

AN ABSTRACT OF THE THESIS OF

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Title: THE EFFECT OF MATERNAL CONDITION ON SEX RATIO OF
OFFSPRING OF GREY-TAILED VOLES

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Approved: _____

Dr. Bruce E. Solentz

The hypothesis that female voles in poor condition produced more female offspring than female voles in good condition was tested. The hypothesis was based on a theory advanced by Trivers and Willard (1973); they stated that a female in good condition that produced a male offspring would leave more surviving third-generation offspring than a female that produced a female offspring, while an adult female in poor condition that produced a female offspring would leave more surviving third-generation offspring than one that produced a male offspring.

Grey-tailed voles (Microtus canicaudus) were chosen as the animal on which to test the hypothesis. Weight was chosen as the index of condition, and quantity of food as the variable to affect weight (and thus condition). From May 1977 to June 1978, two experimental groups of voles, which were fed slightly different restricted diets, and one control group, which received food ad libitum, were

maintained under controlled laboratory conditions. Data were collected on adult weights, number, frequency, and size of litters, weight and sex of offspring, and deaths of adults and juveniles.

It was found that adult male and female weights differed significantly between the groups during part of the experiment, so it was assumed that during the same period, the groups of adult voles showed differences in condition. Since the experimental groups were fed restricted diets and the controls had unlimited access to food, adults in the experimental groups were considered to be in poorer condition than those in the control. Sex ratios of offspring showed no significant differences between the groups, therefore, it was concluded that sex ratios were not affected by female weight, and consequently, the data did not support the hypothesis that female voles in poor condition produced more female offspring than female voles in good condition. Other variables tested, such as weight of offspring, time elapsed between the birth of litters, and number of litters produced, appeared to be related to maternal weight since they showed significant differences between the groups only during the period when the adult females showed the largest differences in weights; thus, these variables supported the relationship of weight to condition.

The Effect of Maternal Condition on Sex Ratio of
Offspring of Grey-tailed Voles

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Debra Lynn Goldenberg

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APPROVED:

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Professor of Wildlife Science
in charge of major

Redacted for Privacy

Head of Department of Fisheries and
Wildlife

Redacted for Privacy

Dean of Graduate School

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Typed by Deanna L. Cramer for Debra Lynn Goldenberg

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THE EFFECT OF MATERNAL CONDITION ON SEX RATIO OF OFFSPRING OF GREY-TAILED VOLES

INTRODUCTION

Several researchers observed unbalanced sex ratios in offspring; these were attributed to various factors: stress (White, 1914; Geiringer, 1961; Snyder, 1976), age of the parent (Robinette et al., 1957; McDowell, 1960; Kamaljan, 1962; Lowe, 1969), sex ratio in the population (Terman and Sassaman, 1967; Snyder, 1976; DeLong, 1978), temporal effects, such as the point during a breeding season that fertilization occurs (Hart and Moody, 1949; Howe, 1977), and nutrition (Verme, 1969). Others (MacArthur, 1965; Hamilton, 1967; Klein, 1968; Alexander, 1974; Spieth, 1974; Snyder, 1976; Werren and Charnov, 1978) suggested that, theoretically, under some conditions, sex ratios that deviated from 1:1 could be beneficial to the reproductive success of individuals that produced them.

Natural selection should favor individuals that maximize their reproductive output. The best reproductive strategy for an individual should be a compromise between the production of the largest number and the highest quality, or fitness, of offspring; this is a trade-off between r and K selection (Pianka, 1974). The success of an individual could be defined as the number of offspring it leaves, however, a better definition is the number of

offspring that survive to reproduce. Those that leave more offspring, or more fit breeding offspring, will introduce a higher proportion of genes into the gene pool than those who leave fewer or less fit offspring.

Manipulation of sex ratio of offspring to that combination which will produce the highest fitness of those offspring is one way by which individuals could maximize their reproductive success. Fisher (1958:162) stated that "...the action of Natural Selection will tend to equalize the parental expenditure devoted to the production of the two sexes." He based his statement on the fact that in sexually reproducing populations, half the ancestry of future generations must be supplied by each sex. If the total parental energy expended on one sex was less than that expended on the other, then parents genetically inclined to produce an excess of the sex which was less common in the population would, for the same amount of expenditure, produce a greater amount of reproductive value, and would consequently be progenitors of a larger fraction of future generations than would parents that produced the more common sex. The result would be the production of greater numbers of the less common sex, and selection would then raise the sex ratio until the expenditure on each sex became equal. Fisher (1958) went on to state, however, that if for any reason sexual differentiation was advantageous, then the numbers attaining sexual maturity may

become unequal. Alexander (1974:337) summarized Fisher's statements on sex ratio: "Fisher realized that the sex ratios of broods of offspring will represent the greatest realized reproduction for the parent."

Kolman (1960) supported Fisher's theory and expanded on it by demonstrating that a population could exhibit any degree of heterogeneity of sex ratio as long as the total energy expended on the production of each sex was equal. He showed mathematically that a population, half of whose members produced only males and the other half only females, was just as stable as one in which each member produced equal numbers of each sex.

Verner (1965:421) responded to Kolman's (1960) statement regarding sex ratio by proposing that "Selection will...favor variations toward a more equal expenditure for each individual and act against deviations in those individuals already having equal expenditures." He showed that any factor, such as genetic recombination, genetic change, immigration or emigration, which resulted in an imbalance of the total mean energy expenditure by parents on offspring of each sex worked to the advantage of individuals who expended equally on each sex.

A theory related to the topic of selection on the sex ratio was presented by Trivers and Willard (1973). They suggested that females could gain advantage if they possessed the ability to vary the sex ratio of offspring

according to their own condition from conception to the end of the period of parental care. By using her own condition as an indicator of her surroundings, and by being able to exert a certain amount of "control" over the sex of her offspring, a female could respond to the environmental conditions by choosing or caring for the sex or combination of sexes most likely to be successful at a particular time, thus enhancing the probability that those offspring would survive to reproduce.

Trivers and Willard (1973) further proposed that under certain conditions, natural selection favored deviations from the usual 1:1 sex ratio. They listed three assumptions that were necessary to their hypothesis: 1) the condition of the young at the end of the period of parental care was correlated with the condition of the mother during this period; 2) differences that might exist in the condition of the young at the end of the period of parental care will tend to be maintained into adulthood; and 3) slight advantages in physical condition will help male reproductive success more than female.

In species in which males compete to inseminate females, a slight advantage in physical condition would be of great importance. In several species that show polygynous mating systems, only a small percentage of the males inseminate females (Kolata, 1977; Pianka, 1974), and these males are usually the strongest or highest in the social

hierarchy (Emlen and Oring, 1977; McCullough, 1969; Geist, 1971; Coblentz, personal comm.), those in possession of superior-quality territories (Cronin and Sherman, 1976; Downhower and Armitage, 1971), or, at least, those that were successful in male-male competition. In contrast, the reproductive success of females may not depend as strongly on the excellence of their condition. Consequently, in species that show polygynous mating systems, male reproductive success should vary more than that of females (Trivers, 1972).

