

THE EFFECT OF SELECTION ON THE HERITABILITY AND GENETIC  
CORRELATION OF TWO QUANTITATIVE TRAITS IN MICE

By

Tsang Kay Cheung

AN ABSTRACT OF A THESIS

Submitted to

The University of Manitoba

in Partial Fulfillment of the Requirements

for the Degree of

MASTER OF SCIENCE

1971



## ABSTRACT

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This study was to examine the effects of different intensities of single trait directional selection on the heritability and genetic correlation of the selected primary and correlated traits in random mating populations of mice. The traits under investigation were six-week body weight and six-week tail length. These two traits are quantitative, easily measured and expressed in both sexes. The mice were divided at random into five groups (A, B, C, D and E). Group A was under 30 percent mass selection for large six-week body weight and Group B was under 60 percent mass selection for large six-week body weight. Group C and Group D were under 30 percent and 60 percent mass selection for long six-week tail length, respectively. Group E acted as a control group with no selection applied. Mating in every group was random over the period of the experiment.

It was found that direct selection had no apparent effect on heritability of the trait selected for and there was no indication that the heritability of the correlated trait changed. The heritability of six-week tail length was

higher than the heritability of six-week body weight. The estimates of heritability of six-week body weight ranged from  $0.00 \pm 0.30$  to  $0.59 \pm 0.49$ , while estimates of heritability of six-week tail length ranged from  $0.19 \pm 0.29$  to  $0.74 \pm 0.35$ . There was no significant difference among the genetic correlations between the two traits in the five selection groups. Estimates of realized genetic correlation between six-week body weight and six-week tail length ranged from 0.35 to 0.44.

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## ACKNOWLEDGEMENT

The author wishes to express his sincere appreciation and gratitude to Dr. R. J. Parker for his encouragement, advice and guidance during the course of graduate study and preparation of this thesis.

Sincere thanks also go to Dr. M. E. Seale and Dr. R. J. Baker for their willingness to be of assistance at any time.

This investigation was financed in part by a grant from the National Research Council of Canada.

## TABLE OF CONTENTS

	Page
Acknowledgments . . . . .	ii
List of Tables . . . . .	iv
List of Figures . . . . .	vii
Introduction . . . . .	1
Literature Review . . . . .	2
Materials and Methods . . . . .	10
Genetic Stock . . . . .	10
Selection Criteria . . . . .	10
Mating and Selection Scheme . . . . .	11
Data Collection . . . . .	12
Analysis of Data . . . . .	14
Results and Discussion . . . . .	20
Response to Selection . . . . .	20
Response in Six-Week Body Weight . . . . .	20
Response in Six-Week Tail Length . . . . .	25
Correlated Response in Litter Size . . . . .	26
Estimates of Heritability . . . . .	27
Realized Heritabilities . . . . .	29
Genetic Correlation . . . . .	35
Summary and Conclusion . . . . .	41
Literature Cited . . . . .	42
Appendix . . . . .	44

## LIST OF TABLES

Table		Page
1	Levels of selection applied to five groups of mice . . . . .	11
2	Selection scheme for groups under 30 percent selection . . . . .	13
3	Selection scheme for groups under 60 percent selection . . . . .	13
4	Analysis of variance and expectation of mean squares . . . . .	16
5	Generation means and standard deviations for six-week body weight (gm.) of all five groups for each of seven generations of selection. . . .	22
6	Generation means and standard deviations for six-week tail length (cm.) of all five groups for each of seven generations of selection. . . .	22
7	Deviation of generation means (gm.) for six-week body weight of Groups A, B, C and D from the control Group E for each of seven generations of selection. . . . .	24
8	Deviation of generation means (cm.) for six-week tail length of Groups A, B, C and D from the control Group E for each of seven generations of selection. . . . .	25
9	Generation means for litter size of all groups for each of seven generations of selection. . . .	27
10	Estimates of heritability of six-week body weight obtained from sire components of variance for all groups from generation 2 to 7 . . . . .	28

