

SELECTION FOR 42-DAY WEIGHT IN MICE ON  
HIGH AND LOW FIBER DIETS

By

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ABSTRACT OF DISSERTATION PRESENTED TO THE GRADUATE COUNCIL  
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By

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Chairman: Marvin Koger  
Major Department: Animal Science

Direct and correlated responses were determined in two lines of mice (L1 and L2) selected for increased 42-day weight on two diets; L1 on D1, a commercial laboratory ration (PLC) and L2 on D2, a ration consisting of 70% PLC and 30% nonnutritive bulk. After 3 generations eight females from each of the original lines were transferred to the opposite diet forming four subgroups. For the next 5 generations sires were selected only from original lines, each being bred to females from his line on both diets. Traits measured were individual weights at weaning, 42 and 60 days; litter size at birth and at weaning and total litter weight at 42 days.

L1 females were heavier on both diets and pupped larger litters due to a positive effect of maternal weight on litter size. L2 surpassed L1 for weaning weight, litter size at weaning, and litter weight at 42 days. L1 individuals were heavier at 42 and 60 days on both diets. Diet x line interaction approached significance ( $P < .075$ ) for litter weight at 42 days as a result of a reversal in line rank with L2 surpassing L1 in the later generations.

Diet effects were significant for all traits. Generation effects were significant for individual 42- and 60-day weights with means for both weights increasing in response to selection for 42-day weight. Diet x generation effects were significant for litter size at birth, litter weight at 42 days and individual weight at all ages. These interactions were explained by generation means increasing in D1 while D2 means decreased or remained unchanged. There was a significant negative regression of individual weight on number weaned for weaning weight and for 42-day weight. Sex differences were significant for all weights, with males being generally heavier than females. A significant sex x line effect for 60-day weights resulted from a larger difference between sexes in L1. All weights showed significant sex x diet interactions caused by smaller sex differences in D2 than in D1. Diet 2 did not allow males to express their superior growth potential.

Genetic parameters for individual weights were estimated from 8 generations of data from L1 D1 and L2 D2 .

Sire effects were significant only for 42- and 60-day weights in L1. Dam effects were significant for all weights in both lines. All weights had a larger additive genetic variance for growth ( $V_{AO}$ ) in L1 and a larger within-litter variance ( $V_{WL}$ ) in L2. Maternal effect ( $V_{Me}$ ) accounted for most of the phenotypic variance ( $V_p$ ) for all weights in L2. Heritability estimates from L1 and L2 data were for weaning weight .21 and .13; for 42-day weight .34 and -.17 and for 60-day weight .48 and .04. Cumulative selection differentials and responses in grams per generation were 2.71 and .87, respectively, for L1 versus 2.40 and .19 for L2. Realized heritabilities and selection intensities were .33 and 1.35 for L1 compared with .08 and 1.20 for L2. In L1, 42-day weight had a realized genetic correlation with weaning weight 1.04 and with 60-day weight of .57.

Selection for 42-day weight in D1 yielded large growth responses on both diets and a negative correlated response for maternal ability in D2. Selection in D2 resulted in a small direct response, a large correlated response for 42-day weight in D1 and a positive correlated response for maternal ability on D1. Growth rate behaved as a maternal trait in D2.

## INTRODUCTION

One of the basic premises of biometrical genetics concerns the nature of the relationship between genetic and environmental variations which together give rise to variation in phenotypes.

Since most breeds of livestock originated in temperate zones, their performance in the tropics may be profoundly influenced by genetic and environmental variations and their interrelationships in the expression of phenotype.

Selective cattle breeding historically has been practiced predominantly in temperate zones. The temperate zones with their short growing seasons produce forages of low fiber content and high nutritional value. As western man began to colonize and use the tropical and subtropical zones for agriculture and animal husbandry, he generally used existing breeds of cattle from the temperate zones as foundation stock.

Cattle breeding techniques in the temperate zone have become increasingly more sophisticated with developments such as performance testing, progeny evaluation, artificial insemination, heat synchronization and embryo transplants. These techniques usually are practiced under intensified management systems with optimum nutritional regimes.

Progressive livestock breeders from the tropical and subtropical zones have engaged in importation of temperate zone cattle into their areas for improvement of foundation stock. Controversy and doubts exist as to whether the genotypes best suited for temperate zones will be most productive in the tropics. Tropical forages due to the interrelationships between plants, soil nutrients, moisture and temperature are high in lignin and fiber resulting in lower quality than temperate-zone forages. One school of thought is that animals selected under a low plane of nutrition for increased growth rate will maintain or excel their level of performance when transferred to a good plane of nutrition.

The study of interactions of environments and genotypes in large animals is a project of long duration and great expense. The small animal model provides a short generation interval, requires only modest facilities, and lends itself better to selection experiments due to the large number of young produced per mating allowing for a higher selection intensity. Data from the small monogastric animal model, however, may not be altogether characteristic of responses from ruminant populations.

Wright (1939) showed that the relationship between genotype and environment need not be additive. He suggested that if nonadditive genotype-environment interactions existed a breed would have to be developed for every ecological niche capable of supporting one. In 1947 Hammond suggested that animals should be bred in a highly

favorable environment in order to maximize expression of the trait.

Falconer and Latyszewski (1952) hypothesized that for Hammond's thesis to be valid there should be no genotype-environment interaction present. They also pointed out that heritability in a good environment must be higher than in a poor environment in order for selection in a good environment to be superior to selection under a poor environment when both lines are measured under the good environment. It was further stated that a good environment should reduce the random environmental variation which normally lowers the correlation between genotype and phenotype. Falconer (1960a), expanding upon his earlier work, demonstrated that selection for growth in mice under a poor environment was superior to selection under a good environment when performance was measured under both environments.

The interrelationship of diet and genotype in the tropics is a condition that is present during the animals' complete life cycle. Most experiments in the literature have been concerned with temporal diet effects where animals did not reproduce or lactate on the poor diet. They were exposed to it for a short postweaning growth period after which the selected individuals were returned to the optimum diet to breed, gestate and raise their young. Experiments in which diets were not temporal in action were reported by Fowler and Ensminger (1960) in swine and by Hardin and Bell (1967) working with the flour beetle

Tribolium castaneum.

This project was designed using diet as a continuous environment with the mice spending their entire life in the diet designated as environment. The objectives were to study the response to selection under two nutritional environments, to assess the performance of the lines both environments and to measure the correlated responses in traits that would be of economic interest if measured in livestock.

## REVIEW OF LITERATURE

### General Review

Genotype-environment interactions have been studied from different approaches by many workers. McBride (1959) presented an extensive review of opposing arguments. As early as 1939 Wright recognized that the relationship between genotype and environment enhanced the effectiveness of selection, while Lush (1945) recommended that the environmental conditions for a breeding herd be similar to those prevailing for the general population or breed under improvement. James (1961) postulated that an unfavorable environment accompanied by increased physiological stress would accelerate genetic improvement.

In order for selection to be more effective in a good environment, the good environment should be capable of reducing the random environmental variation which normally lowers the correlation between genotype and phenotype; in other words, the heritability of the character should be higher in a good environment than in a poor one.

Haldane (1946) made the first attempt to classify genotype-environment interactions. He postulated four types of interactions between two genotypes and two environments. He gave no attention to the type of differences between environments and genotypes. Lerner (1950) intro-

duced the term "nonlinear genotype-environment interaction" to define Haldane's 2, 3, 4a and 4b type interactions while he termed the remainder as "linear."

McBride (1959) postulated a method for classifying genotype-environment interactions. He partitioned environmental differences into two types, micro- and macro-environmental, and treated intra and interpopulation differences separately. Different climates, diets or even different management practices are examples of macroenvironmental differences, whereas the microenvironmental differences are those fluctuations which occur even when all animals apparently are treated alike. These differences were referred to as "intangible" by Wright (1921). An example would be peck order in domestic fowl.

#### Results From Experiments

Falconer and Latyzewski (1952) reported that the improvement made by selection under good conditions may not be expressed when animals were transferred to poor conditions but that the improvement made under less favorable conditions was retained when animals were transferred to favorable conditions.

Falconer (1960a) showed that mice selected for increased growth on a low plane of nutrition, but later reared on a high plane, were similar to those produced by selection on a high plane. Their growth was the same but they were heavier, had less fat and more protein and were better mothers.

The interaction between temperature and lines was studied by Baker and Cockrem (1970). Mice selected for high 42-day weight under cold, medium and high temperatures for four generations were switched at 3 weeks of age to the other two temperatures. No significant interaction for lines x temperature was found.

Dalton (1967) reported a selection experiment with mice on two diets. His design was very similar to that of Falconer (1960a), except that dietary differences were greater. His measurement of growth was the weight gain between 3 to 6 weeks of age. The low plane consisted of 70% cellulose (crude fiber) and 30% regular lab ration. Selection was within litters standardized at birth to eight. He found no adverse effects from natural selection by comparing selection differentials. Estimates of realized heritability were .23 and .03 in the upward direction for good and poor diets, respectively. When both upward selected lines were tested by means of second litters on the diet opposite to that in which they were selected, he found that on the good diet the good line was superior, while on the poor diet the poor line was better. Differences were not significant, however. He concluded that there was no genotype by environment interaction present.

Park et al. (1966), working with rats, measured post-weaning growth (3 to 9 weeks) under full and restricted feeding regimes. Response to selection was higher under the full-feed regime with realized heritability estimates

of  $.127 \pm .02$  and  $.058 \pm .02$ , respectively, for the two regimes. When the performance of both lines was evaluated under the two feeding regimes it was found that a significant line x feeding regime interaction occurred in females, but not in males. He concluded that selection was best practiced under the regime where the animals were to perform. Correlated responses resulting from selection for postweaning gain are reviewed later in this paper.

#### Weaning Weights

Falconer (1960a) found that female mice selected under a poor nutritional plane produced heavier offspring at 21 days of age when lactating on the good plane of nutrition, both in the upward and downward selection groups. Falconer (1955), selecting within litters, reported that upward selection for increased 42-day weight resulted in a slight increase in weaning (21-day) weight up to generation 12 (.75 grams), followed by a decline to the end of the experiment (30 generations). At the end, the large line had a 21-day weight 3 grams below the control line. He further stated that the regression of 21-day weight of the offspring on 42-day weight of the mother was  $.09 \pm .05$ , as compared with  $-.09 \pm .10$  for the unselected group.

Carry-over effects of weaning weight on postweaning growth are to be expected since this represents a part-whole relationship. However, Falconer (1960a) introduced controversy by reporting a higher regression of growth (3

to 6 week weight gains) on weight at 3 weeks for the poor environment than for the good diet. This higher regression was more evident in males than in females, due possibly to a greater growth potential. Sutherland et al. (1970) reported a decrease in weaning (28-day) weights for lines selected for 4 to 11-week weight gains, feed intake and feed efficiency. Decreases per generation were about  $-.30$  grams per generation. He postulated that the decrease might have been due to an increase in inbreeding, as even the unselected line accumulated 56.8% inbreeding.

Selecting for high 42-day weight under hot, medium and cold temperatures, Baker and Cockrem (1970) reported a positive correlated response for weaning weights under the medium and cold environments and a negative one for the hot environment.

Park et al. (1966), working with rats and using post-weaning gains (3 to 6 weeks) as the trait under selection, obtained a negative correlated response for weaning weights under both full feed and restricted regimes.

Maternal environment acting on growth of the offspring through the prenatal and postnatal influences is an important source of variation in body weight of mice. Maternal effects are still evident at 60 days of age. Brumby (1960) studied this area extensively, using techniques of ova transplant and cross-fostering. His experimental material consisted of three lines, one selected for high 42-day weight, one for low 42-day weight and the third an unse-

lected control. He found a deterioration in lactational performance of both selected lines as compared with controls. His results agreed with Bateman (1954) who stated that 73% of the variance associated with 21-day litter weights was due to prenatal influences. The effect of maternal environment was evident at 60 days of age, even when adjustments were made for litter size. These results emphasize the importance of prenatal environment.

Cox, Legates and Cockerham (1959) looked at the relationship of prenatal versus postnatal environments on 12-day, 21-day and 42-day weights of mice. Cross fostering was used in a fashion similar to Bateman (1954). He found no effect of sex on 21-day weights. Postnatal environment accounted for 60% of the variance of 21-day weights, even when litters were standardized to six young at birth. He disagreed with Brumby (1960) by stating that postnatal environment was the main source of variation in weaning weights.

Young and Legates (1965), using a cross-fostering technique with mice, reported upon relationships between postnatal maternal performance and subsequent weights. The genetic correlation between postnatal maternal performance and 21-day weight was .46 using standardized litters of six young. However, they reported negative correlations between preweaning and postweaning gains. Apparently dams that milked well produced young which had lower gains following weaning.

MacDowell et al. (1930) stated that the increase or differences in weights incurred during the nursing period persisted at maturity in mice. Zucker et al. (1941a, b) found the opposite with rats. Butler and Metrakos (1950) working with mice reported data which agreed with MacDowell et al. (1930).