Trivers and Willard (1973) predicted that an adult female in good condition that produces a male offspring will leave more surviving third-generation offspring than a female that produces a female offspring, while an adult female in poor condition that produces a female offspring will leave more surviving third-generation offspring than one that produces a male offspring. In other words, if a female is in good condition, it is likely that her offspring also will be in good condition. Hypothetically, if she can produce a female or a male offspring, it would be to her advantage to produce a male, since a male in good condition has the potential of breeding many times, while a female offspring, also in good condition, is limited to the number of times she can bear young. The male is only limited by his strength and competitive ability and the availability of receptive females. In the reverse situation, if a

female is in poor condition and produces a male offspring, the possibility exists that if he is also in poor condition, he will not breed at all, while a female offspring in a similar condition is more likely to breed than he. Thus, a breeding female that adopts this strategy should have a higher rate of reproductive success than one who does not; the trait, if genetically based, is selectively advantageous and thereby established in a population. Trivers and Willard also predicted that the greater the variability in male reproductive success as opposed to that of females, the greater the tendency should be for females to vary the sex ratio of their offspring as a function of maternal condition.

Trivers and Willard (1973) did not suggest a mechanism by which control of the sex ratio might be achieved; however, they emphasized that deviations from a 1:1 ratio should be produced as a result of differential investment in one sex or the other during the period of parental care, rather than deviations in the primary sex ratio. Differential male mortality was suggested as part of the mechanism by which the sex ratio may be adjusted.

Differential male mortality implies destruction of potential offspring; this is not energetically conservative, even if it is passive, through neglect or differential investment. Myers (1978) critically reviewed Trivers and Willard's (1973) paper and suggested that it would be to

the greater advantage of the individual to produce offspring of the sex which required less expenditure from the parent(s) than to produce offspring with a balanced primary sex ratio and selectively eliminate part of them as conditions require. Trivers and Willard assumed that "for simplicity", parents invested equally in offspring of both sexes, but in birds and mammals, most males are larger than females and therefore more expensive to produce (Myers, 1978), so the assumption of equal investment is not realistic.

Trivers and Willard (1973) implied that females in poor condition were more likely to breed than males in poor condition. A distinction needs to be drawn between females that breed and those that breed and raise offspring that reproduce. It is not apparent from the literature that females in poor condition raise young as successfully as those that are in good condition; there is much evidence to the contrary. However, there is some evidence that breeding and conceiving are not largely affected by female condition; decreased birth rate among females in poor condition was attributed to prenatal and neonatal mortality in deer (Murphy and Coates, 1966) and in mice (Crowcroft and Rowe, 1958). Therefore, although a female in poor condition may breed, her offspring may not survive to reproduce. Unless reproductive success is defined only in terms of offspring produced, Trivers and Willard's

(1973) assumption that a female in poor condition will out-reproduce a male in similar condition is questionable.

Their statement that a female in poor condition will leave more surviving third-generation offspring than a male in poor condition is a clear statement that their definition of reproductive success extends beyond the production of one generation of offspring.

Contrary to their statement that deviations in sex ratio should be a result of differential investment in one sex or the other, Trivers and Willard (1973) stated that natural selection favored individual deviations from a 1:1 sex ratio at conception, and those deviations tended to cancel in the local breeding population. They attributed the deviations to the tendency within a population for adult condition to vary around a mean. Interpretation of their views may differ depending on whether the local population mean is derived at a single point in time, or if it may be summarized over several generations. If the statement is considered in terms of a local population at a point in time, and if the mean condition of individuals in the population does not consistently represent an "average" condition or one that would produce a 1:1 sex ratio, then I believe that the sex ratios will not cancel in the local population. Instead, the sex ratio of the population should reflect the actual mean condition of the population as predicted by Trivers and Willard's theory.

If the sex ratios consistently cancel, regardless of the condition of the average individual, the assumption is required that individuals must possess the ability to assess the condition of other members of the population, a feat not established for most mammals. However, individuals may be able to assess condition of other individuals from their social status if condition and position in social hierarchy are directly related (Schenkel, 1947; Mykytowycz, 1965; Altmann, 1967; Geist, 1971; Wilson, 1975). If the statement that individual deviations from a 1:1 sex ratio tend to cancel in the population is viewed as a long-term effect, skewed sex ratios could cancel each other over several generations, which would allow for variation in the mean individual condition in populations. It was not clear in Trivers and Willard's article if they intended their statement to be viewed as an immediate or as a long-term effect.

Despite the problems that were mentioned, I decided to test Trivers and Willard's (1973) hypothesis. To my knowledge, no one has tested experimentally Trivers and Willard's hypothesis. The purpose of this investigation was to determine if female voles in poor condition (based on restricted diets) produced more female offspring than those in good condition (based on unlimited diets).

METHODS

Voies (Microtus sp.) were chosen as experimental animals because they have a polygynous breeding system (Walker et al., 1964), are highly productive with several litters born annually (Asdell, 1964), and are excellent laboratory animals (Pinter and Negus, 1965). The grey-tailed vole (Microtus canicaudus) was chosen on the basis of its availability and local success as a laboratory animal (Larry Forslund, pers. comm.). The gestation period of this species is 21 days and 1 to 9 offspring are produced per litter (Hagen and Forslund, in press).

I designed a laboratory experiment that allowed the isolation and control of one variable which could affect the condition of the voles. This variable was chosen to be quantity of food, and the measure of condition to be weight of the adult voles. "Condition" is a vague term that can be interpreted in many ways; for this experiment, the definition of condition was body weight of an individual relative to the other voles because this parameter was direct and easy to measure.

Ninety-two pairs of grey-tailed voles obtained from a breeding colony maintained on the Oregon State University campus by L. Forslund were housed in the Mammal Vivarium, Room 110, Nash Hall, Oregon State University from May 1977 to June 1978. Daylength in the vivarium was controlled at

14 h of artificial light per day throughout the experiment, and temperature ranged from a mean minimum of 21.7°C to a mean maximum of 23.3°C, with a mean daily fluctuation of 1.3°C.

A 19-day feeding trial was conducted prior to the initiation of the primary experiment to determine the rate of food consumption for male and female voles. Thirty-five males and 27 females between 8 and 12 weeks of age were placed singly in cages made from 60 by 15 by 15-cm fiberglass flower boxes fitted with 1.2-cm wire mesh tops. Each was provided with alder shavings and cotton batting for bedding material. Each cage also contained a stainless steel food cup with a tight-fitting rim, under which was a perforated plate through which food could be removed. Dishes were filled with Alber's Rabbit Ration and Purina Rat Chow in similar proportions (75% Rabbit Ration and 25% Rat Chow) to that which I planned to feed during the main experiment. Water was provided ad libitum from glass bottles with ball-bearing sipper tubes placed through the lid of the cage.