Table	Page
11 Estimates of heritability of six-week tail length obtained from sire components of variance for all groups from generation 2 to 7 . . . . .	28
12 Estimates of heritability for both traits for all five groups by method of pooled analysis of variance . . . . .	30
13 Estimates of heritability of six-week body weight obtained from the regression of offspring on mid-parent for all groups from generation 2 to 7. . . . .	31
14 Estimates of heritability of six-week tail length obtained from the regression of offspring on mid-parent for all groups from generation 2 to 7. . . . .	32
15 Cumulated selection differentials of six-week body weight (gm.) in Groups A and B and of six-week tail length (cm.) in Groups C and D over the seven generations . . . . .	33
16 Estimates of realized heritability for six-week body weight in Groups A and B and realized heritability for six-week tail length in Groups C and D. . . . .	33
17 Genetic correlation estimates from product-moment correlation of genotypic values for all groups in every generation . . . . .	35
18 Estimates of genetic correlation for all groups in each generation by arithmetic method . . . . .	36
19 Estimates of genetic correlation for all groups in each generation by geometric method . . . . .	36



Table		Page
20	Cumulative direct response (R) and cumulative correlated response (CR) in Groups A, B, C and D from generation 2 to 7 . . . . .	39
21	Realized genetic correlation in the two group pairs. . . . .	39
22	Rate of gain in direct response and rate of gain in correlated response in Groups A, B, C and D. . . . .	40

## LIST OF FIGURES

Figure		Page
1	Generation means for six-week body weight (gm.) of Groups A, B, C, D and E for each of seven generations of selection . . . . .	23
2	Generation means for six-week tail length (cm.) of Groups A, B, C, D and E for each of seven generations of selection. . . . .	23

## INTRODUCTION

Quantitative geneticists have long been aware that correlated responses are common in populations under different types of selection. The primary implication of a correlated response is that the character under selection is genetically correlated with another character, although other parameters can affect the magnitude of the correlated response.

There has not been enough study of the effects of selection on the genetic correlation between traits and on the correlated response of traits not under selection to adequately account for their behaviour or to answer questions such as to what extent correlations can be changed by selection, over how many generations correlated responses continue, or what is the total correlated response when the selection limit is reached.

The present investigation was to examine the effects of different intensities of single trait directional selection in random mating populations of mice upon the genetic correlation between the selected trait and other traits not selected and upon the correlated response of traits not directly selected. Also of interest was the effect that different levels of heritability in the selected trait might have on genetic correlation and what changes might result in the heritabilities of both the selected and correlated traits themselves.

## REVIEW OF LITERATURE

Selection applied to one trait generally results in correlated changes in other traits not under selection. This 'correlated response' depends primarily upon the genetic correlation. The following statement by Darwin (1875) indicates that he had noted the importance of correlated variation:

"Hence, if man goes on selecting, and thus augmenting, any peculiarity, he will almost certainly modify unintentionally other parts of the structure, owing to the mysterious laws of correlation".

According to Falconer (1960), the genetic cause of correlation is chiefly pleiotropy. Pleiotropy is simply the property of a gene whereby it affects two or more characters; if the gene is segregating, it causes simultaneous variation in the characters it affects. The degree of correlation arising from pleiotropy expresses the extent to which two characters are influenced by the same genes.

Other possible causes of genetic correlation are usually regarded as minor or transient. For example, Lush (1948) stated that linkage can be an important cause only in a population where either the coupling or repulsion phase of the double heterozygote is far more abundant than the other. Such a condition would only persist for a few generations after a cross because in a freely interbreeding population, the coupling

and repulsion phase of the double heterozygote tend rapidly to become equally frequent.

Lerner (1958) presented a simple theoretical model, suggesting that the genetic correlation between two traits would eventually become negative if selection were applied to both traits simultaneously. Those alleles which affect one trait alone or both traits in a plus direction would eventually become fixed under selection for both traits while those alleles having a negative effect on one or both traits would be eliminated. The net result of selection would be to leave segregating only those alleles which have opposite effects on the two traits resulting in a negative genetic correlation. Lush (1948) makes essentially the same point when discussing the effect of selection on genetic correlation. While this theory seems sound, there has been little research reported on whether the theoretical treatment of correlated response to selection in terms of genetic correlation is adequate to explain the responses realized in experimental results.