Neville et al. (1962), working with Hereford cattle, reported a lower partial regression between preweaning growth and milk yield on high nutritional levels than for cattle on lower levels of nutrition, indicating less dependence of calf gains on milk supply as nutrition improves.

#### 42-Day Weights

Sudden increases in the trait under selection as a selection experiment progresses are not uncommon. Roberts (1966) found a marked increase in 42-day weight between generations 43 and 44, from 32 to 35 grams. He believed at first that the change was environmental since the small line (SC) also showed an increase at this point. In addition, the diet had been modified at the time. He concluded that the changes probably were genetic in origin, basing his hypothesis on the fact that no such increases were observed in four other lines derived from the same line. Furthermore, the SC line was notorious for its fluctuations between generations, also the diet modification was of a minor nature.

The number of young born or weaned in a litter has been reported to have a marked effect on individual weight

of the mice at 42 days of age. Roberts (1966) reported a regression of  $-.6$  grams for each mouse born, whereas Falconer (1960b) reported a lower value of  $-.34$  for an unselected line. However, Roberts (1966) further stated that correction of 42-day weights using within-generation regressions resulted in such a small correction that no experimental conclusion could possibly be affected.

Baker and Cockrem (1970) reported results of a selection experiment with mice under three temperatures, high ( $29^{\circ}\text{C}$  to  $33^{\circ}\text{C}$ ), medium ( $19^{\circ}\text{C}$  to  $23^{\circ}\text{C}$ ) and low ( $6^{\circ}\text{C}$  to  $8^{\circ}\text{C}$ ). The trait under selection was 42-day weight and the correlated response was tail length. After four generations, mice from the second litters of all three lines of generation four were allotted at random to the other two temperatures at weaning (3 weeks) and their growth to 6 weeks recorded. He obtained realized heritabilities of  $.64 \pm .05$ ,  $.38 \pm .09$  and  $.52 \pm .07$  for hot, medium and cold temperatures, respectively. Since litter size was not adjusted at birth, the experiment afforded an opportunity to study effects of litter size on 42-day weight. All regressions were negative. The maximum was  $-.5$  grams per mouse weaned. However, since litter size at weaning differed by only  $.7$  mice between the three lines, there were no significant differences in the regressions between lines.

Cox et al. (1959), using a cross-fostering technique, reported an estimate of the effects of postnatal environment on 42-day weight. Using standardized litters of six

mice, he reported that 26% of the variation in 42-day weight could be attributed to postnatal environment.

A limit was reached by Roberts (1966) after 20 generations of selecting for increased 42-day weight in mice. Neither reversed nor relaxed selection yielded change, indicating an exhaustion of additive genetic variance. Falconer (1955) found a high correlation of .90 between postweaning growth and 42-day weight.

Young and Legates (1965) reported a genetic correlation between postnatal maternal performance and 42-day weight of .37 using standardized litters of six young. The phenotypic correlation between 21-day and 42-day weights was .68.

Working with Hereford cattle, Neville et al. (1962) reported a lower partial regression coefficient between milk yield of dam and postweaning performance of the calf under a high nutritional level than under a low nutritional level, indicating a higher dependency on maternal performance under poor nutritional regimes.

#### Fertility

Roberts (1966) demonstrated that cessation of selection for large or small size at 42 days of age resulted in increased fertility of exposed females.

The effect of temperature on fertility was briefly discussed by Baker and Cockrem (1970). They reported a longer interval between pairing and birth of first litter

in cold or hot environments than for normal temperatures.

The interval from first exposure to birth of first litter was used by Park et al. (1966) as a fertility criterion in rats. When the response of the correlated trait was regressed on the cumulative selection differential of the selection trait (3 to 6 weeks growth), estimates obtained were  $.00 \pm .01$  and  $-.005 \pm .01$  for full-fed and restricted-fed lines, respectively.

#### Litter Size

MacArthur (1949) with mice, and Hetzer and Birer (1940) with swine, found a direct association between body weight at maturity and litter size. Wright (1922) and Eaton (1941), working with guinea pigs, observed that a decline in growth from inbreeding was correlated with reduced litter size, while growth heterosis was associated with large litters. Dickerson et al. (1954), working with swine, found that selection for increased litter size and growth was not effective in improving genetic worth of these traits. They postulated a negative genetic correlation between the traits concerned. Cockerham (1952) estimated that the genetic correlation between growth rate and litter size did not differ significantly from zero.

Rahnefled, Boylan and Comstock (1962) reported a heritability based on paternal half-sib correlation of  $.11 \pm .04$  for litter size in mice. The genetic correlation between litter size and growth rate was  $.15$ , but not

significantly different from zero. The genetic change in average litter size for the line selected for growth rate during 13 generations, expressed as a linear regression, was  $.082 \pm .04$  per generation.

Falconer (1955) reported a dam-daughter regression for litter size of virtually zero. However, the standardized regression coefficient, holding the daughter's 42-day weight constant, gave a value of  $.10 \pm .05$  for a heritability of 20%.

It has been demonstrated in swine by Dickerson et al. (1954) that inbreeding was detrimental to prolificacy, even when upward selection for that trait was applied. Coefficients of variation of 35% for number born per litter and 54% for number weaned were reported.

The effect of temperature on litter size in mice was reported by Baker and Cockrem (1970). No significant difference between hot, cold and medium environments for litter size was found.

The correlated response in litter size to selection for postweaning growth (3 to 9 weeks) in rats was studied by Park et al. (1966). It was expressed as the regression of the correlated trait on the weighted selection differential for postweaning gains. The value was  $-.006 \pm .004$  under the full-fed regime and  $.002 \pm .005$  under the restricted regime.

### Literature Summary

Conflicting reports are found in the literature concerning the results of selection in mice and rats for increased body weight on two nutritional environments. Falconer and Latyzewski (1952) and Falconer (1960a) reported an advantage for selection under the poor environment. Dalton (1967), Korkman (1961), Park et al. (1966) and Bateman (1971) recommended that selection should be practiced on the nutritional environment in which the offspring are expected to perform.

Females from a line selected in a low nutritional environment were found to be better mothers (Falconer, 1960a) than those selected on a high plane when both were reared on the high plane.

Selection for growth rate was found to be negatively associated (Roberts, 1966) with fertility in mice. Park et al. (1966) in rats found no significant effects on fertility due to selection for growth rate.

A positive relationship between increased body weight and large litters in mice was reported by MacArthur (1949), Rahnefeld et al. (1962), Falconer (1960b), Eisen (1970), Falconer and King (1953) and Dinsley (1966). Cockerham (1952) estimated a genetic correlation between growth rate and litter size not significantly different from zero. Korkman (1961) found a decrease in litter size in mice selected for increased growth rate.

Kownacki (1971) reported higher survival to weaning

in mice selected in a high plane of nutrition as compared to those selected on a low plane.

A negative effect on weaning weights as a result of selection for increased 42-day weight was reported by Falconer (1955) and Brumby (1960). No significant sex effects at weaning were reported by Cox et al. (1959). A larger difference between the sexes in a good environment was reported by Butler and Metrakos (1950) and Korkman (1957).

Roberts (1966) and Falconer (1960b) reported a marked negative effect of the number weaned per litter on individual weight of mice at 42 days of age. Postnatal environment was found to be a highly significant source of variance for preweaning and postweaning weight by Cox et al. (1959), Young and Legates (1965), Jinks and Broadhurst (1963), Rutledge et al. (1972) and Moore et al. (1970).

Small responses to selection for growth rate in the low plane were reported in mice (Korkman, 1961; Dalton, 1967; Kownacki, 1971) and in rats (Park et al., 1966).

Phenotypic variances were found to be larger in the low plane as compared to the high plane by McLaren and Michie (1956) and Bateman (1971).

Non-Mendelian transmitted maternal effects were reported by Morton (1970), Brumby (1960) and Reutzel (1970).

## MATERIALS AND METHODS

### Collection of Data

Two lines were formed in 1967 allocating eight males and twenty-four females randomly from a population of random bred ICR mice from Dublin Laboratories to each of two diets. Diet one (D1) consisted of Purina Laboratory Chow. Diet two (D2) was 70% Purina Laboratory Chow and 30% Alphacel, a nonnutritive bulk. Both diets were fed ad libitum with feed and water present at all times.

Mass selection was practiced from first litters only for increased individual weight at 42 days of age for eight generations. Mice were weighed after feed had been withheld for approximately 24 hours. Selections were made only from litters in which at least six mice were weaned. Litters were reduced to 10 mice at birth by sacrifice of all young exceeding 10. Mice were bred at  $65 \pm 2$  days of age. No full- or half-sib mating were permitted, nor was it allowed for two full-sib females to be bred to the same male. The mating design employed is presented in Table 1.

Eight third-generation females were selected from each diet and placed on the opposite diet at 60 days of age, thus forming four groups. Mice selected originally on diet 1 were referred to as line L (L1), and those from diet 2 as line 2 (L2). The four groups consisted of the two original

TABLE 1. MATING DESIGN EMPLOYED IN DEVELOPING THE TWO LINES AND IN SUBSEQUENT TESTING OF THE TWO LINES ON THE OPPOSITE DIETS

Offspring Generation	Line 1		Line 2		Sire #	Sire #	Diet 1		Diet 2	
	Sire #	Females/Sire	Sire #	Females/Sire			Females/Sire	Females/Sire	Females/Sire	Females/Sire
1	1- 5	5	-	-	6- 10	-	-	-	-	4
2	11- 18	3	-	-	19- 26	-	-	-	-	3
3	27- 34	3	-	-	35- 42	-	-	-	-	3
4	43- 50	3	1	1	51- 58	1	1	1	1	3
5	59- 66	3	1	1	67- 74	1	1	1	1	3
6	75- 82	3	1	1	83- 90	1	1	1	1	3
7	91- 98	3	1	1	99-106	1	1	1	1	3
8	107-114	3	1	1	115-122	1	1	1	1	3

groups, L1/D1, L2/D2, and the two new groups, L1/D2 and L2/D1.

Breeding males were selected only from the original two groups in all succeeding generations, whereas breeding females were selected from all four groups. Females were bred only to males of their own line, i.e., L1/D1 and L1/D2 females were bred to L1/D1 males whereas L2/D2 and L2/D1 females were bred to L2/D2 males. This was accomplished by changing males from diet 1 to diet 2, or from diet 2 to diet 1, every 24 hours during the breeding season so that the females underwent no change of diet. Offspring from the four groups were grown, selected and bred with no change of diet for the next five generations with the exception of males during the breeding season. Selection criteria were the same for females in all four groups.

Each breeding male was mated to three females from his own line-diet group and to one female from his line on the opposite diet. The mating period continued for 18 days after which all females were placed on individual solid bottom cages using treated corncob grounds as bedding.

All litters were weighed at birth and if larger than ten in size they were reduced to 10 by sacrificing at random except for weak or deformed pups.

The mice were weaned at 21 days of age. At this time they were weighed, ear marked and separated by sex. They were raised in 3 x 3 mesh wire cages in groups of approximately 10. The cross-over mice (L1D2, L2D1) were inter-

mingled with the selection group on the same diet. At 41 days of age feed was withdrawn from the mice for a period of 24 hours. The mice then were weighed at day 42 on an empty basis. The same procedure was followed in obtaining 60-day weights.

#### Description of Data

The data were partitioned into two distinct sets. One set consisted of 8 generations from L1/D1 and L2/D2 and is referred to as the selection experiment. The other set involved the last 5 generations which compared contemporaneously L1/D1, L1/D2, L2/D1 and L2/D2. This set is referred to as the genotype by environment interaction (GEI) experiment.

A portion of the results from the selection experiment have been reported by Rodriguez, Koger and Franke (1970).

The data represented two types of traits, dam traits and individual weight data. Dam traits included pregnancy rate (a trait common to all selected females) and the litter traits, litter size at birth, litter size at weaning, average within litter 42-day weight and total litter weight at 42 days of age. The individual weight data included weaning weights, 42-day weights and 60-day weights.

Pregnancy rate, litter traits and individual weights were analysed by fitting different models to the GEI data (Tables 2 to 4). Genetic parameters for individual

TABLE 2. EFFECTS FITTED, DEGREES OF FREEDOM AND THEIR EXPECTED MEAN SQUARES FOR MODEL 1 EMPLOYED IN ANALYZING PREGNANCY RATE

SOURCE	df	E (MS)
Generations (G)	4	$\sigma^2_w + k_{15}\sigma^2_s + k_{16}\sigma^2_g$
Lines (L)	1	$\sigma^2_w + k_{13}\sigma^2_s + k_{14}\sigma^2_e$
G x L	4	$\sigma^2_w + k_{11}\sigma^2_s + k_{12}\sigma^2_{gl}$
Sires/GL (S)	70	$\sigma^2_w + k_{10}\sigma^2_s$
Diet (D)	1	$\sigma^2_w + k_8\sigma^2_{ds} + k_9\sigma^2_d$
D x G	4	$\sigma^2_w + k_6\sigma^2_{ds} + k_7\sigma^2_{dg}$
D x L	1	$\sigma^2_w + k_4\sigma^2_{ds} + k_5\sigma^2_{dl}$
D x G x L	4	$\sigma^2_w + k_2\sigma^2_{ds} + k_3\sigma^2_{dgl}$
D x S	70	$\sigma^2_w + k_1\sigma^2_{ds}$
Within	160	$\sigma^2_w$

weights were obtained from the selection experiment (Table 5). Complete confounding of sires and dams in L1/D2 and L2/D1 precluded the unbiased estimation of random variances in these two groups.