Weight of each animal was recorded weekly. At 1000 ± 2 h each day, food cups were weighed with all remaining food plus any food cached in the cage. Dishes were re-filled every 1 to 2 days as necessary.

Females voles consumed an average of 0.228 g food/g body weight and male voles consumed an average of 0.218 g

food/g body weight each 24-hour period. Despite the fact that the food was the same variety fed to these animals in their original breeding colony, and that it was available ad libitum, 97% of all animals lost weight the first week of the feeding trial, 76% during the second week, and 53% during the third week.

On the basis of the results of the feeding trial, two experimental groups were established which represented what I considered to be two slightly different levels of dietary restriction, but not sufficiently severe to suppress reproduction. Since most animals lost weight during the trial, Group I was fed 1 standard deviation above the mean amount consumed during the feeding trial, or 0.265 g food for males and 0.284 g food for females/g of body weight each day, and Group II was fed the mean amount consumed during the trial. Group III was established as the control group and received food ad libitum. Water was provided ad libitum to all groups.

Because it was not possible to obtain 92 pairs of voles of approximately the same age at one time, I received 4 increments of animals over a 16-week period; all animals were maintained under as nearly identical conditions as possible. The first increment, animals used in the feeding trial, was received on 11 June 1977; the second was received on 24 August, the third on 28 September and the fourth on 5 October. Upon receipt, each animal was

weighed and placed in its own cage, where it received food and water ad libitum and was weighed once weekly for 3 weeks to simulate conditions during the feeding trial, which only involved animals from the first increment. After the 3-week period, females were paired randomly with males, then pairs were placed randomly into one of the three groups. Pairs remained together for the duration of the experiment, and young were weaned at approximately 12 days of age when they began to consume solid food.

Voles were fed each morning at 0900 ± 1 h. Food rations were adjusted each week according to the weight of each animal; the male and female portions of the ration were calculated separately and then combined when the food was weighed. To minimize the effects of male-female competition for food, half of each ration was placed at opposite ends of the cages.

Data were collected on each pair of animals for 26 weeks or until death of one of a pair. Recorded were weekly adult weights, date of birth and weight of individuals in each litter, and weight and sex of all offspring at 1 week of age. Death of young and adults was recorded and an attempt made to determine the cause.

To use weight as the measure of condition in the adult voles, it was important to test for differences in weight between the three groups. To more accurately compare weights of the adult females, an attempt was made to

remove part of the pregnancy-induced variations in weight from the set of female weights. To determine the point at which females began a rapid weight gain, a line was fitted by the least-squares method to female weight in relation to the duration of gestation, thus establishing a curve which represented weight gain during pregnancy (Fig. 1). The regression had weight as the dependent variable and days (days of pregnancy), days squared, and days cubed as the initial independent variables. The initial variables were retained as all were found to be important to the model. To use all of the data, I ignored independence criteria; therefore, no tests of significance were necessary. Utilizing the fitted line, I selected weights which represented females pregnant more than 9 days as those appropriate to remove from the set of female weights.

All data, with the exception of variables representing mortality, fecundity, and female weight during pregnancy, were analyzed with a packaged computer program, Statistical Package for the Social Sciences (SPSS), another program, Statistical Interactive Programming System (SIPS), was used to analyze weights of females during pregnancy. Both packages were available on Oregon State University's CYBER computer system.

Analysis of variance was used to examine the relationship between the control and the experimental groups in adult weights, sex ratios, litter size, time elapsed

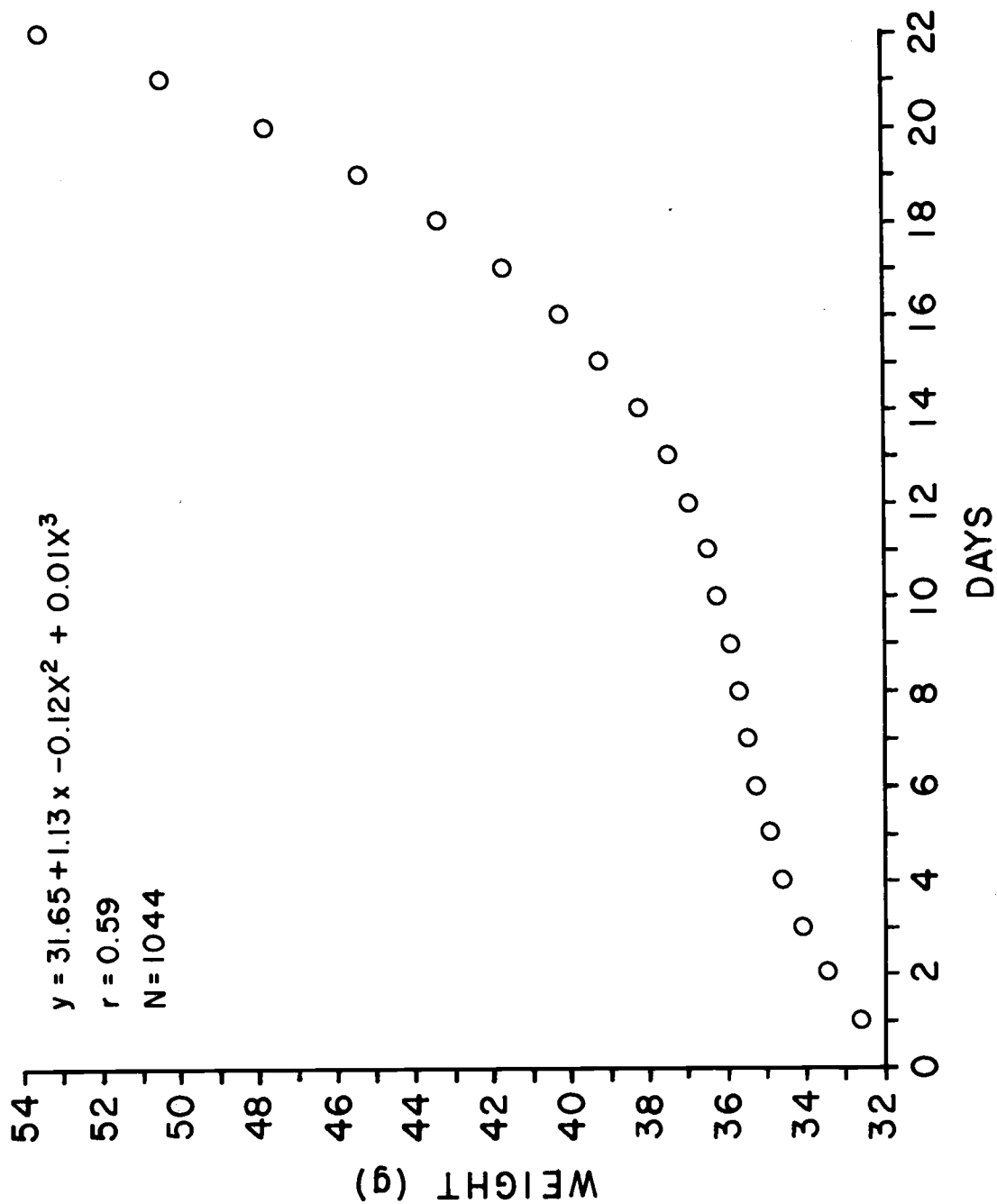


Fig. 1. Predicted values of female weight during pregnancy in grey-tailed voles.