Falconer (1953), selecting for large and small body size at six weeks of age in mice reported changes over time in estimates of genetic correlation among various correlated traits. The correlated response of tail length to selection for body size became irregular after generation five; the large line showed little further increase in tail length but the small line showed a sudden and rapid decrease from generation eight onwards.

He suggested that the apparent cessation of correlated response in tail length in the large line after generation five might be due to the genetic correlation between body weight and tail length having been broken down but emphasized that the facts were not clear enough to warrant speculation on this point. The observed correlated response of 12-day weight was also irregular. The large line increased rapidly until generation four and then showed no further increases. The small line, on the other hand, showed little decline up to generation five, after which the decline was rapid.

The correlated response of weaning weight differed in the two lines. The decrease in weaning weight in the small line was much greater than the increase in the large line. The large line increased by about 0.5 gm. while the small line decreased by about 2.5 gm., so that the change was about five times greater in the small line. The cause of this asymmetry of response could not be determined but it was suggested that it might be due to inbreeding or that weaning weight was a component of fitness, so that more litters with a small weaning weight of offspring were produced.

Rahnefeld et al. (1966) studied the genetic correlation between growth rate and litter size in mice. The genetic correlation and additive genetic covariance of post-weaning gain and litter size were estimated for a genetically variable population of mice during a 29 generation span in which recur-

rent selection for post-weaning gain was practiced. Estimates indicated a high positive genetic correlation (0.89) between the two traits and no clear indication of change in response to selection was observed during the 29 generations. Rahnefeld's report of this positive response of litter size to selection for post-weaning growth is comparable to the responses in litter size that MacArthur (1949) and Falconer (1955) observed in populations selected for large body size. However, in their experiments, the correlated response ceased after a very few generations (five in one case and six in the other). This difference is probably a function of the difference in selection criterion. For dams of equal size, there would be a negative correlation between litter size and weight of offspring at 42 or 60 days and a resulting tendency for mice largest in size to be found in smaller litters. The litter size effect on post-weaning growth is much less than on weight at 42 days and not sufficient to dampen the correlated response.

Clayton et al. (1957), studied correlated response in Drosophila melanogaster. They found that the genetic correlation between the primary trait (abdominal bristle number) and the secondary trait (sternopleural bristle number) was small though positive (0.05 to 0.10) in the base population. Moderate agreement with predicted correlated response was observed in the earlier generations while inbreeding was quite low. The correlated response became entirely unpredictable with further se-

lection in later generations. They concluded that if the genetic correlation is low, to measure it by correlated response is unwise, unless the inbreeding each generation can be kept at a very low level; and careful experimental design is required to estimate genetic correlations from correlated responses.

Festing et al. (1967) studied the response to selection for body weight and egg weight in chickens. Four lines of Leghorns, of common origin, were each selected for a single quantitative trait. The four lines consisted of a two-way set (lines B and C) selected for body weight (W), high and low, respectively, and another set (lines D and E) selected for egg weight (Z) high and low, respectively. The selected breeders consisted of eight sires each mated to eight to ten females per line per year. The Cornell White Leghorn Random-bred was the control population used each year. In addition, Line A selected for high rate of egg production, served as a quasicontrol population. This line responded little to selection, and its origin was in common with the other selected lines. Selections were based on measurements at approximately 32 weeks of age. Responses to selection over seven generations were immediate, large, and essentially linear. Realized heritabilities calculated from the regression of the selected trait on cumulative selection differential were asymmetrical with respect to the direction of selection. In contrast, heritabilities estimated from variance components were symmetrical and intermediate with



heritabilities largest in the lines selected upwards but smallest in the lines selected downwards. The estimation of genetic correlations from variance components and from realized selection response between W and Z paralleled those for the estimation of heritabilities. The agreement between realized and variance component correlations was good in the downward selected lines (C and E) but poor in the upward selected lines (B and D). The trends in the heritabilities were not statistically significant, but both the phenotypic and genetic correlations declined significantly over generations. In the upward selection lines (B and D), genetic correlations estimated from variance components declined from 0.6 to 0.2-0.3 in generation six. In the downward selected lines (C and E), they declined less (to 0.4-0.5). In control A line, no decline was observed. The rates of decline between the lines were statistically significant. Body weight and egg weight were evidently controlled by both independent and pleiotropic genes.