#### Analyses of Data

The data were analyzed employing least squares techniques described by Harvey (1960), utilizing the Ohio State University Computer Least Squares Program written by Dr. Harvey. The data were analyzed according to procedures described by Harvey (1964) using absorption techniques in the analysis of split-split plot designs.

#### Pregnancy Rate

Pregnancy rate was expressed as the presence or absence (recorded as 1 or 0, respectively) of a litter resulting from the pairing of 240 females with 80 sires. Model 1 was fitted and the effects, degrees of freedom and expected mean squares appear in Table 2. Sires in the model represent males mated with females, not sires of females.

#### Litter Traits

Litter traits are those in which the litter measurement is the observation. Litter size at birth and at weaning, were unadjusted observations. Total litter weight at 42 days of age was obtained by totaling individual records of litter mates adjusted for sex. Least squares constants obtained from fitting a model containing sex as a

single effect were employed to adjust data. Average within-litter 42-day weight was obtained by dividing total litter weight by the number of litter mates at 42-days of age.

The data included 175 litters by 54 sires. There were 74 litters by 23 sires in line 1, and 101 litters by 31 sires in line 2. Sires were considered random in model 2, with all other effects (Table 3) assumed to be fixed.

#### Individual Weights

Weaning weight (21-day weight), 42-day weight and 60-day weight were the individual weights analyzed. Unadjusted observations were analyzed by fitting model 3 (Table 4). The number of pups weaned per litter was used as a covariate to remove environmental effects due to variations in litter size.

The data consisted of 1312 records, representing 51 sires and 162 dams. Only sires with progeny on both diets and litters of at least three young at weaning were included. This restriction was imposed to prevent distortion of sire x diet effects by insuring at least three observations in sire x diet subcells.

#### Random Variances

Estimates of random variances were obtained for weaning weight, 42-day weight and 60-day weight by analyzing individual weight data from 8 generations. Line 1 data consisted of 1113 mice representing 50 sires and 125 dams, while line 2 had 878 records by 46 sires and 115

TABLE 3. EFFECTS FITTED, DEGREES OF FREEDOM AND THEIR EXPECTED MEAN SQUARES FOR MODEL 2 EMPLOYED IN ANALYZING LITTER TRAITS

SOURCE	df	E (MS)
Generations (G)	4	$\sigma^2_w + k_{15}\sigma^2_s + k_{16}\sigma^2_g$
Lines (L)	1	$\sigma^2_w + k_{13}\sigma^2_s + k_{14}\sigma^2_l$
G x L	4	$\sigma^2_w + k_{11}\sigma^2_s + k_{12}\sigma^2_{gl}$
Sires/GL (S)	44	$\sigma^2_w + k_{10}\sigma^2_s$
Diet (D)	1	$\sigma^2_w + k_8\sigma^2_{ds} + k_9\sigma^2_d$
D x G	4	$\sigma^2_w + k_6\sigma^2_{ds} + k_7\sigma^2_{dg}$
D x L	1	$\sigma^2_w + k_4\sigma^2_{ds} + k_5\sigma^2_{dl}$
D x G x L	4	$\sigma^2_w + k_2\sigma^2_{ds} + k_3\sigma^2_{dgl}$
D x S	44	$\sigma^2_w + k_1\sigma^2_{ds}$
Within	67	$\sigma^2_w$

TABLE 4. EFFECTS FITTED, DEGREES OF FREEDOM AND THEIR EXPECTED MEAN SQUARES FOR MODEL 3 EMPLOYED IN ANALYZING INDIVIDUAL WEIGHT DATA

SOURCE	df	E (MS)
Generations (G)	4	$\sigma_w^2 + k_{28}\sigma_i^2 + k_{29}\sigma_s^2 + k_{30}\sigma_g^2$
Lines (L)	1	$\sigma_w^2 + k_{25}\sigma_i^2 + k_{26}\sigma_s^2 + k_{27}\sigma_l^2$
G x L	4	$\sigma_w^2 + k_{22}\sigma_i^2 + k_{23}\sigma_s^2 + k_{24}\sigma_{gl}^2$
Sires/GL (S)	41	$\sigma_w^2 + k_{20}\sigma_i^2 + k_{21}\sigma_s^2$
Diet (D)	1	$\sigma_w^2 + k_{17}\sigma_i^2 + k_{18}\sigma_{ds}^2 + k_{19}\sigma_d^2$
D x G	4	$\sigma_w^2 + k_{14}\sigma_i^2 + k_{15}\sigma_{ds}^2 + k_{16}\sigma_{dg}^2$
D x L	1	$\sigma_w^2 + k_{11}\sigma_i^2 + k_{12}\sigma_{ds}^2 + k_{13}\sigma_{dl}^2$
D x G x L	4	$\sigma_w^2 + k_8\sigma_i^2 + k_9\sigma_{ds}^2 + k_{10}\sigma_{dgl}^2$
D x S	41	$\sigma_w^2 + k_6\sigma_i^2 + k_7\sigma_{ds}^2$
Dams/SDGL (I)	58	$\sigma_w^2 + k_5\sigma_i^2$
No. Weaned (Linear)	1	$\sigma_w^2 + K_{31}\sigma_{bl}^2$
No. Weaned (Quadratic)	1	$\sigma_w^2 + K_{32}\sigma_{bq}^2$
Sex (Z)	1	$\sigma_w^2 + k_4\sigma_z^2$
Z x G	4	$\sigma_w^2 + k_3\sigma_{zg}^2$
Z x L	1	$\sigma_w^2 + k_2\sigma_{zl}^2$
Z x D	1	$\sigma_w^2 + k_1\sigma_{zd}^2$
Within	1141	$\sigma_w^2$

dams. Data from line 1 and line 2 were analyzed separately by fitting model 4 (Table 5).

### Genetic Parameters

#### Variance Components

Estimates of the components of random variances were obtained using the method of King and Henderson (1954) for unequal number of progeny per dam and unequal number of dams per sire.

$$\sigma^2_S = \frac{MS_S - MS_W - \frac{K_2}{K_1} (MS_D - MS_W)}{K_3}$$

$$\sigma^2_D = \frac{MS_D - MS_W}{K_1}$$

$$\sigma^2_W = MS_W$$

$K_1$  = number of offspring per dam

$K_2$  = number of offspring per dam/sire

$K_3$  = number of offspring per sire

$\sigma^2_S$  = sire variance

$\sigma^2_D$  = dam variance

$\sigma^2_W$  = within-litter variance

The K values were computed as suggested by Becker (1964).

$$K_1 = \frac{\text{Total No.} - \frac{\sum (\text{number/dam})^2}{\text{number/sire}}}{\text{d.f. dams}}$$

TABLE 5. EFFECTS FITTED, DEGREES OF FREEDOM AND THEIR EXPECTED MEAN SQUARES FOR MODEL 4 EMPLOYED IN ANALYZING INDIVIDUAL WEIGHT DATA WITHIN LINE AND DIET

SOURCE	df	E (MS)
Generations (G)	GEN - 1	$\sigma^2_w + k_6\sigma^2_i + k_7\sigma^2_s + k_8\sigma^2_g$
Sires/G (S)	SIR - GEN	$\sigma^2_w + k_4\sigma^2_i + k_5\sigma^2_s$
Dams/S (I)	D - SIR - 2	$\sigma^2_w + k_3\sigma^2_i$
No. Weaned (Linear)	1	$\sigma^2_w + K_9\sigma^2_{b1}$
No. Weaned (Quadratic)	1	$\sigma^2_w + K_{10}\sigma^2_{bq}$
Sex (Z)	1	$\sigma^2_w + k_2\sigma^2_z$
Z x G	GEN-1	$\sigma^2_w + k_1\sigma^2_{zg}$
Within	Total-Reduction-1	$\sigma^2$

GEN = number of generations

SIR = number of sires

D = number of dams

$$K_2 = \frac{\frac{\Sigma (\text{number/dam})^2}{\text{number/sire}} - \frac{\Sigma (\text{number/dam})^2}{\text{total number}}}{\text{d.f. sires}}$$

$$K_3 = \frac{\text{Total No.} - \frac{\Sigma (\text{number/sire})^2}{\text{total number}}}{\text{Sires} - 1}$$

### Estimates of $h^2$

The estimates of  $h^2$  and their standard errors were computed as suggested by Dickerson (1960).

$$h^2 = \frac{4\sigma^2_S}{\sigma^2_W + \sigma^2_D + \sigma^2_S} = \frac{V_A}{V_P}$$

$$\text{s.e.}h^2 = \frac{4 \cdot 2/K^2_3 \cdot \frac{MS^2_S}{S+1} + \frac{MS^2_D}{D-S-2}}{\sigma^2_W + \sigma^2_D + \sigma^2_S}$$

$\text{s.e.}h^2$  = standard error of the  $h^2$

s = number of sires

D = number of dams

### Causal Components of Variance

The causal components were computed from the observational components as described by Falconer (1964), with modifications introduced by Willham (1963) and Miller, Legates and Cockerham (1963).

The phenotypic variance ( $V_P$ ) of mice weights can be expressed in terms of its components as

$$V_p = \sigma^2_{Ao} + \sigma^2_{Do} + \sigma_{AoAm} + \sigma^2_{Am} + \sigma^2_{Dm} + \sigma^2_{Ec} + \sigma^2_{Ew} + \sigma^2_I$$

$\sigma^2_{Do}$  = nonmaternal dominance variance

$\sigma_{AoAm}$  = covariance of maternal and nonmaternal components

$\sigma^2_{Ao}$  and  $\sigma^2_{Am}$  = additive nonmaternal and maternal variances

$\sigma^2_{Dm}$  = maternal dominance variance

$\sigma^2_{Ec}$  = random environmental variance common to litters

$\sigma^2_{Ew}$  = random environmental variance within-litter

$\sigma^2_I$  = epistasis variance

Miller et al. (1963) found no nonadditive genetic variance due to dominance or epistasis in 21- and 42-day weights in mice. Similar results were reported by Cox, Legates and Cockerham (1959). On the basis of these findings it was assumed that dominance and epistasis effects are not different from zero. The expression then reduces to a simpler form.

$$V_p = \sigma^2_{Ao} + \sigma_{AoAm} + \sigma^2_{Am} + \sigma^2_{Dm} + \sigma^2_{Ec} + \sigma^2_{Ew}$$

This expression can then be defined in terms of the observational components.

$$\sigma^2_S = 1/2 \sigma^2_{Ao}$$

$$\sigma^2_D = 1/4 \sigma^2_{Ao} + \sigma_{AoAm} + \sigma^2_{Am} + \sigma^2_{Dm} + \sigma^2_{Ec}$$

$$\sigma^2_W = 1/2 \sigma^2_{Ao} + \sigma^2_{Ew}$$

The causal components can then be computed from the observational components.

$$\begin{aligned} \text{Nonmaternal additive variance } (V_{Ao}) &= 4 \sigma^2_S \\ \text{Maternal effect } (V_{Me}) &= \sigma^2_D - \sigma^2_S \\ \text{Within-litter variance } (V_{WL}) &= \sigma^2_W - 2 \sigma_S \\ \text{Phenotypic variance } (V_p) &= \sigma^2_S + \sigma^2_D + \sigma^2_W \end{aligned}$$

Therefore:

$$V_{Ao} = \sigma^2_{Ao}$$

$$V_{Me} = \sigma^2_{Am} + \sigma_{AmAo} + \sigma^2_{Dm} + \sigma^2_{Ec}$$

$$V_{WL} = \sigma^2_{Ew}$$

$$V_p = V_{Ao} + V_{Me} + V_{WL}$$

### Realized Genetic Correlations

Falconer (1952) developed the first genetic correlation formula based on direct and correlated responses:

$$r_A = \frac{CR_Y \sigma_{ax}}{R_X \sigma_{ay}}$$

Where:

$r_A$  = realized genetic correlation

$CR_Y$  = correlated response in trait y to selection for trait x

$R_X$  = direct response to selection for trait x

$\sigma_{ax}$  = additive standard deviation of trait x

$\sigma_{ay}$  = additive standard deviation of trait y

Standard errors of the realized genetic correlations were calculated according to Robertson (1959).

$$\sigma(r_A) = \frac{1-r_A^2}{\sqrt{2}} \cdot \sqrt{\frac{(h_x^2) \sigma(h_y^2)}{h_x^2 h_y^2}}$$

Where:

$\sigma(r_A)$  = standard error of the genetic correlation estimate

$r_A^2$  = square of the genetic correlation

$\sigma(h_x^2)$  = standard error of the heritability estimate of trait x

$\sigma(h_y^2)$  = standard error of the heritability estimate of trait y

## RESULTS AND DISCUSSION

Both the direct and correlated responses to selection enter into total response which is generally the item of greatest interest in selection experiments. In single trait selection, the aggregate of correlated responses generally are of greater impact than direct response. This is true especially of experiments involving genotype by environment interactions. The present trial fits into this category.