between the birth of litters, and weights of the young. A one-way randomized block design was used, with "batches" (increments) as blocks and "groups" (feeding groups) as the single factor. Because weekly adult weights were dependent on the original weight of the animals, weights taken at the beginning of the experiment were used as covariates in the analysis of adult weights. Similarly, weight of the female and size of the litter were used as covariates in the analysis of litter weights at birth and at 1 week of age. The Student-Newman-Keuls mean separation test was used to determine which of the two experimental groups differed from the control in those analyses which yielded significant F values.

Student's t -test was used to determine if the experimental groups produced a different number of litters or a different number of offspring than the control. A chi-square contingency table was used to determine if there was a difference in adult or juvenile mortality between the control and the experimental groups.

Results showing differences at the $\alpha = 0.05$ level of significance or less were accepted as being significant for all analyses performed.

RESULTS

Adult male voles showed significant differences in weight between Group II and the control from the 5th to the 14th week, a trend which was maintained until the end of the experiment (Fig. 2). Adult females showed significant differences in weight between groups from the 8th to the 16th week (Fig. 3); during this period Group II differed from the control for all but the 15th week and Group I differed from the control for all but the 12th and 14th weeks. Animals' weights at the outset of the experiment, which was used as a covariate, was found to have a significant relationship with their weekly weights throughout the experiment for both male and female voles.

No significant differences were found in proportion of males in the offspring between groups when analyzed by litter size (Table 1) with the exception of two young per litter; I attribute the difference found between groups in this litter size to an effect of small sample size and of the limited combinations of the two sexes in a litter size of two. With the exception of the eighth litter, which had a low sample size, proportion of males in each sequential litter (Table 2) showed no significant differences between groups.

No significant differences were found in weight of the young at birth between groups (Appendix Table B),

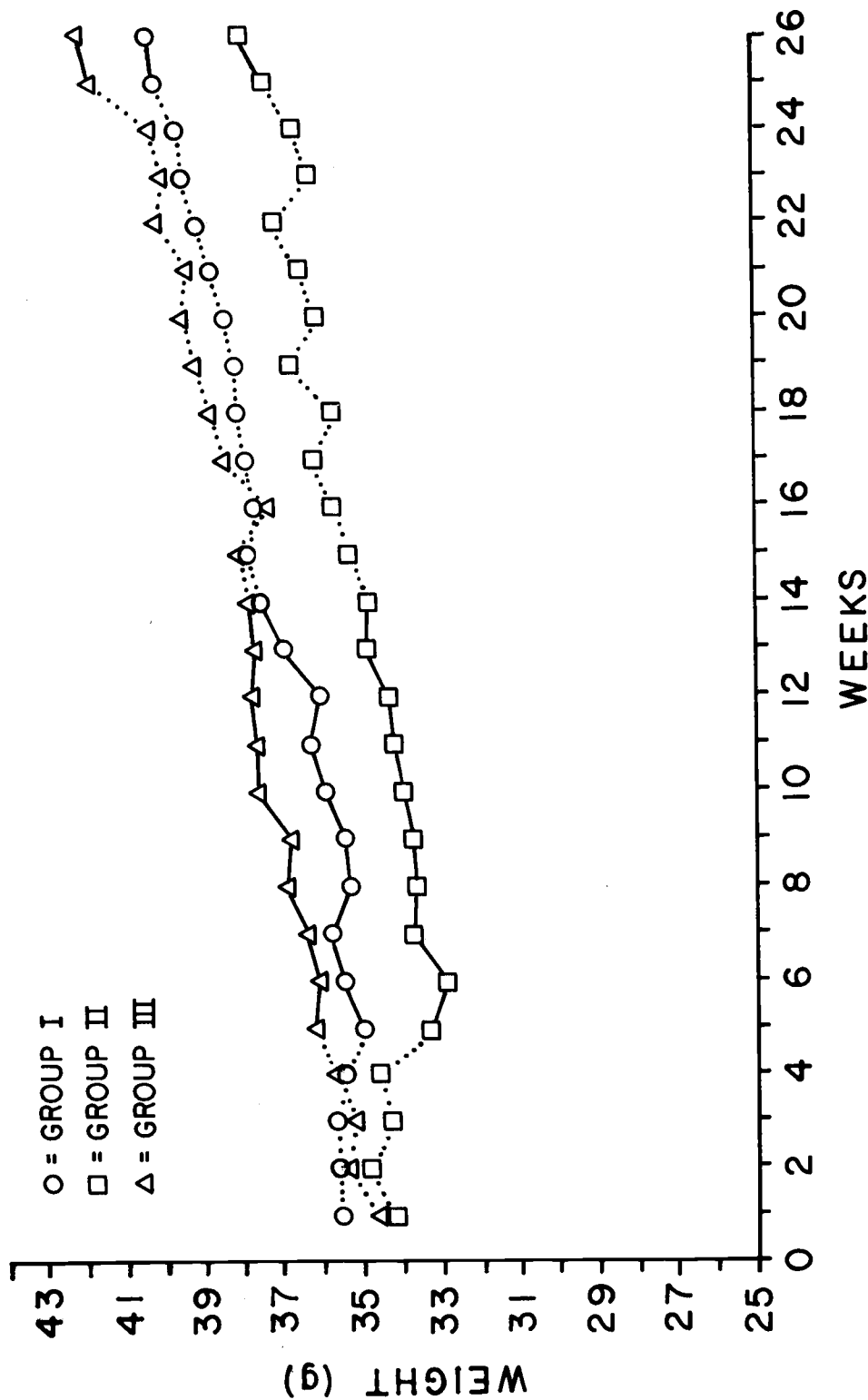


Fig. 2. Adult male weights of grey-tailed voles on restricted diets. Group III = control, Group II = low (0.218 g food for males and 0.228 g for females/g body weight), Group I = intermediate (0.265 g food for males and 0.284 g for females/g body weight). Solid lines represent areas of significant difference between groups.