Parker et al. (1969, 1970a,b) have examined the effect of truncation selection of a primary trait upon the genetic correlation and the correlated response in a secondary trait for a simulated population. The size of the parent population was 48 in each generation. Three levels of selection, 0.8, 0.5 and 0.2, three genetic correlations between traits 0.75, 0.50 and 0.25 and three levels of heritability for both traits 0.7, 0.4 and 0.1 were simulated. Each trait was controlled by 48 loci

segregating independently, effects were equal at every locus, and gene frequency was arbitrarily set at 0.5 at each locus in the initial generation. Two models of gene action, additive and complete dominance, were discussed and each parameter set was under selection for 30 generations.

The results from the additive model indicated that high selection intensity resulted in a decline in genetic correlation while low selection intensities maintained the genetic correlation. In the model of complete dominance, the change in genetic correlation where selection was by upper truncation, followed essentially the same patterns as in the additive model. Selection by lower truncation was similar except that decreases in the correlation at high intensity of selection was more rapid. The estimates of genetic correlation computed from phenotypic covariances between parents and offspring fluctuated markedly from the true correlation.

The effect of selection on genetic correlation has been of considerable interest to research workers. Both theoretical and experimental studies have been carried out in an attempt to clarify this problem. Although the general trend seems to be that continuous selection will eventually cause a decrease in genetic correlation, there are still many questions unanswered. There is insufficient information about the behaviour of the genetic correlation under selection or about correlated response to selection, to allow conclusions to be drawn

for questions such as:

"Does the change in the size of the genetic correlation depend more on the intensity of selection, on the heritability of selected trait, or on the initial degree of correlation?"

"Does the process of selection affect the relative accuracy of the different methods of estimating the genetic correlation differently?"

An understanding of the changes likely to occur in genetic correlation between traits under selection is rather important. In order to achieve accurate prediction of response in a selection programme and to accurately construct a selection index, it is essential for the animal breeder to have a knowledge of the effects of selection on genetic correlation.

## MATERIALS AND METHODS

A selection experiment, using mice as the experimental animal, was initiated in May, 1967 to study the effects of varying levels of selection and varying heritabilities on genetic correlation. This thesis will report on the analysis of the data generated from generations one to seven.

Genetic Stock. A random sample of 30 males and 60 females were obtained and random mated for one generation, one male being mated to two females. The offspring were divided at random into five groups A, B, C, D and E, with each group consisting of fifteen males and fifteen females. These groups were then mated at random and their offspring (generation 1) were the animals used for the first generation of selection.

Selection Criteria. The traits selected for were six-week body weight and six-week tail length. These two traits are quantitative, easily measured and expressed in both sexes. The genetic correlation between them is considered high ( $r_G = 0.6$ ) (Falconer, 1960). Their heritabilities are reasonably large and yet different from each other. Heritability of tail length is generally considered to be about 0.6 and heritability of six-week body weight about 0.3. It was considered that such reasonably high heritabilities and high genetic correlation would more easily allow detection of any change in the genetic correlation between them and the effect of heritability

on this change.

The selection applied was directional for large six-week body weight or long six-week tail length. Two levels of selection were applied to each trait. There was also a control group where no selection was applied. The five groups and the selection applied to each are shown in Table 1. Group A was under 30 percent mass selection for six-week body weight and Group B was under 60 percent mass selection for six-week body weight. Group C and Group D were under 30 percent and 60 percent mass selection for tail length respectively. Group E was the control group with no selection applied.

Table 1. Levels of selection applied to five groups of mice

Group	Selection Criterion	Level of Selection (b)
A	Six-week body weight	0.30
B	Six-week body weight	0.60
C	Six-week tail length	0.30
D	Six-week tail length	0.60
E	Control	0

Mating and Selection Scheme. The number of mice saved for breeding each generation was 15 males and thirty females. Each male was mated to two females, with the mating period being of ten days duration. The males were then discarded and the females placed in separate cages. The number of offspring per litter was counted at birth and the offspring weaned at three weeks of age. At six weeks of age, body weight and tail length of each mouse in the litter were measured and these were the

measurements used as the basis of selection of the parents of the subsequent generation. For the group under 30 percent mass selection for either six-week body weight or six-week tail length, 75 males and 75 females per group were selected at random and ranked in descending order in the trait selected for. The top 30 females in the rank and the top 15 males in the rank were saved and mated at random to produce the next generation (Table 2); with the restriction of no full-sib matings.