To gain the best comprehension of results from the experiment requires the presentation of correlated responses both within and across diets. Consequently, the GEI data set will be presented first. The data include those from generations 4 through 8. Estimates of direct and important correlated responses along with total productivity in the two dietary environments will be presented first.

Data from the two selection groups, D1/L1 and D2/L2, across all eight generations will then be presented along with certain genetic parameters having a bearing on the results from the GEI phase of the trait.

The unadjusted means and standard deviations for the traits measured in the project are presented in Table 6.

TABLE 6. AVERAGES AND STANDARD DEVIATIONS FOR DEPENDENT VARIABLES

	$\bar{X}$	Standard Deviation	Number of Observations
Pregnancy Rate	83.75%	36.95	320
Litter Size at Birth	9.62	2.62	175
Litter Size at Weaning	7.90	2.24	175
Litter Size at 60 Days of Age	7.69	2.26	175
Average Within Litter 42-Day Weight	21.36 grams	4.19	175
Total Litter Weight at 42-Days of Age	164.69 grams	59.08	175
Weaning Weight (21-day weight)	9.69 grams	2.83	1312
42-Day Weight	21.44 grams	4.41	1312
60-Day Weight	26.77 grams	5.00	1312

### Pregnancy Rate

Pregnancy rate was analyzed by fitting model 1. The analysis of variance is shown in Table 7. Generation and sires were the only significant ( $P < .05$ ) sources of variation. Least squares means for pregnancy rate are presented in Table 8.

While generation effects were evident, they did not appear to follow a trend attributable to a response to selection for body weight. The first four generations were suggestive of a negative trend. During the last generation, however, pregnancy rate returned approximately to the level of generation 4. The regression of generation means on generation number was not significant.

When generation and sires were considered together, it appeared that random sire differences were the major cause of fluctuations in generation means. Sire differences appeared to be the result of an occasional sterile sire within a particular generation. These results disagree with those obtained by Roberts (1966) with mice and Park et al. (1966) with rats who reported a decrease in pregnancy rate as a result of selection for increased weight.

### Litter Size at Birth

Physiological aspects of reproductive responses in this project were reported previously by Dickens (1970). Litter size at birth, weaning and 60 days of age were included in the present study as dependent variables to help

TABLE 7. LEAST SQUARES ANALYSIS OF VARIANCE FOR PREGNANCY RATE, MODEL 1

SOURCE	df	SS	MS	F
Generations (G)	4	1.86	.46	2.52*
Lines (L)	1	.15	.15	.83
G x L	4	.89	.22	1.21
Sires/GL (S)	70	12.76	.18	1.62*
Diet (D)	1	.04	.04	.33
D x G	4	.19	.05	.42
D x L	1	.07	.07	.58
D x G x L	4	.61	.15	1.25
D x S	70	9.20	.12	1.11
Within	160	18.00	.11	

\* P &lt; .05.

TABLE 8. LEAST SQUARES MEANS AND STANDARD ERRORS FOR PREGNANCY RATE (%) BY DIET, LINE AND GENERATION, MODEL 1

Line & Diet	Generations						Means
	4	5	6	7	8		
L1 D1	85.1±.04	85.1±.04	82.5±.04	54.9±.04	88.2±.04	79.2±.03	
L1 D2	94.7±.08	94.7±.08	77.5±.08	60.3±.08	97.8±.08	85.0±.06	
L2 D1	94.7±.08	82.2±.08	90.0±.08	85.3±.08	85.3±.08	87.5±.06	
L2 D2	97.6±.04	85.1±.04	78.3±.04	84.0±.04	88.2±.04	86.7±.03	
L1	89.9±.07	89.9±.07	80.0±.07	57.6±.07	93.0±.07	82.1±.03	
L2	96.1±.07	83.6±.07	84.2±.07	84.7±.07	86.8±.07	87.1±.03	
D1	89.9±.07	83.6±.07	86.2±.07	70.0±.07	86.8±.07	83.3±.03	
D2	96.1±.07	89.9±.07	78.0±.07	72.2±.07	93.0±.07	85.8±.03	
All Groups	93.0±.05	86.8±.05	82.1±.05	71.1±.05	89.9±.05	84.58±.02	

characterize the litters used in these analyses. Litter size was analyzed using Model 2.

The variance analysis for litter size at birth is shown in Table 9. Two main effects (line and diet) and one interaction (generation x diet) were found to be significant ( $P < .05$ ). The subclass least squares means for litter size at birth are shown in Table 10.

Larger litters were born on diet 1 than on diet 2. With successive generations of selection, diet 1 litters became larger, while diet 2 litters became smaller, resulting in a significant ( $P < .05$ ) diet x generation interaction. The positive effect of maternal body weight on litter size at birth has been reported for mice by Falconer and King (1953), Dinsley (1966), Rahnefeld et al. (1962) and MacArthur (1949); by Hetzer and Brier (1940) for swine, and by Robens (1968) in golden hamsters. The 60-day weights of mice taken just prior to pairing appear in Table 23. It is evident that an increase both in 60-day weight and litter size at birth occurred in diet 1. It also appears that L1/D2 mice were heavier and had larger litters than L2/D2.

Significant ( $P < .05$ ) line effects on litter size may also be attributed to the relationship between body weight and litter size at birth. Line 1 mice were bigger at 60 days of age and had larger litters than line 2 mice in both diets. The regression coefficient of litter size on dam's weight in L1/D1 for all 8 generations of the selection experiment was .37 ( $P < .001$ ). This was similar to results with mice

TABLE 9. LEAST SQUARES ANALYSIS OF VARIANCE FOR LITTER SIZE AT BIRTH, MODEL 2

SOURCE	df	SS	MS	F
Generations (G)	4	33.54	8.38	1.23
Lines (L)	1	40.71	40.71	5.95*
G x L	4	8.43	2.11	.31
Sires/GL (S)	44	300.83	6.84	1.25
Diet (D)	1	34.37	34.37	5.89*
D x G	4	60.57	15.14	2.59*
D x L	1	12.44	12.44	2.13
D x G x L	4	48.48	12.12	2.08
D x S	44	256.77	5.84	1.07
Within	67	366.33	5.47	

\*P < .05

TABLE 10. LEAST SQUARES MEANS AND STANDARD ERRORS FOR LITTER SIZE AT BIRTH BY DIET,  
LINE AND GENERATIONS, MODEL 2

Line & Diet	Generations						Means
	4	5	6	7	8	8	
L1 D1	10.41± .72	10.48± .69	10.79±1.00	11.22±1.36	12.01±1.14	10.98±.38	
L1 D2	10.61±1.11	10.04±1.03	8.73±1.36	8.06±1.92	9.47±1.36	9.39±.54	
L2 D1	8.83± .76	7.86± .90	9.00± .83	10.02± .72	10.59± .90	9.25±.45	
L2 D2	10.23± .49	8.62± .55	8.14± .57	8.06± .56	9.25± .76	8.86±.30	
L1	10.52± .58	10.26± .55	9.76± .72	9.63±1.02	10.74± .76	10.18±.34	
L2	9.53± .53	8.24± .61	8.56± .58	9.04± .54	9.92± .70	9.06±.27	
D1	9.61± .55	9.16± .60	9.89± .64	10.62± .74	11.30± .72	10.12±.29	
D2	10.43± .55	9.33± .56	8.43± .64	8.06± .77	9.37± .74	9.12±.31	
All Groups	10.02± .38	9.25± .39	9.16± .44	9.33± .57	10.33± .51	9.62±.22	

reported by Eisen (1970). He concluded that the sum of additive covariance between maternal effects for litter size and maternal effects for body weight; and for additive covariance between maternal effects for litter size and direct effects for adult weight must be positive. He hypothesized that covariances must have been the result of pleiotropic effects of genes influencing litter size and body weight. Korkman (1961) reported that selection for body weight in crosses between certain inbred mice lines resulted in a decrease in litter size and an increase in weight.

Litter size at birth for L1/D1, L2/D1, L1/D2 and L2/D2 were consistent with ovulation rates reported by Dickens (1970) for these same groups.

#### Litter Size at Weaning

According to the analysis shown in Table 11, the only significant effects influencing litter size at weaning were generation ( $P < .05$ ) and diet ( $P < .01$ ). Least squares generation means were variable and seemingly without pattern (Table 12). Generation 7 means were low for all groups due to an unspecific pathogen causing death in preweaning pups.

Diet had a marked effect on number weaned, with means of 8.42 for diet 1 and 7.04 for diet 2. At least two cumulative effects were involved. Diet 1 females had larger litters than diet 2, as discussed in the previous section. The survival rates of pups to weaning, Table 14, in diets 1 and 2 were 88.6 and 74.3%, respectively. The combination

TABLE 11. LEAST SQUARES ANALYSIS OF VARIANCE FOR LITTER SIZE AT WEANING, MODEL 2

SOURCE	df	SS	MS	F
Generations (G)	4	67.99	17.00	2.93*
Lines (L)	1	.56	.56	.10
G x L	4	9.86	2.47	.42
Sires/GL (S)	44	255.66	5.81	1.60
Diet (D)	1	66.32	66.32	15.72**
D x G	4	22.36	5.59	1.32
D x L	1	8.56	8.56	2.03
D x G x L	4	16.02	4.01	.95
D x S	44	185.65	4.22	1.16
Within	67	243.50	3.63	

\* P < .05

\*\* P < .01

TABLE 12. LEAST SQUARES MEANS AND STANDARD ERRORS FOR LITTER SIZE AT WEANING BY DIET, LINE AND GENERATION, MODEL 2

Line & Diet	Generations						Means
	4	5	6	7	8		
L1 D1	9.36±.52	8.36±.50	8.65±.73	7.94± .99	8.70±.83	8.61±.32	
L1 D2	8.59±.80	7.14±.74	6.27±.99	5.11±1.40	6.50±.99	6.73±.46	
L2 D1	8.50±.70	7.21±.83	8.51±.76	8.16± .66	8.81±.83	8.24±.38	
L2 D2	8.75±.45	6.99±.50	7.12±.52	6.32± .51	7.62±.69	7.36±.26	
L1	8.98±.49	7.76±.46	7.46±.61	6.53± .87	7.61±.65	7.67±.29	
L2	8.62±.45	7.10±.52	7.82±.49	7.24± .46	8.21±.59	7.80±.23	
D1	8.94±.47	7.79±.51	8.58±.55	8.05± .63	8.76±.66	8.42±.25	
D2	8.67±.47	7.07±.48	6.70±.55	5.71± .66	7.06±.63	7.04±.26	
All Groups	8.80±.32	7.43±.33	7.64±.38	6.88± .48	7.92±.43	7.73±.19	

of larger litters and better survival in diet 1 resulted in a highly significant difference between diet means. Kownacki (1971) reported larger litters at birth and higher survival for mice selected on a high protein diet than for a line selected on a low protein level.

The data showed some interesting nonsignificant trends as the project progressed. Some of these trends, however, were evident enough to merit discussion.

As selection progressed from generation 4 to generation 8, line 1 increased in litter size at birth. A negative trend, however, was evident in L1/D2. In generation 8, litter size at weaning in line 2 (8.21) was superior to that of line 1 (7.61). Litter size at weaning in L1/D2 responded negatively to selection for increased body weight in L1/D1, while litter size at weaning in L2/D1 responded positively to selection for body weight in L2/D2. Oddly enough, litter size at weaning in the parental lines L/D1 and L2/D2 showed little change.