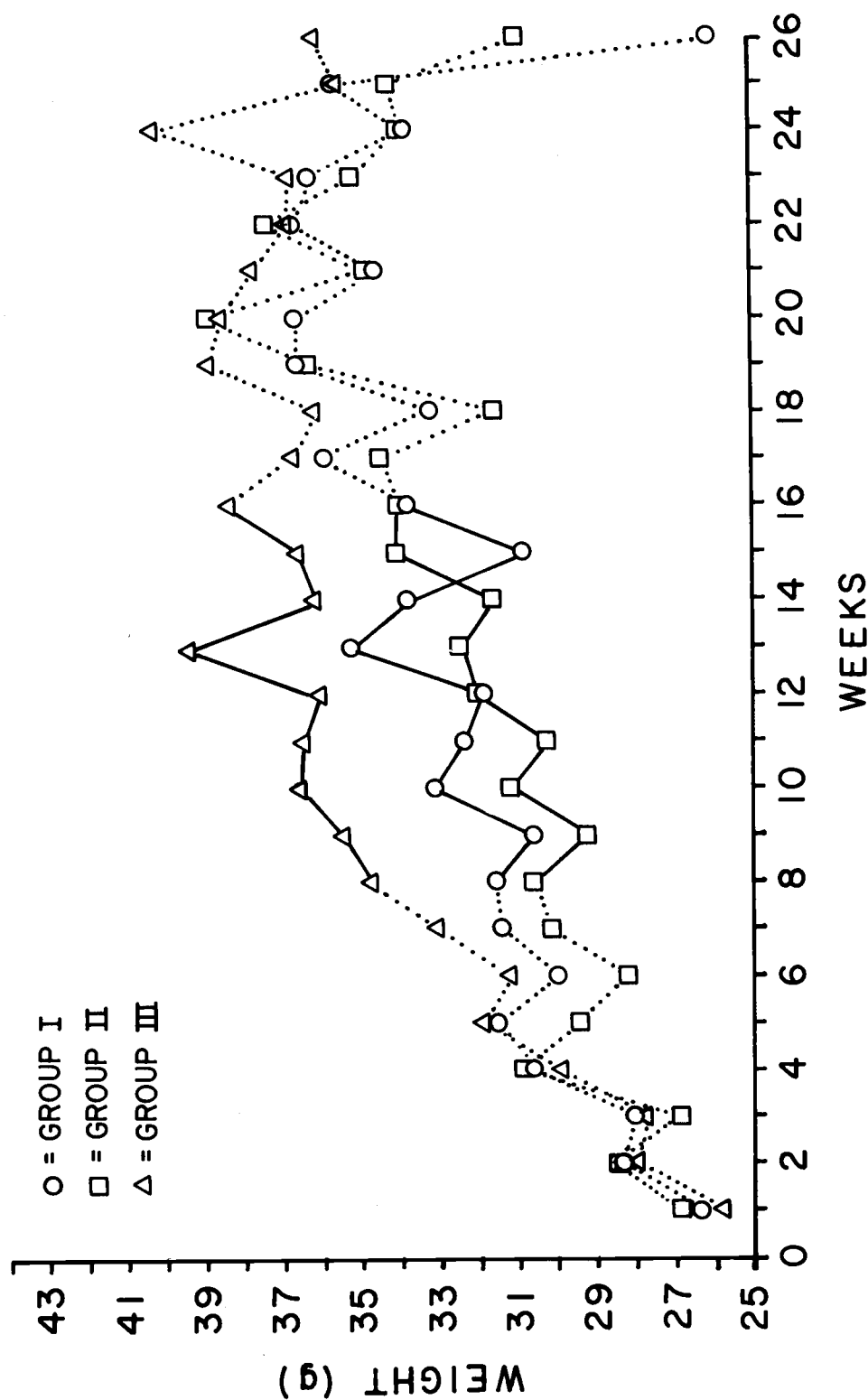


Fig. 3. Adult weights of female grey-tailed voles on restricted diets. Group III = control, Group II = low (0.218 g food for males and 0.228 g for females/g body weight), Group I = intermediate (0.265 g food for males and 0.284 g for females/g body weight). Solid lines represent areas of significant difference between groups.

Table 1. Proportion of males in each litter size of grey-tailed voles on restricted diets. Group III = control, Group II = low (0.218 g food for males and 0.228 g for females/g body weight), Group I = intermediate (0.265 g food for males and 0.284 g for females/g body weight). Values in parenthesis indicate sample size.

# YOUNG/ LITTER	GROUP I	GROUP II	GROUP III	F
2	0.60 (5)	0.61 (7)	0.29 (6)	5.224*
3	0.55 (9)	0.38 (10)	0.64 (12)	2.356
4	0.56 (13)	0.51 (14)	0.53 (16)	0.085
5	0.53 (19)	0.47 (10)	0.47 (17)	0.639
6	0.44 (13)	0.56 (5)	0.48 (14)	0.464
7	0.52 (7)	0.54 (5)	0.55 (6)	0.829
8	0.42 (2)	0.56 (1)	0.53 (5)	-----

*Significant at $\alpha = 0.05$.

Table 2. Proportion of males in each litter of grey-tailed voles on restricted diets. Group III = control, Group II = low (0.218 g food for males and 0.228 g for females/g body weight), Group I = intermediate (0.265 g food for males and 0.284 g for females/g body weight). Values in parenthesis indicate sample size.

LITTER	GROUP I	GROUP II	GROUP III	F
1	0.54 (26)	0.44 (21)	0.54 (24)	1.372
2	0.53 (19)	0.50 (17)	0.43 (23)	0.940
3	0.52 (18)	0.50 (16)	0.44 (20)	0.865
4	0.43 (17)	0.52 (15)	0.51 (14)	0.243
5	0.48 (16)	0.48 (13)	0.54 (14)	0.432
6	0.60 (13)	0.65 (9)	0.49 (13)	0.898
7	0.49 (11)	0.80 (2)	0.51 (14)	1.079
8	1.00 (1)	0.71 (2)	0.52 (8)	10.567*

*Significant at $\alpha = 0.05$.

however, at 1 week of age, analysis of variance showed significant differences in weight between groups in the third and fourth litters (Table 3). Mean separation tests showed Group II to be different from the control in the third litter, but no differences were detected in the fourth litter. Examination of covariates showed adult female weight at the outset of the experiment to be significantly related to weight of the young at birth for all eight litters, but only in the third and seventh litters at 1 week of age. Litter size was significantly related to litter weight at birth and 1 week only in the third litter.

When weight gain between birth and 1 week was analyzed, analysis of variance showed that there was a significant difference between groups in the fourth litter (Table 4), but these differences were not detectable with the mean separation test.

Periods elapsed between the birth of the second, third, and fourth litters were significantly different between groups (Table 5); Group II differed from the control in all three cases while Group I differed from the control only in the third litter.

Both Group I and Group II produced significantly fewer litters than the control, however, there were no significant differences observed between groups in total

Table 3. Weight (g) at 1 week of age of offspring of grey-tailed voles on restricted diets. Group III = control, Group II = low (0.218 g food for males and 0.228 g for females/g body weight), Group I = intermediate (0.265 g food for males and 0.284 g for females/g body weight). Values in parenthesis indicate sample size.