For the group under 60 percent mass selection for either six-week body weight or six-week tail length, 36 males and 36 females per group were selected at random and ranked in descending order in the trait selected for. The top 30 females in the rank and the top 15 males in the rank were saved and mated at random to produce the next generation (Table 3). In the control Group E, 30 females and 15 males were chosen at random and mated at random to produce the next generation.

Data Collection. The following data were collected on each mouse: date of birth, coat color, sex, four-week body weight, six-week body weight and six-week tail length.

The populations throughout the course of the experiment appeared in good health. No cases of disease among mice were found at any time during the course of the experiment.

Table 2. Selection scheme for groups under 30 percent selection

(Groups A and C)			
	*	**	
Females	b	Z/b	Average Z/b
30/75	0.4	0.97	
Males			1.19
15/75	0.2	1.40	

Table 3. Selection scheme for groups under 60 percent selection

(Groups B and D)			
	*	**	
Females	b*	Z/b**	Average Z/b
30/36	0.83	0.34	
Males			0.65
15/36	0.41	0.97	

\* the proportion of animals selected

\*\* the ordinate at the point of truncation

Analysis of Data. All but the more easily computed statistics were obtained using an I.B.M. 360 computer. Analyses were performed within each group for each generation and in addition, a pooled analysis was carried out across generations. Standard statistical procedures were employed in the estimation of all parameters. Heritabilities and genetic correlations were estimated both from parent-offspring covariances and regressions and from analysis of variance and covariance.

a) Parent-offspring covariances and regressions:

Heritability was estimated from the regression of offspring on mid-parent. In any mid-parent offspring regression the form of analysis is similar to the following:

$$b = \frac{\text{Cov } XY}{\sigma^2_X}$$

where  $b$  is an estimate of heritability,  $\text{Cov } XY$  is the covariance between the phenotypic mean ( $X$ ) of the two parents and the phenotype of the offspring ( $Y$ ) and  $\sigma^2_X$  is the phenotypic variance of the mean of the two parents. The standard error of the estimate of heritability was estimated according to Becker (1967) as

$$\text{S.E. } (h^2) = \sqrt{\frac{S_b^2}{\Sigma X^2}}$$



where  $S_b^2$  is the mean square deviation from regression, and  $\Sigma X^2$  is the corrected sum of squares of mid-parents.

Genetic correlation was estimated each generation by the method proposed by Hazel (1943) utilizing phenotypic covariances between parent and offspring. Two variations of Hazel's method were used to compare the relative accuracy of the two methods. The two methods were:

$$i) r_{G1} = [(\text{CovP}_{xp} P_{yo})(\text{CovP}_{yp} P_{xo}) / (\text{CovP}_{xp} P_{xo})(\text{CovP}_{yp} P_{yo})]^{1/2}$$

$$ii) r_{G2} = (\text{CovP}_{xp} P_{yo} + \text{CovP}_{yp} P_{xo}) / 2 [(\text{CovP}_{xp} P_{xo})(\text{CovP}_{yp} P_{yo})]^{1/2}$$

where  $P_{xp}$  and  $P_{xo}$  are the phenotypic values for six-week body weight in the parent and offspring respectively, and  $P_{yp}$  and  $P_{yo}$  are the phenotypic values for six-week tail length in the parent and offspring respectively.

The standard error of the genetic correlation coefficient was estimated according to Reeve (1955) and Robertson (1959) as

$$\text{S.E. } (r_G)^* = \frac{1 - r_G^2}{\sqrt{2}} \cdot \sqrt{\frac{\text{S.E. } h_x^2 \cdot \text{S.E. } h_y^2}{h_x^2 \cdot h_y^2}}$$

where  $h_x^2$  is the estimate of heritability for trait X and  $h_y^2$  is the estimate of heritability for trait Y and S.E.