Table 14 indicates superior survival for pups of line 2 in both diets. If survival to weaning is a function of maternal ability, then line 2 females were superior to mothers from line 1. As females of line 1 became heavier, their maternal performance suffered, especially in diet 2. Visual observation of carcasses of these mice indicated an increasing predisposition to fatness in L1/D1 animals as body weight increased in response to selection. Anus to tip of snout measurements, Table 13, revealed no increased

TABLE 13. NUMBER OF OBSERVATIONS AND AVERAGE LENGTH IN CENTIMETERS FROM ANUS TO TIP OF SNOOT BY LINE, SEX AND GENERATION

Generation	Males		Females	
	L1/D1	L2/D2	L1/D1	L2/D2
	Number of Observations			
2	19	20	19	20
3	20	20	20	20
4	14	13	13	15
5	17	15	18	11
6	18	16	13	18
7	14	14	13	14
8	<u>17</u>	<u>17</u>	<u>19</u>	<u>19</u>
Total	119	115	115	117
	Length in Centimeters			
2	9.88	9.27	9.54	8.76
3	9.89	9.18	9.29	8.85
4	9.80	9.57	9.41	8.60
5	9.66	9.55	9.20	8.45
6	10.37	9.59	9.71	8.90
7	9.97	9.65	9.24	8.24
8	<u>9.84</u>	<u>9.30</u>	<u>9.20</u>	<u>8.75</u>
Aver.	9.89	9.44	9.37	8.65

TABLE 14. LEAST SQUARES MEANS FOR SURVIVAL TO WEANING (%) BY DIET, LINE AND GENERATION

Line & Diet	Generations						Means
	4	5	6	7	8		
L1 D1	90.4	90.4	95.0	62.0	89.3	87.0	
L1 D2	89.2	69.2	41.8	56.0	32.6	60.7	
L2 D1	92.1	92.3	95.2	95.8	91.5	93.6	
L2 D2	90.9	82.2	78.6	60.7	78.8	79.2	
L1	90.1	84.9	84.4	60.4	78.2	79.6	
L2	91.2	84.2	83.2	72.8	82.0	82.7	
D1	90.8	90.7	95.0	74.1	89.8	88.6	
D2	90.5	78.3	63.4	59.5	68.0	74.3	
All Groups	90.6	84.6	83.9	67.1	80.0	81.0	

skeletal length in L1/D1. Korkman (1961) has reported an increase in length of mice selected for increased 40-day weight on a high plane of nutrition. It is a prima facie assumption that the increase in body weight which occurred in L1/D1 was the result of a genetic ability to accumulate fat. L2/D2 mice visually were leaner and more active than L1/D1 individuals. It appears reasonable, then, to theorize that selected breeders from L1/D1 were in effect selected on the basis of ability to accumulate fat under an optimum nutritional regime, while in the L2/D2 group selected individuals were heavier because they or their dams were better adapted to the adverse nutritional regime under which they were selected.

When the line 1 females were forced to grow and reproduce under the adverse nutritional regime of diet 2, there was a tendency to utilize available nutrients for fat deposition rather than for milk for the young, resulting in pup survival of 18.5% less than that for line 2. Inability of a line selected under a good plane of nutrition to adapt to a low plane was encountered also by Falconer (1960a). He referred to it as the "susceptibility" of the good line to the low plane.

On diet 1, differences between line 1 and line 2 were mainly a function of initial litter size and survival. Both lines showed increased litter size at birth, Table 10. For example, in generation 8, litter size for line 1 was 12.01 and for line 2, 10.59; however, after

adjustment for litters to a maximum of 10 pups the two lines had nearly an equal starting point. Survival to weaning in line 1 was 89.3% and in line 2, 91.5% resulting in line 2 having an advantage over line 1 (8.81 vs. 8.70) in litter size at weaning.

#### Total Litter Weight at 42 Days of Age

Litter weight is a good indication of total performance since it combines litter size, survival and growth rate. The least squares analysis for this trait is presented in Table 15. Factors affecting this trait significantly were generation ( $P < .05$ ), diet ( $P < .01$ ) and their interaction  $G \times D$  ( $P < .01$ ).

Diet effects again were highly significant with least squares means of 208.96 grams for diet 1 and 119.10 grams for diet 2. Generation effects also were significant as were  $G \times D$  interaction effects. Means for generations (Table 16) in diet 1 became progressively larger while means for generations in diet 2 declined, particularly those for L1/D2. The  $L \times D$  interaction component approached significance ( $P < .10$ ).

As discussed in the section on litter size at weaning, line 2 females appeared to be superior in maternal performance to line 1 females. Even though line 2 females gave birth to smaller litters adjustment to 10 pups per litter at birth and superior survival to weaning resulted in larger litters at 42 days of age for line 2 than for line 1.

TABLE 15. LEAST SQUARES ANALYSIS OF VARIANCE FOR TOTAL LITTER WEIGHT AT 42-DAYS OF AGE, MODEL 2

SOURCE	df	SS	MS	F
Generations (G)	4	14,878.29	3,719.57	2.69*
Lines (L)	1	9.33	9.33	.01
G x L	4	5,529.31	1,382.33	.76
Sires/GL (S)	44	80,141.40	1,821.40	1.37
Diet (D)	1	281,456.04	281,456.04	173.66**
D x G	4	33,993.65	8,498.41	5.24**
D x L	1	6,046.94	6,046.94	3.73***
D x G x L	4	9.033.30	2,258.33	1.39
D x S	44	71,311.20	1,620.71	1.22
Within	67	89,154.54	1,330.66	

\* P < .05

\*\* P < .01

\*\*\*P < .10

TABLE 16. LEAST SQUARES MEANS AND STANDARD ERRORS IN GRAMS FOR TOTAL LITTER WEIGHT AT 42-DAYS OF AGE BY LINE, DIET AND GENERATION, MODEL 2

Line & Diet	Generations						Means
	4	5	6	7	8		
L1 D1	215.58±11.03	199.46±10.64	220.70±15.41	212.34±20.93	231.32±17.62	215.88±6.15	
L1 D2	155.54±17.10	122.22±15.82	110.50±20.93	87.88±29.61	87.48±20.93	112.72±8.70	
L2 D1	187.90±12.11	172.86±14.33	202.42±13.08	211.14±11.33	235.86±14.33	202.04±7.21	
L2 D2	154.46± 7.71	122.22± 8.68	118.82± 8.99	113.28± 8.81	118.62±11.99	125.48±4.89	
L1	185.56± 9.22	160.85± 8.75	165.60±11.47	150.10±16.48	159.40±12.20	164.30±5.49	
L2	171.19± 8.53	147.55± 9.81	160.62± 9.29	162.21± 8.60	177.24±11.18	163.76±4.37	
D1	201.75± 8.85	186.17± 9.55	211.56±10.36	211.74±11.89	233.59±11.53	208.96±4.71	
D2	155.00± 8.89	122.22± 9.00	114.66±10.32	100.58±12.40	103.05±11.83	119.10±5.00	
All Groups	178.38± 6.06	154.20± 6.32	163.11± 7.12	156.16± 9.15	168.32± 8.16	164.03±3.51	

Selection for 42-day weight in L1/D1 resulted also in an increase in total litter weight in diet 1. The correlated response in diet 2, however, was negative and large. The responses were linear in both cases with a gain of 15.74 grams in diet 1 and a loss of 68.06 grams in diet 2.

As line 1 mice became heavier, litter size increased in both diets. Survival of the pups, however, decreased (Table 14). The resulting decreased litter size at weaning explains why at generation 8, line 1 was below line 2 in total litter weight in both diets. This occurred even though individual 42-day weights were heavier in line 1 than in line 2.

L2/D2 mice maintained a near constant level of performance during the five generations. The lack of direct response in this line apparently resulted from the nutritional level being below the threshold required for phenotypic expression of genotype. The effectiveness of selection in line 2 in changing genotype, however, was evident from the correlated response in L2/D1. The superior survival to weaning for L2/D1 over L1/D1 and their similarity in average 42-day weights enabled L2/D1 to surpass the performance of L1/D1 in generation 8.

Superior mothering ability of low plane females was encountered by Falconer and Latyszewski (1952) who described them as heavier with less fat and more protein when reared on the high plane.

Productivity as measured by total litter weight at 42 days of age responded well to selection for 42-day weight in the optimum environment, diet 1. There was a negative correlated response in productivity when the line selected under optimum environment was reared under the unfavorable environment of diet 2.

In the unfavorable environment, productivity was not measurably responsive to selection for increased 42-day weight on diet 2. There was a highly positive correlated response in productivity when the line selected for increased 42-day weight on diet 2 was reared in diet 1, the optimum environment. The correlated response in diet 1 to selection for increased 42-day weight in diet 2 was as effective as the response obtained from selection for increased 42-day weight in diet 1.

Among the most interesting results from this trial was that selection for increased body weight under an unfavorable nutritional regime resulted in better total productivity in a favorable regime than selection for the same trait under an optimal nutritional plane.

#### Weaning Weight (21-Day Weight)

Individual weaning weights were analyzed using model 3, Table 17. No significant differences were found for lines, generations or their interaction (L x G). Sire effects within line and generation approached significance ( $P < .10$ ).

Table 18 contains least squares subclass means and

TABLE 17. LEAST SQUARES ANALYSIS OF VARIANCE FOR WEANING WEIGHT, MODEL 3

SOURCE	df	SS	MS	F
Generations (G)	4	250.60	62.65	2.19
Lines (L)	1	15.91	15.91	.55
G x L	4	58.03	14.51	.51
Sires/GL (S)	41	1174.52	28.65	1.52***
Diet (D)	1	5703.98	5703.98	302.40**
D x G	4	309.38	77.34	4.10**
D x L	1	22.88	22.88	1.21
D x G x L	4	38.33	9.58	.60
D x S	41	773.30	18.86	1.18
Dams/SDGL (I)	58	927.16	15.98	24.97**
No. Weaned (Linear)	1	149.62	149.62	233.80**
No. Weaned (Quadratic)	1	51.07	51.07	79.80**
Sex (Z)	1	9.07	9.07	14.20**
Z x G	4	2.76	.69	1.07
Z x L	1	.49	.49	.76
Z x D	1	12.17	12.17	19.01**
Within	1141	734.48	.64	

\* P &lt; .05

\*\* P &lt; .01

\*\*\*P &lt; .10

TABLE 18. LEAST SQUARES MEANS AND STANDARD ERRORS IN GRAMS FOR WEANING WEIGHT BY LINE, DIET AND GENERATIONS, MODEL 3

Line & Diet	Generations						Means
	4	5	6	7	8		
L1 D1	11.81±.12	11.00±.12	12.23±.12	12.52±.18	13.28±.13	12.17±.09	
L1 D2	7.83±.75	6.38±.26	6.97±.38	5.82±.34	6.54±.51	6.71±.16	
L2 D1	11.26±.28	10.79±.35	11.70±.27	13.47±.25	13.38±.32	12.13±.11	
L2 D2	7.92±.11	6.81±.13	7.08±.14	7.41±.17	7.28±.13	7.29±.08	
L1	9.82±.13	8.69±.14	9.60±.20	9.17±.27	9.91±.22	9.44±.10	
L2	9.59±.13	8.80±.17	9.39±.15	10.44±.14	10.33±.16	9.71±.07	
D1	11.54±.13	10.90±.15	11.96±.16	13.00±.19	13.34±.17	12.15±.07	
D2	7.87±.13	6.59±.16	7.02±.19	6.61±.22	6.61±.22	7.00±.09	
All Groups	9.71±.09	8.75±.11	9.49±.12	9.80±.15	10.12±.13	9.58±.06	

standard errors for weaning weights by line, diet and generation. Diet effects were highly significant ( $P < .01$ ) as would be expected because of the superior nutritional plane provided by diet 1.

A significant ( $P < .01$ ) D x G interaction resulted from weaning weights in diet 1 increasing from generation 4 through generation 8, while in diet 2 weights were decreasing. The increase in weaning weights in diet 1 was larger than the one obtained by Falconer (1955), where in 12 generations of selection for increased 42-day weight the total increase in weaning weight was .75 grams. L1/D1 increased 2.83 grams from generation 1 to generation 8. The correlated response in L2/D1 was positive also and slightly larger for generations 5 to 8 than in L1/D1. Falconer (1960a) obtained similar results when he reared a low-plane selection group in a good environment. Weaning weight in L1/D2 showed a negative response to selection for 42-day weight in diet 1. These results are in agreement with those reported by Sutherland et al. (1970) in rats, Falconer (1955) in mice and by Park et al. (1966) in rats. The only negative correlated response in this study occurred for weaning weight in L1/D2. The L2/D2 mice exhibited no apparent response in weaning weight to selection for increased 42-day weight.

Superior weaning weights for line 2 in both diets at generation 8 most likely are explained in part by a progressive loss of milking ability in line 1. This loss probably

was the result of increased fatness in line 1. M.G. Godwin (unpublished data) compared milk yield of females from generation 9 of this project with that of females from the random-bred base population. She found that L1/D1 females produced 25% less milk per day than base population females. L2/D2 females produced more gross milk than L1/D1 even though they were on a lower plane of nutrition. This loss in milk yield in line 1 apparently was more pronounced in diet 2 where both survival and the weaning weight of the surviving pups were reduced drastically during the latter generations. Brumby (1960) reported a loss of lactational performance in lines of mice selected for increased or decreased 42-day weights. Cox et al. (1959) reported that postnatal environment accounted for 60% of the variance of 21-day weights, even when litters were standardized to six young at birth.

Regression of weaning weight on number weaned, both linear and quadratic, was highly significant ( $P < .01$ ). These significant regressions ( $-1.93 \pm .27$  and  $.07 \pm .02$ ) indicate a dependency of weaning weight on the amount of milk available to the pup. Significant dam effects which remained with number weaned in the model suggest significant individual differences between dams for milk production.