LITTER	GROUP I	GROUP II	GROUP III	F
1	5.28 (23)	5.13 (19)	5.61 (23)	1.469
2	5.25 (18)	5.18 (17)	5.49 (18)	2.464
3	5.26 (15)	4.49 (15)	5.43 (15)	3.416*
4	5.38 (12)	5.10 (14)	6.53 (11)	3.704*
5	5.42 (13)	5.23 (11)	5.56 (10)	0.999
6	5.26 (11)	5.36 (7)	5.24 (9)	0.012
7	5.36 (10)	5.63 (2)	5.71 (12)	1.331
8	5.32 (1)	5.57 (2)	4.91 (7)	1.911

*Significant at $\alpha = 0.05$.

Table 4. Weight gain (g) between birth and 1 week in grey-tailed voles on restricted diets. Group III = control, Group II = low (0.218 g food for males and 0.228 g for females/g body weight), Group I = intermediate (0.265 g food for males and 0.284 g for females/g body weight). Values in parenthesis indicate sample size.

LITTER	GROUP I	GROUP II	GROUP III	F
1	2.85 (20)	2.63 (19)	3.20 (23)	1.658
2	2.93 (17)	2.79 (17)	3.13 (18)	0.896
3	2.89 (15)	2.85 (15)	3.06 (15)	0.445
4	3.02 (12)	2.87 (13)	3.99 (10)	3.480*
5	2.94 (13)	2.75 (11)	3.11 (10)	1.240
6	2.76 (10)	2.81 (7)	2.76 (8)	0.102
7	2.78 (8)	3.09 (2)	3.22 (12)	0.764
8	2.81 (1)	3.36 (2)	2.42 (7)	4.711

*Significant at $\alpha = 0.05$.

Table 5. Days elapsed between the birth of each litter of offspring of grey-tailed voles on restricted diets. Group III = control, Group II = low (0.218 g food for males and 0.228 g for females/g body weight), Group I = intermediate (0.265 g food for males and 0.284 g for females/g body weight). Values in parenthesis indicate sample size.

LITTER	GROUP I	GROUP II	GROUP III	F
1	37.07 (29)	31.43 (21)	29.77 (26)	1.364
2	28.46 (22)	34.40 (20)	22.76 (21)	6.541*
3	28.75 (16)	32.13 (16)	23.13 (16)	9.361*
4	25.88 (16)	32.39 (13)	23.64 (14)	4.209*
5	23.00 (14)	24.90 (10)	22.67 (12)	0.636
6	22.44 (9)	24.71 (7)	23.88 (8)	0.806
7	21.55 (11)	22.00 (1)	22.80 (10)	0.434
8	22.00 (1)	21.00 (2)	22.14 (7)	0.768

*Significant at $\alpha = 0.05$.

production of offspring (Table 6) or in litter size (Table 7).

There were no significant differences in mortality between groups of adult voles, but significant differences were observed between both of the experimental groups and the control in mortality of juvenile voles (Table 6).

Table 6. Mortality and fecundity of grey-tailed voles on restricted diets. Numbers in parenthesis represent dead animals. Group III = control, Group II = low (0.218 g food for males and 0.228 g for females/g body weight), Group I = intermediate (0.265 g food for males and 0.284 g for females/g body weight). Values in parenthesis indicate sample size.

VARIABLE	GROUP I	GROUP II	GROUP III
MORTALITY: ADULT	21.2% (7)	37.0% (10)	40.6% (13)
MORTALITY: JUVENILE	11.9%* (26)	7.6%* (17)	8.8% (19)
LITTERS PER PAIR	5.12*	4.82*	6.56
OFFSPRING PER PAIR	24.54	22.77	30.63

*Significantly different from control at $\alpha = 0.05$.

Table 7. Litter size of grey-tailed voles under dietary restriction. Group III = control, Group II = low (0.218 g food for males and 0.228 g for females/g body weight), Group I = intermediate (0.265 g food for males and 0.284 g for females/g body weight). Values in parenthesis indicate sample size.

LITTER	GROUP I	GROUP II	GROUP III	F
1	4.16 (31)	4.00 (22)	3.63 (27)	1.210
2	4.31 (26)	4.14 (21)	4.83 (24)	1.644
3	5.10 (21)	4.83 (18)	5.55 (22)	0.728
4	5.05 (19)	4.94 (16)	5.00 (20)	0.154
5	5.56 (18)	5.15 (13)	5.82 (17)	0.734
6	5.07 (14)	5.10 (10)	5.07 (14)	0.046
7	5.75 (12)	5.00 (3)	5.43 (14)	0.166

DISCUSSION

Among both adult males and adult females, there was a period of time during which there were significant differences in weights between groups, and periods during which weights between groups were not significantly different (Fig. 2, Fig. 3). Voles on restricted diets possibly began to compensate in some way during the second half of the experiment for the lower amounts of food. Voles could have compensated by curbing reproduction, reducing activity, or both. Voles in the two experimental groups produced significantly fewer litters than did the controls (Table 6).

Sex ratios of the young showed no significant differences during the entire experiment (Table 1, Table 2). It appeared as though sex ratios were not related to weights of females.

Weights of the young at birth were not affected by restricted maternal diets, but after 1 week, offspring in the experimental groups were significantly lighter than offspring in the control (Table 3). These differences occurred in the third and fourth litters, during the period when adult females showed the largest differences in weights. Millar (1978) found similar results for the white-footed mouse (Peromyscus leucopus); he observed that the weight of neonates was not related to maternal weight, but

by the 13th day post partum, offspring weight was related to female weight. Females that were lighter were thought to be less able to nourish their young than females that were heavier.

The relationship between maternal weight and weight of the offspring demonstrated by the analysis of covariates appears contradictory to results obtained by between-groups analysis of offspring weight. At birth there was a significant relationship between maternal and offspring weight but at 1 week of age only two of eight litters showed this relationship. Possibly, the relationship shown at birth was masked at 1 week by a large amount of variation present in weight of the offspring at that time. This variation accompanied the between-groups difference in weight at 1 week but was not present to as large a degree in the weight at birth, a time at which between-groups weights were shown not to be different. Examination of the mean-square error in the analysis of offspring weight at birth and at 1 week showed a consistently higher value at 1 week throughout the eight litters, which indicated a higher degree of variation in weights of offspring at 1 week. Therefore, I believe that, despite the lack of female-to-young relation in weight at 1 week, the offspring reflected the condition of the mother by 1 week of age; offspring of lighter mothers were not nourished as well as those of heavier mothers.

Weight gain between birth and 1 week was significantly different between groups in the fourth litter in the analysis of variance (Table 4); the fourth litter was born during the period of time when females showed significant differences in weight between groups. Post-partum weight gain appeared to be temporally related to maternal weight, and, as in the weight of the young at 1 week, weight gain of offspring could be related to the weight of the mother during lactation.

The control group produced litters more frequently than the experimental groups (Table 5) which could imply that females which were fed restricted diets (and consequently weighed less than the controls) required a longer period of post-partum recovery than the controls before mating or conceiving again. Weight (as related to nutrition) was found to have a direct relationship with fecundity in sheep (Coop, 1966) and in deer (Verme, 1969).

The group that produced the most litters showed the highest level of adult mortality (Table 6). Spencer and Steinhoff (1966) assumed that parental mortality varied directly with litter size; survivorship varied inversely with fecundity in general (Murdoch, 1966; Williams, 1966; Tinkle, 1969, Ricklefs, 1973; Pianka, 1974; Wilson, 1975). A large expenditure of energy on reproduction could result in the decline of individual condition; the more energy channeled into reproduction, the less there is left for maintenance.

The effect of various nutritional factors on litter size has been documented; some found no effect (Pinter and Negus, 1965; Negus and Pinter, 1966), but others found maternal level of nutrition to show a direct relation to litter size (Spencer, 1896; Hoffman, 1908; Lamming et al., 1954; Hamilton, 1962; Williams and Caskey, 1965; Verme, 1969). Millar (1978) found that energy for female maintenance increased with increased litter size; he also found that mean litter size was different for wild and captive mice. I found that litter size did not change (Table 7) despite differences in female weights, assumed to be caused by dietary restrictions.

Out of a total of 27 variables which were found to have significant F values and therefore represented differences between groups, mean separation tests showed Group II to be different from the control 24 times and Group I to be different from the control 10 times. This imbalance was probably a reflection of the different levels of dietary restriction imposed on the two groups.

CONCLUSIONS

Prior to the initiation of the experiment, weight of individuals was chosen as the index of condition. Significant differences in individual weights were demonstrated to exist between the three groups of adult voles for at least part of the experiment. In addition, other variables such as weight of offspring, weight gain of offspring, number of litters produced, and length of time elapsed between the birth of litters showed significant differences between the groups only during the period of time during which the adults showed significant differences in weights. Many of these variables have been shown to reflect maternal condition (Millar, 1978; Hamilton, 1962; Verme, 1969; Murphy and Coates, 1966; Crowcroft and Rowe, 1958). Therefore, I am confident that, for at least part of the experiment, the adult female voles in the experimental groups were in different condition than the voles in the control, and because the voles in the experimental groups were on restricted diets and the voles in the control group were not, those in the experimental groups were considered to be in poorer condition relative to the controls. I believe, then, that the data I collected on sex ratios did not support the hypothesis that female voles in poor condition produce more female offspring than female voles in good condition.

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APPENDIX

Appendix Table A. Mean ($\bar{X}$), standard deviation (S), and sample size (N) of adult male weights, adult female weights, and weight of young at birth of grey-tailed voles on restricted diets. Group III = control, Group II = low (0.218 g food for males and 0.228 g for females/g body weight), Group I = intermediate (0.265 g food for males and 0.284 g for females/g body weight).

VARIABLE	GROUP I			GROUP II			GROUP III		
	$\bar{X}$	S	N	$\bar{X}$	S	N	$\bar{X}$	S	N
ADULT MALE WEIGHT:									
WEEK 1	35.62	4.84	33	34.33	5.88	27	34.66	3.62	32
WEEK 2	35.63	4.30	33	34.93	5.43	27	35.37	3.54	32
WEEK 3	35.74	4.13	33	34.33	5.11	27	35.27	3.91	30
WEEK 4	35.60	4.07	33	34.61	4.99	27	35.73	3.85	28
WEEK 5	35.00	4.64	33	33.29	5.30	27	36.21	3.99	28
WEEK 6	35.51	4.59	31	32.89	5.51	27	36.16	3.81	28
WEEK 7	35.84	4.70	30	33.75	5.68	25	36.43	4.25	28
WEEK 8	35.36	5.18	30	33.66	5.81	25	36.90	4.18	27
WEEK 9	35.51	5.39	30	33.73	5.24	24	36.80	4.29	26
WEEK 10	36.02	5.43	30	33.98	4.02	23	37.66	4.04	26
WEEK 11	36.36	5.57	29	34.27	4.35	22	37.70	4.43	26
WEEK 12	36.15	6.16	28	34.35	5.30	22	37.78	4.52	25
WEEK 13	37.02	5.21	27	34.92	4.70	20	37.76	4.26	24
WEEK 14	37.60	5.58	27	34.85	5.02	20	37.89	4.40	23
WEEK 15	37.97	5.43	27	35.38	4.24	20	38.13	4.34	21
WEEK 16	37.76	5.34	27	35.77	3.83	19	37.36	3.89	21
WEEK 17	38.00	5.52	26	36.34	4.22	19	38.54	4.78	20

Appendix Table A (continued)

VARIABLE	GROUP I			GROUP II			GROUP III		
	$\bar{X}$	S	N	$\bar{X}$	S	N	$\bar{X}$	S	N
ADULT MALE WEIGHT: (continued)									
WEEK 18	38.18	5.34	26	35.90	4.28	19	38.93	5.25	20
WEEK 19	38.25	5.45	26	36.78	4.66	17	39.35	4.93	19
WEEK 20	38.48	5.59	26	36.31	5.01	17	39.55	4.79	19
WEEK 21	38.89	5.70	26	36.62	4.72	17	39.48	4.54	19
WEEK 22	39.23	5.52	26	37.29	4.56	17	40.23	5.33	19
WEEK 23	39.62	5.90	26	36.39	4.93	16	40.19	4.82	18
WEEK 24	39.76	6.31	26	36.81	4.75	16	40.52	5.36	18
WEEK 25	40.39	5.71	26	37.48	5.32	16	42.05	3.96	17
WEEK 26	40.52	6.38	26	38.14	5.54	16	42.26	3.98	17
ADULT FEMALE WEIGHT: (ADJUSTED FOR PREGNANCY) *									
WEEK 1	26.41	4.62	33	26.90	3.98	27	25.84	3.15	29
WEEK 2	28.38	4.18	32	28.43	4.33	21	28.00	3.96	27
WEEK 3	27.97	3.90	16	26.94	4.20	11	27.91	3.97	10
WEEK 4	30.56	5.28	20	30.90	4.48	20	29.97	4.14	18
WEEK 5	31.53	6.22	24	29.46	4.14	22	31.87	5.22	24
WEEK 6	30.11	5.88	18	28.24	3.96	20	31.29	4.65	10
WEEK 7	31.42	6.29	19	30.25	4.19	17	33.04	3.99	11
WEEK 8	31.57	5.56	23	30.65	5.76	16	34.76	5.31	16
WEEK 9	30.64	5.13	19	29.31	3.77	19	35.46	5.99	12

Appendix Table A (continued)