Effects for sex and sex x diet interaction were significant ( $P < .01$ ). Male pups were heavier than female pups across diets; but within diets, male pups were heavier in diet 1 while females were slightly heavier in diet 2,

resulting in the significant interaction, Table 19. This interaction apparently was due to the inability of the sexes to express their differences in growth potential on the low plane of nutrition provided by diet 2. In diet 1, energy intake was higher and differences in growth potential were expressed. This diet induces sexual dimorphism is common (Korkman, 1957; Butler and Metrakos, 1950) in mice selection experiments under two planes of nutrition.

These results disagree with Cox et al. (1959) who reported no sex effects on 21-day weight of mice on a regular diet.

#### Individual 42-Day Weight

The trait under direct selection in this project was 42-day weight, equivalent approximately to that of puberty in farm animal species. This trait is a composite of preweaning and postweaning growth, being influenced by both the maternal performance of the dam and the genetic growth potential of the individual. It corresponds roughly to yearling weight in cattle. This trait was analyzed by fitting model 3. Results are presented in Table 20. Significant ( $P < .05$ ) effects were found for line, generation and the linear regression on number weaned. Significant ( $P < .01$ ) effects included diet, diet x generation, dams, sex and sex x diet.

Least squares means for 42-day weight are presented in Table 21. Line 1 mice were heavier than line 2 mice in both diets by an average of .75 grams. Generation means

TABLE 19. LEAST SQUARES MEANS AND STANDARD ERRORS IN GRAMS FOR INDIVIDUAL WEIGHT PARAMETERS BY SEX, LINE AND DIET, MODEL 3

	Weaning Weight		42-Day Weight		60-Day Weight	
	Male	Female	Male	Female	Male	Female
L1	9.55±.13	9.33±.12	23.60±.17	19.90±.17	30.33±.19	24.48±.19
L2	9.78±.09	9.64±.10	22.64±.13	19.37±.13	28.74±.14	23.74±.15
D1	12.34±.10	11.95±.10	27.49±.13	22.98±.14	33.95±.15	27.31±.15
D2	6.98±.12	7.02±.12	18.74±.17	16.29±.16	25.24±.18	20.90±.18
Mean	9.66±.08	9.48±.08	23.12±.11	19.64±.11	29.59±.12	24.11±.12

TABLE 20. LEAST SQUARES ANALYSIS OF VARIANCE FOR INDIVIDUAL 42-DAY WEIGHT, MODEL 3

SOURCE	df	SS	MS	F
Generations (G)	4	402.57	100.64	3.42*
Lines (L)	1	117.77	117.77	4.01*
G x L	4	18.00	4.50	.15
Sires/GL (S)	41	1204.39	29.38	1.22
Diet (D)	1	12818.19	12818.19	533.65**
D x G	4	1104.61	276.15	15.81**
D x L	1	42.99	42.99	2.46
D x G x L	4	108.45	27.11	1.55
D x S	41	716.22	17.47	.73
Dams/SDGL (I)	58	1393.10	24.02	7.90**
No. Weaned (Linear)	1	16.75	16.75	5.41**
No. Weaned (Quadratic)	1	.31	.31	.10
Sex (Z)	1	3497.79	3497.79	1150.60**
Z x G	4	21.59	5.40	1.78
Z x L	1	11.13	11.13	3.66
Z x D	1	283.07	283.07	93.12**
Within	1141	3466.17	3.04	

\* P &lt; .05

\*\*P &lt; .01

TABLE 21. LEAST SQUARES MEANS AND STANDARD ERRORS IN GRAMS FOR INDIVIDUAL 42-DAY WEIGHT BY LINE, DIET AND GENERATIONS, MODEL 3

Line & Diet	Generations						Means
	4	5	6	7	8	8	
L1 D1	23.52±.18	24.66±.19	26.02±.18	26.93±.27	28.01±.19	25.82±.13	
L1 D2	18.53±.39	17.87±.42	17.40±.61	17.14±.54	17.41±.81	17.67±.22	
L2 D1	22.56±.31	23.32±.38	24.39±.30	26.13±.28	26.82±.35	24.65±.15	
L2 D2	18.43±.18	17.40±.20	16.66±.22	17.23±.26	17.10±.21	17.36±.11	
L1	21.03±.19	21.26±.20	21.71±.30	22.04±.37	22.71±.30	21.75±.13	
L2	20.50±.18	20.36±.24	20.53±.20	21.68±.20	21.96±.21	21.00±.09	
D1	23.05±.18	23.99±.21	25.21±.22	26.52±.26	27.41±.23	25.24±.10	
D2	18.48±.18	17.63±.22	17.03±.26	17.19±.30	17.25±.28	17.52±.12	
All Groups	20.77±.12	20.81±.15	21.12±.16	21.86±.21	22.34±.18	21.38±.08	

increased steadily from generation 4 to generation 8. Diet 1 mice averaged 7.72 grams heavier than diet 2 mice.

A significant diet by generation interaction ( $P < .01$ ) was caused by a linear increase for generation means in diet 1 while a slight decrease occurred in diet 2.

Dams had a persistent significant ( $P < .01$ ) effect on 42-day weight of their progeny. Since regressions for number weaned (linear and quadratic) were in the model, this effect for dams was independent of litter size. Rutledge et al. (1972) concluded that growth in mice until about 7 weeks of age is influenced more by postnatal maternal differences than by direct genetic differences. Jinks and Broadhurst (1963) stated that maternal effects in rats are more important at 50 days of age than at weaning (21 days).

The significant ( $P < .01$ ) linear regression of 42-day weight on number weaned was  $-.65 \pm .37$  grams for each mouse weaned in the presence of a nonsignificant quadratic of  $-.005 \pm .03$ . This agrees with Roberts (1966) and Falconer (1960b) who reported regressions of  $-.6$  and  $.34$  grams per mouse born. Roberts (1966), however, reported that corrections for this regression were so small that no conclusions were affected. At 42 days of age, males were 3.48 grams heavier than females ( $P < .01$ ).

Significant ( $P < .01$ ) sex x diet interaction was the result of sex difference being larger in diet 1 than in diet 2. In diet 1, males and females weighted an average

of 27.49 and 22.98 grams, respectively, for a difference of 4.51 grams. In diet 2, the respective means for the two sexes were 18.74 and 16.29 for a difference of only 2.45 grams.

Direct response to selection for 42-day weight in line 1 was positive. Correlated response in L1/D2, however, was slightly negative. In L2/D2, the direct phenotypic response to selection was slightly negative. Correlated response in L2/D1, however, was positive and almost as effective as direct selection in diet 1. L1/D1 had a direct response of 4.48 grams while L2/D1 had a correlated response of 4.26 grams. As was the case for 21-day weights the nutritional regime in line 2 apparently prevented the expression of any increase in genotype for growth rate. The positive correlated response in L2/D1, however, indicates that animals with superior growth rates were selected as breeders.

Diet 2 apparently provided a more severe nutritional stress than Falconer and Latyszewski (1952) provided in their poor environment. They were able to obtain a response in the poor environment; however, the mice were on the poor environment for only 3 weeks (3 to 6 weeks of age). Failure to show response to selection under a low plane has been demonstrated in mice by Korkman (1961), Bateman (1971) and Dalton (1967), and in rats by Park et al. (1966). The high correlated response in L2/D1 to selection for increased 42-day weight in diet 2 was very similar to the one reported in mice by Falconer (1960a).

The lack of significant line x diet and sire x diet interaction effects together with heavier weights for line 1 in both diets indicates an absence of genotype x environment interaction for this trait.

#### 60-Day Weight

This is the weight at which the mice in this project were bred. It was assumed to be sufficiently removed from maternal environmental effects to yield a good estimate of additive nonmaternal effects for weight.

Table 22 shows the least squares analysis for this trait. Line, generation, diet, diet x generation, dam, sex, sex x line and sex x diet all had highly significant ( $P < .01$ ) effects. Sire effects were significant ( $P < .05$ ).

Generation means increased steadily for the duration of the project. Line 1 mice were significantly heavier than line 2 mice in both diets. Diet 1 mice were 7.56 grams (Table 23) heavier than diet 2 mice. The large increase in generation means in diet 1, while generation means in diet 2 exhibited a small increment, resulted in a highly significant diet x generation interaction.

The effect of dams persisted at 60 days of age, even though the effects due to regressions of 60-day weight on number weaned (linear and quadratic) were small.

Sex effects were highly significant ( $P < .01$ ) with males being heavier than females. Sex effect differed with line resulting in a sex x line interaction (Tables 19 and

TABLE 22. LEAST SQUARES ANALYSIS OF VARIANCE FOR 60-DAY  
WEIGHT, MODEL 3

SOURCE	df	SS	MS	F
Generations (G)	4	1384.60	346.15	10.41**
Lines (L)	1	261.93	261.93	7.88**
G x L	4	9.94	2.48	.07
Sires/GL (S)	41	1363.18	33.25	1.63*
Diet (D)	1	12308.52	12308.52	604.20**
D x G	4	1113.25	278.31	13.66**
D x L	1	30.57	30.57	1.50
D x G x L	4	55.41	13.85	.50
D x S	41	835.33	20.37	.73
Dams/SDGL (I)	58	1608.58	27.73	6.86**
No. Weaned (Linear)	1	6.56	6.56	1.62
No. Weaned (Quadratic)	1	1.02	1.02	.25
Sex (Z)	1	8691.02	8691.02	2151.20**
Z x G	4	17.72	4.43	1.10
Z x L	1	32.83	32.83	8.13**
Z x D	1	352.46	352.46	87.20**
Within	1141	4605.77	4.04	

\* P < .05

\*\*P < .01

TABLE 23. LEAST SQUARES MEANS AND STANDARD ERRORS IN GRAMS FOR 60-DAY WEIGHTS BY LINE, DIET AND GENERATION, MODEL 3

Line & Diet	Generations						Means
	4	5	6	7	8		
L1 D1	28.61±.20	29.69±.20	30.65±.20	34.10±.30	33.76±.21	31.37±.14	
L1 D2	23.71±.19	23.33±.46	22.49±.67	23.64±.60	24.06±.89	23.37±.24	
L2 D1	27.25±.38	28.04±.46	29.50±.36	32.33±.33	32.35±.42	29.90±.17	
L2 D2	23.07±.19	22.40±.21	22.06±.24	22.59±.28	23.37±.23	22.70±.12	
L1	26.16±.20	26.51±.22	26.57±.31	28.89±.41	28.91±.33	27.40±.14	
L2	25.16±.19	25.22±.26	25.78±.22	27.46±.22	27.86±.24	26.30±.10	
D1	27.94±.20	28.87±.23	30.08±.24	33.21±.29	33.06±.26	30.63±.11	
D2	23.39±.20	22.86±.25	22.27±.29	23.11±.33	23.71±.31	23.07±.14	
All Groups	25.66±.14	25.86±.16	26.18±.18	28.16±.23	28.39±.19	26.85±.09	

22). The difference between male and female weights in line 1 was larger than in line 2. Moore, Eisen and Ulberg (1970) encountered a similar sex x line interaction involving lines of large mice. The response may be the result of scale effects increasing the magnitude of the differences between the sexes in the larger lines. A significant ( $P < .01$ ) sex x diet interaction likewise resulted from a larger sex difference in diet 1 than in diet 2.

Sire effects for 60-day weight were significant ( $P < .05$ ). Absence of sire effects on growth traits taken at younger ages (weaning and 42-day weight) points to the higher maternal components present in those traits. Variance due to dams is the within variance of sire groups. The magnitude of this variance in the younger weights in combination with small number of dams per sire was responsible for nonsignificant sire effects. The presence of significant sire effect on 60-day weights is the result of a reduction of within sire variance due to a smaller dam effect at this age. This point will be discussed further in the section on genetic parameters.

As was the case for 42-day weight, there was no indication of diet x genotype interaction present for this trait.

#### Genetic Parameters

Response to selection and genetic parameters can be ascertained by various techniques. The three approaches used in this study were, (1) to compute selection differ-

entials, selection intensities and realized heritabilities for the traits under selection, (2) to obtain estimates of observational and causal components of random variances and (3) to obtain estimates for heritabilities and realized genetic correlations for individual weights at weaning, 42 days and 60 days of age.

Since sires and dams were completely confounded in L1/D2 and L2/D1, the estimates for random variances were obtained only from the eight generations of L1/D1 and L2/D2. Data from each line was analyzed by fitting model 4.