VARIABLE	GROUP I			GROUP II			GROUP III		
	$\bar{X}$	S	N	$\bar{X}$	S	N	$\bar{X}$	S	N
ADULT FEMALE WEIGHT: (continued)									
WEEK 10	33.14	6.00	17	31.20	5.34	20	36.55	5.01	13
WEEK 11	32.42	6.39	17	30.25	4.98	14	36.48	4.95	14
WEEK 12	31.95	5.95	15	32.08	4.52	15	36.05	5.79	8
WEEK 13	35.29	6.64	20	32.49	4.77	13	39.45	5.13	10
WEEK 14	33.89	6.20	19	31.69	3.76	11	36.20	3.57	12
WEEK 15	30.91	4.48	13	34.09	6.60	8	36.65	4.53	8
WEEK 16	33.82	7.56	11	33.33	3.27	9	38.36	5.04	8
WEEK 17	35.97	6.92	19	34.49	6.11	10	36.68	4.17	9
WEEK 18	33.33	5.13	16	31.71	7.18	7	36.18	4.21	9
WEEK 19	36.61	9.21	15	36.28	6.11	12	38.87	4.93	12
WEEK 20	36.73	7.91	15	38.96	6.74	8	38.57	4.79	10
WEEK 21	34.62	6.23	15	34.82	6.07	6	37.79	4.07	9
WEEK 22	36.66	6.56	14	37.41	5.30	14	36.85	3.13	11
WEEK 23	36.37	8.33	12	35.21	7.03	8	36.84	3.22	8
WEEK 24	33.91	8.72	9	33.98	7.41	5	40.32	8.04	6
WEEK 25	35.74	7.74	9	34.34	5.36	5	35.64	2.15	5
WEEK 26	26.16	12.18	7	31.00	0.00	1	36.20	0.00	1

Appendix Table A (continued)

VARIABLE	GROUP I			GROUP II			GROUP III		
	$\bar{X}$	S	N	$\bar{X}$	S	N	$\bar{X}$	S	N
WEIGHT OF YOUNG AT BIRTH IN:									
LITTER 1	2.40	0.26	25	2.54	0.27	22	2.39	0.26	26
LITTER 2	2.43	0.19	21	2.35	0.28	21	2.37	0.18	22
LITTER 3	2.37	0.15	17	2.10	0.90	16	2.35	0.21	17
LITTER 4	2.43	0.26	17	2.48	0.27	15	2.51	0.22	14
LITTER 5	2.49	0.19	15	2.48	0.21	11	2.41	0.26	13
LITTER 6	2.42	0.22	11	2.55	0.24	7	2.43	0.22	9
LITTER 7	2.39	0.20	9	2.63	0.16	3	2.47	0.19	13
LITTER 8	2.51	0.00	1	2.22	0.01	2	2.48	0.26	8

*Weights representing >9 days of pregnancy were removed prior to these calculations.

Appendix Table B. Analysis of variance table for adult male weights, adult female weights, and weight of young at birth of grey-tailed voles on restricted diets. Group III = control, Group II = low (0.218 g food for males and 0.228 g for females/g body weight), Group I = intermediate (0.265 g food for males and 0.284 g for females/g body weight). D.f. = 2 for all variables.

VARIABLE	SUM OF SQUARES	MEAN SQUARE	F	SIGNIF OF F
ADULT MALE WEIGHT:				
WEEK 1	39.36	19.68	0.87	0.430
WEEK 2	8.26	4.13	1.88	0.160
WEEK 3	11.18	5.59	1.33	0.271
WEEK 4	16.92	8.46	2.21	0.117
WEEK 5	127.58	63.79	7.55	0.001
WEEK 6	141.81	70.91	7.99	0.001
WEEK 7	89.41	44.70	4.91	0.010
WEEK 8	145.68	72.84	7.15	0.001
WEEK 9	98.64	49.32	4.37	0.016
WEEK 10	146.78	73.39	5.52	0.003
WEEK 11	135.74	67.87	4.55	0.014
WEEK 12	134.44	67.22	4.04	0.022
WEEK 13	90.94	45.47	3.75	0.029
WEEK 14	99.58	49.79	4.24	0.019
WEEK 15	76.48	38.24	2.95	0.060
WEEK 16	24.37	12.19	0.89	0.415
WEEK 17	37.85	18.92	1.33	0.274
WEEK 18	74.59	37.30	2.17	0.124
WEEK 19	55.89	27.95	1.92	0.157
WEEK 20	69.67	34.83	2.51	0.090
WEEK 21	53.58	26.79	2.07	0.144
WEEK 22	57.69	28.85	1.89	0.161
WEEK 23	89.40	44.70	2.78	0.071
WEEK 24	94.98	47.49	2.87	0.066
WEEK 25	128.79	64.39	4.98	0.010
WEEK 26	109.48	54.74	3.59	0.035

Appendix Table B (continued)

VARIABLE	SUM OF SQUARES	MEAN SQUARE	F	SIGNIF OF F
ADULT FEMALE WEIGHT:				
WEEK 1				
WEEK 2	5.79	2.90	0.93	0.401
WEEK 3	6.76	3.38	0.41	0.669
WEEK 4	11.58	5.79	0.56	0.576
WEEK 5	154.85	77.42	5.50	0.006
WEEK 6	62.83	31.41	2.27	0.116
WEEK 7	107.73	53.86	2.80	0.073
WEEK 8	226.96	113.48	7.30	0.002
WEEK 9	226.59	113.29	9.94	0.001
WEEK 10	347.99	174.00	14.71	0.001
WEEK 11	421.48	210.74	12.67	0.001
WEEK 12	194.63	97.32	6.39	0.005
WEEK 13	343.97	171.99	7.54	0.002
WEEK 14	212.99	106.49	8.02	0.001
WEEK 15	126.19	63.10	5.70	0.010
WEEK 16	124.68	62.34	4.30	0.027
WEEK 17	29.77	14.89	0.77	0.471
WEEK 18	101.18	50.59	2.31	0.120
WEEK 19	72.22	36.11	0.79	0.462
WEEK 20	20.79	10.39	0.33	0.723
WEEK 21	71.77	35.89	1.71	0.204
WEEK 22	13.26	6.63	0.43	0.655
WEEK 23	178.99	89.49	6.40	0.007
WEEK 24	77.41	38.71	2.20	0.150
WEEK 25	7.00	3.50	0.18	0.839
WEEK 26	-----	-----	-----	-----
WEIGHT OF YOUNG AT BIRTH IN:				
LITTER 1	0.17	0.09	1.40	0.254
LITTER 2	0.09	0.05	1.06	0.353
LITTER 3	0.03	0.02	0.43	0.654

Appendix Table B (continued)

VARIABLE	SUM OF SQUARES	MEAN SQUARE	F	SIGNIF OF F
WEIGHT OF YOUNG AT BIRTH IN: (continued)				
LITTER 4	0.14	0.07	1.30	0.283
LITTER 5	0.05	0.03	0.59	0.562
LITTER 6	0.03	0.01	0.37	0.699
LITTER 7	0.02	0.01	0.60	0.562
LITTER 8	0.24	0.12	8.81	0.034