#### Realized Heritabilities for 42-Day Weight

This parameter is the ratio of the response to selection divided by the cumulative selection differential. Regression of least squares generation means on generation number (Table 24) was considered the response for each trait. Regression of generation means of cumulative selection differential on generation number was the measure of selection differential. The responses per generation for the two lines were .87 and .19 grams, respectively. The corresponding selection differentials per generation (Table 25) were 2.61 and 2.39 grams. Realized heritabilities were .33 and .08, respectively for the two lines. These estimates are similar to those found in the literature. Korkman (1961) obtained estimates of .22 and .06 on optimum and restricted regime, respectively. Park et al. (1966) in rats obtained a  $h^2$  estimate of .105 and .058 on a full fed and

TABLE 24. LEAST SQUARES MEANS IN GRAMS OF INDIVIDUAL WEIGHT PARAMETERS BY LINE AND GENERATION, MODEL 4

Trait	1	2	3	Generation					8	Means
				4	5	6	7	8		
Weaning Weight										
Line 1	10.84	11.99	10.93	11.36	10.50	11.26	12.21	14.30	11.68	
Line 2	8.71	7.27	7.03	8.43	7.12	7.07	7.64	7.55	7.60	
42-Day Weight										
Line 1	21.40	23.45	23.88	23.24	24.37	24.36	26.64	29.23	24.45	
Line 2	15.51	16.53	17.78	19.04	18.09	16.85	17.23	17.80	17.35	
60-Day Weight										
Line 1	25.80	26.96	28.83	28.30	29.57	29.24	34.05	35.13	29.74	
Line 2	19.24	21.49	22.78	23.51	23.26	22.26	22.56	24.02	22.40	

restricted diets. Kownacki (1971) obtained estimates of .251 and .135, respectively, for high and low protein diets. A limited response to selection under poor nutritional regimes appears to be a general response.

#### Selection Intensities

Intensity of selection depends only on the proportion of the population included in the selected group, provided the distribution of phenotypic values is normal. Intensities for this project appear in Table 25, and were obtained by calculating the proportion of males and females selected. These proportions yielded the values of  $i$  from the tables of Fisher and Yates (1943). Sufficient offspring were produced in each generation by both lines to insure similar selection intensities.

#### Relation to Natural Selection

Relation of natural selection to the trait under selection is an important factor influencing response. Ratio of effective over expected selection differentials, if different than 1, indicates a conflict between the direction of natural and artificial selection (Falconer, 1964). The effective selection differential was calculated by weighting the selected parents by the number of offspring produced. If the more extreme selected individuals have a tendency to be less viable or fertile, they will produce fewer offspring than the remainder of the selected breeders. This may result in a difference between expected and effective selection differentials.

TABLE 25. SELECTION DIFFERENTIALS AND INTENSITIES FOR LINE 1 AND 2 BY SEX

Gener- ation	Intensities				Selection Differentials (g)			
	L 1		L 2		L 3		L 4	
	Males	Females	Males	Females	Males	Females	Males	Females
1	1.450	.903	.963	0	3.2	1.6	3.3	0
2	1.884	1.231	1.569	.970	4.5	1.7	2.3	1.3
3	1.823	.979	1.867	1.116	3.9	1.3	3.6	1.2
4	1.767	1.138	1.848	1.174	3.3	1.3	3.6	1.8
5	1.752	1.092	1.707	.929	3.5	2.2	3.6	1.5
6	1.867	1.081	1.679	.876	3.6	2.6	4.8	1.8
7	1.368	.573	1.501	.687	3.3	.5	3.2	1.5
Ave. Sex	1.702	1.000	1.591	.882	3.6	1.6	3.5	1.3
Ave. Line	1.351		1.202		2.61		2.39	
Cumulative	9.45		8.44		18.25		16.75	

The ratios for this project were, 1.0266 and .9962 for lines 1 and 2, respectively, suggesting no conflict between natural and artificial selection in this trial.

#### Observational and Causal Components of Random Variances

Analyses of variance for individual weights appear on Tables 31 to 36. In line 1, sire effects were positive for all ages and significant for 42- and 60-day weights, whereas in line 2 sire effects were not significant for any weight with a negative sire component for 42-day weight. Dam effects were significant ( $P < .01$ ) for all weights in both lines.

Nonsignificant and negative sire variances in line 2 indicated that sire components were not significantly different from zero. Observational components are listed in Table 26.

Partitioned dam components were larger for line 2 for all traits, indicating a large common maternal effect in line 2. Dam variance accounted for most of total random variance in line 2.

Moore et al. (1970) indicated that maternal effects in mice were significant at all ages reaching a maximum at 21 days and decreasing as the mice became older. Monteiro and Falconer (1965) believed maternal effects in mice to be the most important source of variance up to 4 weeks of age. Jinks and Broadhurst (1963) reported that maternal effects in that data were higher for 50-day weight than for

TABLE 26. ESTIMATES OF OBSERVATIONAL COMPONENTS OF VARIANCE  
FOR WEANING WEIGHT, 42-DAY WEIGHT AND 60-DAY  
WEIGHT, MODEL 4

Source	Weaning Weight		42-Day Weight		60-Day Weight	
	Line 1	Line 2	Line 1	Line 2	Line 1	Line 2
<u>Components</u>						
Sires	.15	.07	.40*	-.20	.73**	.06
Dams/Sire	1.90*** <sup>a</sup>	1.47**	1.56**	2.61**	1.71**	2.66**
Within	.62	.50	2.70	2.38	3.67	3.06
Total	2.66	2.04	4.65	4.99	6.11	5.77

<u>As % of Total</u>						
Sires	5	3	8	0	12	1
Dams/Sire	71	72	34	52	28	46
Within	23	24	58	48	60	53
Total	100	100	100	100	100	100

<sup>a</sup>Significance of tests of ratios of mean squares

\*P < .05

\*\*P < .01

TABLE 27. ESTIMATES OF CAUSAL COMPONENTS OF VARIANCE FOR WEANING WEIGHT, 42-DAY WEIGHT AND 60-DAY WEIGHT

	<u>Weaning Weight</u>		<u>42-Day Weight</u>		<u>60-Day Weight</u>	
	Line 1	Line 2	Line 1	Line 2	Line 1	Line 2
	<u>Components</u>					
Phenotypic ( $V_p$ )	2.66	2.04	4.65	4.99	6.11	5.77
Additive ( $V_{A_0}$ )	.58	.27	1.59	0	2.93	.24
Maternal Effect ( $V_{ME}$ )	1.75	1.40	1.16	2.61	.97	2.60
Within-Litter ( $V_{WL}$ )	.33	.37	1.90	2.38	2.20	2.94
	<u>As % of <math>V_p</math></u>					
$V_p$	100	100	100	100	100	100
$V_{A_0}$	22	13	34	0	48	4
$V_{ME}$	66	69	25	52	16	45
$V_{WL}$	12	18	41	48	36	51

21-day weight. This study agrees with these authors in regard to line 1; however, line 2 presents a case not covered in the literature. Maternal effects persisted up to 60-day weight as 45% of the total phenotypic variance. Line 1 behaved similarly to the mice of Rutledge et al. (1972), who concluded that up to 7 weeks of age growth was influenced more by postnatal maternal differences than by genetic differences.  $V_{AO}$  for line 1 was 34% and  $V_{ME}$  25% at 42 days of age or of about equal magnitude.

Within-litter variances were smaller in line 2 as a result of scale effects since all traits in line 2 were smaller in magnitude. Within-litter variance as a percent of total random variance increased as mice became older.

Causal components were estimated from observational components, Table 27, using the method of Falconer (1963).

Additive variance ( $V_{AO}$ ) components in line 2 were small. In line 1,  $V_{AO}$  components were larger and accounted for a greater percentage of total phenotypic variance ( $V_p$ ) as mice became older. Schmitz (1970) working with the Goodale large strain of mice estimated values of  $V_{AO}/V_p$  at 28, 42 and 60 days of age to be 17.6%, 21.6%, and 33.9%, respectively. Line 1 in this project had values of 22%, 34% and 48%, respectively.

Maternal effect ( $V_{ME}$ ) accounted for most of the total phenotypic variance in line 2. Maternal effects were large in line 1 but decreased markedly with age. Within-litter environmental variance ( $V_{WL}$ ) increased with age in both lines.

Total phenotypic variance was smaller for line 2 than for line 1 in all traits with the exception of 42-day weight. This is in disagreement with results from other selection experiments on different nutritional regimes. McLaren and Michie (1956) in mice, Becker and Berg (1959) in poultry, and Bateman (1971) in mice all observed higher phenotypic variances on the low plane of nutrition.

#### Heritability Estimates

When sire variances are not significant, heritability estimates are not reliable. This is evident from the standard errors shown in Table 28. Only two estimates were significant, those for 42- and 60-day weights in line 1.

Lack of significant sire mean squares in most traits made it difficult to estimate additive genetic variances and heritabilities. Large maternal effects between litters accounted for most of total phenotypic variance in all traits measured. Line 2 mice were particularly affected by maternal environment.

Under a poor environment  $V_{ME}$  accounts for most of the  $V_p$ . This indicates a major role played by maternal effects in selection under a poor environment. The high correlated response in diet 1 for selection in diet 2 demonstrates an additive maternal component. The correlated response was cumulative and nearly as effective as direct response in diet 1. This mechanism is in general agreement with the views of M. Koger (personal communication) who proposed

TABLE 28. WITHIN-LINE HERITABILITY ESTIMATES FOR WEANING WEIGHT, 42-DAY WEIGHT, AND 60-DAY WEIGHT, MODEL 4

	Line 1		Line 2	
	$h^2$	s.e.	$h^2$	s.e.
Weaning Weight				
21-Day Weight	.2145	.3378	.1309	.3449
42-Day Weight	.3422*	.2210	-.1692	.2351
60-Day Weight	.4798**	.2240	.0407	.2334
K 3	8.8500		7.5382	
K 4	8.9880		7.7749	
K 5	22.2225		19.0556	

\*  $P < .05$

\*\* $P < .01$

that adaptability to unfavorable environments generally behaves essentially as a maternal trait.

It has been postulated (Eisen, 1973) that rapid growth enhanced by the mother's high lactational output is one way in which the dam could increase the offspring's fitness. Natural selection among dams for the ability to provide a superior maternal environment (Naylor, 1964) may have resulted in a reduction of additive nonmaternal genetic variance. Other works with diallel crosses designed to partition maternal effects into its components and their interactions have been published. Cock and Morton (1963) demonstrated line maternal effects in poultry up to 20 weeks posthatching. Morton (1970) in mice postulated an interaction between genotype of a sire strain and cytoplasm of the female strain. This has been demonstrated with ova transplants (Brumby, 1960) in mice where cytoplasmic factors were apparent. Non-Mendelian transmitted maternal effects were found in the Falconer and Goodale mice lines (Reutzel, 1970). Incorporation of genetic material from the cytoplasm into the genome with a resulting additive genetic action can not be discarded as a possibility for acquired fitness.

#### Realized Genetic Correlations

Estimates of realized genetic correlations ( $r_A$ ) from the data are presented in Table 29. Only in line 1 could the estimates be computed. The trait under selection, 42-day weight, in line 2 had an estimated additive genetic variance of zero.

The  $r_A$  between 42-day weight and 60-day weight was  $1.04 \pm .03$ , indicating that genes influencing 42-day weight were also influencing 60-day weight. This was to be expected since a part-whole relationship existed.

Genetic correlation between 42-day weight and weaning weight was  $.57 \pm .48$ . Larger standard error and smaller magnitude of the estimate as compared with that of 60-day weight was the result of environmental variations in weaning weight.

Phenotypic (.73 and .50) and genetic (1.04 and .57) correlation coefficients were similar in magnitude when 42-day weight was correlated with 60-day weight and weaning weight in line 1. Phenotypic correlations appear in Table 30.

Positive phenotypic and genetic correlations in mice between early postweaning growth (21 - 42 days of age) and late post-weaning growth (42- 60 days of age) were reported by Wilson (1973). He found a genetic correlation of .9 between early and late growth in mice selected for early growth.

Data from GEI were not suited for genetic correlation estimates. Additive variance was 0 for 42-day weight in line 2, and sires and dams were completely confounded in L1/D2 and L2/D1.

TABLE 29. REALIZED GENETIC CORRELATIONS ( $r_A$ ) BETWEEN WEIGHT PARAMETERS, STANDARD ERRORS AND THE GENETIC ESTIMATES NEEDED FOR THEIR COMPUTATION

Trait	Response/ generation		$h^2$		$V_A$		$\sigma(h^2)$		$r_A$ with Line 1 42-Day Weight <sup>a</sup>
	L1	L2	L1	L2	L1	L2	L1	L2	
	g								
Weaning Weight	.303	-.089	.215	.131	.58	.27	.338	.345	.57±.48
42-Day Weight	.873	.188	.342	-.169	1.59	0	.221	.235	-
60-Day Weight	1.229	.440	.480	.041	2.93	.24	.224	.233	1.04±.03

a.  $r_A$  in line 2 could not be estimated because of negative half-sib heritability estimates.

TABLE 30. WITHIN LINE CORRELATIONS BETWEEN WEIGHTS AT DIFFERENT AGES<sup>a</sup>

	Weaning Weight	42-Day Weight	60-Day Weight
Weaning Weight	--	.64	.54
42-Day Weight	.50	--	.82
60-Day Weight	.38	.73	--

<sup>a</sup>Correlations within line 1 are to the left of the diagonal, those for line 2 to the right.

TABLE 31. LEAST SQUARES ANALYSIS OF VARIANCE FOR WEANING  
WEIGHT IN LINE 1, MODEL 4

SOURCE	df	SS	MS	F
Generations (G)	7	1376.53	196.65	9.40**
Sires/G (S)	42	878.23	20.91	1.20
Dams/S (I)	73	1270.58	17.40	28.06**
No.Weaned (Linear)	1	3.07	3.07	4.95*
No.Weaned (Quadratic)	1	1.10	1.10	1.77
Sex (Z)	1	34.36	34.36	55.42**
Z x G	7	4.93	.70	1.13
Within	980	610.96	.62	

\* P < .05

\*\*P < .01

TABLE 32. LEAST SQUARES ANALYSIS OF VARIANCE FOR 42-DAY  
WEIGHT IN LINE 1, MODEL 4

SOURCE	df	SS	MS	F
Generations (G)	7	5342.99	763.28	29.88**
Sires/G (S)	42	1072.55	25.54	1.55*
Dams/S (I)	73	1202.95	16.48	6.10**
No. Weaned (Linear)	1	12.20	12.20	4.52*
No. Weaned (Quadratic)	1	.38	.38	.14
Sex (Z)	1	4687.10	4687.10	1735.96**
Z x G	7	140.48	20.07	7.43**
Within	980	2643.44	2.70	

\* P < .05

\*\*P < .01

TABLE 33. LEAST SQUARES ANALYSIS OF VARIANCE FOR 60-DAY  
WEIGHT IN LINE 1, MODEL 4

SOURCE	df	SS	MS	F
Generations (G)	7	8468.80	1209.83	34.27**
Sires/G (S)	42	1482.67	35.30	1.88**
Dams/S (I)	73	1370.98	18.78	5.12**
No. Weaned (Linear)	1	16.39	16.39	4.46*
No. Weaned (Quadratic)	1	5.00	5.00	1.36
Sex (Z)	1	10189.80	10189.80	2776.50**
Z x G	7	208.2	29.73	8.10**
Within	980	3598.76	3.67	

\* P < .05

\*\*P < .01

TABLE 34. LEAST SQUARES ANALYSIS OF VARIANCE FOR WEANING  
WEIGHT IN LINE 2, MODEL 4

SOURCE	df	SS	MS	F
Generations (G)	7	257.86	36.84	2.79*
Sires/G (S)	38	501.88	13.21	1.14
Dams/S (I)	67	776.74	11.59	23.18**
No. Weaned (Linear)	1	64.48	64.48	128.96**
No. Weaned (Quadratic)	1	25.85	25.85	51.70**
Sex (Z)	1	10.12	10.12	20.24**
Z x G	7	6.62	.94	1.88
Within	755	377.52	.50	

\* P < .05

\*\*P < .01

TABLE 35. LEAST SQUARES ANALYSIS OF VARIANCE FOR 42-DAY  
WEIGHT IN LINE 2, MODEL 4

SOURCE	df	SS	MS	F
Generations (G)	7	649.20	92.74	4.93**
Sires/G (S)	38	714.53	18.80	.86
Dams/S (I)	67	1476.37	22.04	9.26**
No. Weaned (Linear)	1	31.64	31.64	13.29**
No. Weaned (Quadratic)	1	5.25	5.25	2.20
Sex (Z)	1	914.13	914.13	384.09**
Z x G	7	32.84	4.69	1.97
Within	755	1798.45	2.38	

\* P < .05

\*\*P < .01

TABLE 36. LEAST SQUARES ANALYSIS OF VARIANCE FOR 60-DAY  
WEIGHT IN LINE 2, MODEL 4

SOURCE	df	SS	MS	F
Generations (G)	7	867.85	123.98	4.99**
Sires/G (S)	38	943.42	24.83	1.08
Dams/S (I)	67	1546.12	23.08	7.54**
No. Weaned (Linear)	1	66.36	66.36	21.69**
No. Weaned (Quadratic)	1	28.33	28.33	9.26**
Sex (Z)	1	2618.73	2618.73	855.79**
Z x G	7	54.77	7.82	2.56*
Within	755	2314.55	3.06	

\* P < .05

\*\*P < .01

## SUMMARY AND CONCLUSIONS

An investigation was performed to evaluate response to mass selection in two lines of mice (L1, L2) for increased 42-day weight on two diets (D1, D2). Diet 1 was Purina Lab Chow and D2 consisted of 30% nonnutritive bulk and 70% Purina Lab Chow. After 3 generations of selection, mice from the original two lines were transferred to the opposite diet forming L1/D1, L1/D2, L2/D1 and L2/D2. Line 1 was originally selected in D1 and line 2 in D2.

### Analyses of Data From Four Subgroups, Generations 4 to 8

#### Pregnancy Rate

The overall least squares mean for pregnancy rate in 240 females mated to 80 males was 84.58%. The only variables having significant effects ( $P < .05$ ) were generation and sires. Sire effects appeared to be due to random sterility while generation means were affected both by this factor and by a nonspecific pathogen encountered in generation 7.

#### Litter Size at Birth

There were 175 litters by 54 sires involved in the analyses of the three litter traits. The overall least squares mean was 9.62. Significant effects ( $P < .05$ ) were

found for line (10.18 vs. 9.06), diet (10.12 vs. 9.12) and D x G. Line differences probably were attributable to larger weights in line 1 as suggested by a significant positive within-line regression of litter size on weight of dam. Litter size in L1/D1 and L2/D1 increased over time while decreasing slightly in L2/D2 and L1/D2, resulting in a significant D x G interaction.

#### Survival and Litter Size at Weaning

Survival to weaning was higher in line 2 than in line 1 (82.7% vs. 79.6%). Thus, at weaning time the two lines had changed rank in litter size with line 2 having a non-significant advantage over line 1 (7.80 vs. 7.67). As expected, there was a significant difference ( $P < .01$ ) in litter size due to diet (8.42 vs. 7.04). Diet x line interaction was nonsignificant.

#### Total Litter Weight at 42 Days of Age

Lines averaged across diets did not differ significantly for total litter weight (164.30 vs. 163.76 grams). There was an interaction of line with diet ( $P < .075$ ), however, with the lines changing rank on the two diets (L2/D1, L1/D1, L2/D2, L1/D2 = 235.86, 231.32, 118.62, 87.48 grams). During generations 7 and 8 line 2 females produced heavier litters than line 1 in both diets for a complete reversal from generation 4.

### Individual Weaning Weights

Records from 1312 mice, 51 sires and 162 dams were utilized in the analyses of the three individual weights. Sub-line group means varied from a low of 6.71 grams for Ll/D2 to 12.17 grams for Ll/D1, with average values of 9.44 for line 1 and 9.71 for line 2. Diet means were 12.15 and 7.00 grams ( $P < .01$ ), respectively. Sire effects were significant ( $P < .10$ ) as were dam effects ( $P < .01$ ). Sex x diet interaction means were significant ( $P < .01$ ) with males being heavier on diet 1 (12.34 vs. 11.95 grams) and females slightly heavier on diet 2 (7.02 vs. 6.98 grams). Diet x generation was significant with generation means becoming progressively heavier for diet 1 while for diet 2 generation means declined.

### Individual 42-Day Weight

Weight at 42 days showed trends similar to those at weaning except that the effects of superior preweaning maternal performance for line 2 had decreased and evidences of genotype for slightly heavier weights for line 1 had emerged. Line effects were significant ( $P < .05$ ) with line 1 being heavier than line 2 on both diets and for all generations. Diet x generation interaction was significant ( $P < .01$ ) with mice on diet 1 becoming progressively heavier over generations while diet 2 mice declined in weight. There was a significant sex x diet interaction due largely to scale effects in the two diets.

### Individual 60-Day Weight

Weight at 60 days showed the same general response as 42-day weight, the principal difference being that line and diet effects were greater in 60-day weight. The effect of litter size on weight had disappeared. Both sire ( $P < .05$ ) and dam ( $P < .01$ ) effects were significant. Diet x generation interaction was again highly significant with diet 1 mice increasing in weight at a much higher rate than diet 2 mice over generations. Sex x diet interaction was significant with sex differences being larger in D1 than in D2.

### Genetic Parameters

The data for 42-day weight over eight generations along with correlated responses in litter size, survival, weaning weights and 60-day were utilized to obtain genetic parameters.

### Growth and Maternal Components in Weight Data

Since early growth in mice is known to be maternally influenced weight data were partitioned into causal components for growth ( $V_{AO}$ ), total maternal impact ( $V_{ME}$ ) and within-litter environmental effects ( $V_{WL}$ ). For this phase of the study  $V_{EM}$  was not further partitioned into its components. The percentages of total random variance accounted for by  $V_A$ ,  $V_{ME}$  and  $V_{WL}$ , respectively were as follows: weaning weight, 22%, 66% and 12% for line 1; 13%, 69% and 18% for line 2. Weight at 42-days, 34%, 25% and 41% for line 1; 0%, 52% and 48% for line 2. Weight at 62-

days, 48%, 16% and 36% for line 1; 4%, 45% and 51% for line 2. Thus, for line 2 mice  $V_A$  was nil or very low while maternal effects accounted for 45% to 69% of total variance.

Paternal half-sib estimates of heritability for the nonmaternal component of weight at 21, 42 and 60 days, respectively were  $.21 \pm .34$ ,  $.34 \pm .22$  and  $.48 \pm .22$  for line 1 and  $.13 \pm .34$ ,  $-.17 \pm .24$  and  $.04 \pm .23$  for line 2.

#### Realized Heritabilities

In line 1 the average selection differential for 42-day weight was 2.61 grams. The response was .87 grams per generation for a realized heritability of .33. In line 2 selection differential, response and realized heritability were 2.41, .19 and .08, respectively. Intensities of selection ( $i$ ) were: 1.35 for line 1, and 1.20 for line 2. The ratio of effective to expected selection differentials were 1.03 for line 1 and .996 for line 2, indicating that natural selection was not in opposition to selection for 42-day weight.

Selection for increased 42-day weight on diet 1 resulted in positive responses in litter size, 42- and 60-day weight in both diets. In line 1, 42-day weight had a  $r_A$  with weaning weight of  $.57 \pm .48$ ; and with 60-day weight  $1.04 \pm .03$ . An apparent loss of lactational performance in line 1 resulted in smaller weaning weights in both diets and a drastic decrease in survival for L1/D2. This loss of lactational performance may have been related to

increased obesity in L1. Selection in L2 resulted in little response for any trait on D2. Responses were marked in L2/D1, however, and during later generations it surpassed L1/D1 for litter size at weaning, litter weight at 42-days and weaning weight. The superiority of line 2 females for milk yield and survival of young was evident in these traits.

In summary, selection on a favorable nutritional regime yielded larger responses for the trait under selection in both the favorable and unfavorable regimes. Selection in the unfavorable regime produced little direct response but resulted in a correlated response for the selected trait in the favorable regime almost as effective as the direct one. Females from the line selected under the unfavorable regime were superior in total productivity on both regimes. Females selected under the favorable regime experienced a decrease in maternal ability as a result of selection.

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## BIOGRAPHICAL SKETCH

Rafael Efren Rodriguez was born at Ponce, Puerto Rico, February 1, 1939. He attended school in Puerto Rico through the eleventh grade and completed his senior year at Cheshire Academy, Connecticut in 1956. He was then accepted for college work at the University of Florida. He attended the University of Florida from 1956 to 1959 when he began work as a production chemist at Peninsular Chemical Research Company of Gainesville, Florida. He continued work there until October, 1961, when a plant explosion placed him in the hospital for a period of 17 weeks with burns over 71% of his body. Upon release from the hospital, he was employed by the Department of Psychiatry, University of Florida College of Medicine, under the direction of Dr. Aaron H. Anton. During this period he attended the University on a part-time basis. In 1964 he became a full-time student and continued his research for Dr. Anton on a part-time basis. He received his B.S. in Agriculture in December, 1965. He worked with Dr. Anton from January, 1965 to August 1966, when he was awarded an NDEA IV fellowship to study under the direction of Dr. Marvin Koger in the field of Animal Breeding in the Department of Animal Science, College of Agriculture at the University of Florida. He commenced his research project in March, 1967.

In the summer of 1967, he was encouraged to undertake a position as a part-time Ranch Manager for Dorado Ranch. This position he maintained until the ranch was sold in 1969. In the winter of 1971, he took a position teaching Animal Breeding at Santa Fe Community College which he maintained until the summer of 1972. He then took the position of Manager with Johnny Cake Florida Division, a 1,000 acre purebred Charolais cattle operation near Gainesville, Florida.

Rafael E. Rodriguez is currently the Manager of Johnny Cake, Inc. He is married to the former Mary Dena Long of Gainesville. He has four children by a previous marriage and they reside with the former Mrs. Rodriguez in Gainesville, Florida.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.



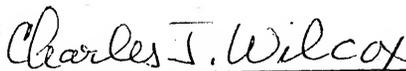
Marvin Koger, Chairman  
Professor of Animal Science

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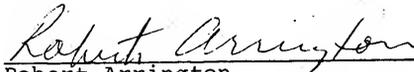
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Professor of Animal Science

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Science

This dissertation was submitted to the Dean of the College of Agriculture and to the Graduate Council, and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

December, 1974

  
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Dean, Graduate School