\* Used to estimate standard error of  $r_{G1}$  only

$h^2_x$  and S.E.  $h^2_y$  are the standard errors of the estimates of heritability of the two traits determined from the formula indicated previously.

b) Analysis of variance and covariance:

The form of the analysis of variance and the expectation of mean squares are presented in Table 4. Separate analyses were conducted for each group within each generation. A pooled analysis across generations was also performed for each of the five groups the form of which was similar to that in Table 4 with the addition of another source of variation, i.e. between generations.

Table 4. Analysis of variance and expectations of mean squares

Source	d.f.	Mean Square	Expectation of Mean Square
Between Sires	s-1	$M_1$	$W + k_2D + k_3S$
Between Dams within Sires	d-s	$M_2$	$W + k_1D$
Within full Sibs	N-d	$M_3$	W

where s = total number of sires

d = total number of dams

N = total number of progeny

$$k_1 = \frac{1}{d - s} \cdot \left[ N - \sum_i \frac{\sum_j n_{ij}^2}{n_i} \right]$$

$$k_2 = \frac{1}{s - 1} \cdot \left[ \sum_i \frac{\sum_j n_{ij}^2}{n_i} - \frac{\sum_i \sum_j n_{ij}^2}{N} \right]$$

$$k_3 = \frac{1}{s - 1} \cdot \left[ N - \frac{\sum_i n_i^2}{N} \right]$$

$n_i$  = total number of offspring from the  $i^{\text{th}}$  sire

$n_{ij}$  = total number of offspring from the  $j^{\text{th}}$  dam

S = variance due to differences among sires

D = variance due to differences among dams

W = variance due to differences among sibs

The variances of variance component estimates were obtained according to Anderson and Bancroft (1952) as follows:

The estimate of S was

$$S = \left[ M_1 - M_3 - \frac{k_2}{k_1} (M_2 - M_3) \right] / k_3$$

It follows that

$$V(S) = \left[ V(M_1) + \left( \frac{k_2}{k_1} \right)^2 \cdot V(M_2) + \left( \frac{k_2 - k_1}{k_1} \right)^2 \cdot V(M_3) \right] / k_3^2$$

where:  $V(S)$  = variance of S

$V(M_1)$  = variance of the mean square for the between sires source of variance

$V(M_2)$  = variance of the mean square for the dams within sire source of variance

$V(M_3)$  = variance of the mean square for the within litters source of variance

The variances of the mean squares were approximated by substitution of the observed mean square for its expectation in the general expression

$$V(M) = \frac{2[E(M)]^2}{d.f.}$$

where: M = any mean square

E(M) = expectation of M

d.f. = degrees of freedom for the mean square M

Since S represents one-quarter the additive genetic variance, and the sum S + D + W represents the total phenotypic variance of the population, it is necessary to solve for each of these components in order to compute estimates of heritability. The formula used for these computations was as follows:

$$h_S^2 = \frac{4S}{S+D+W}$$

The standard error of heritabilities (modified from Dickerson, 1960)\* is

$$S.E. (h_S^2) = \sqrt{\frac{4 \text{Var}(\sigma_s^2)}{\sigma_s^2 + \sigma_D^2 + \sigma_W^2}}$$

The genetic correlation was also computed using sire components of variance and covariance as follows:

\* as described by Becker, W. A. 1967

$$r_G = \frac{\text{Cov}_{xy}(s)}{\sqrt{\sigma_s^2(x) \cdot \sigma_s^2(y)}}$$

where:  $s(x)$  = six-week body weight of sire

$s(y)$  = six-week tail length of sire

$\text{Cov}_{xy}(s)$  is the estimate of the sire component of covariance,  $\sigma_s^2(x)$  and  $\sigma_s^2(y)$  are the sire components of variance for six-week body weight and six-week tail length respectively.

The variance of  $r_G$  was computed as follows (Mode and Robinson, 1959):

$$\begin{aligned} \text{Var}(r_G) \cong r_G^2 \cdot & \frac{\text{Var}(\text{Cov}_{xy}(s))}{\text{Cov}_{xy}^2(s)} + \frac{\text{Var}(\sigma_s^2(x))}{4(\sigma_s^2(x))^2} + \frac{\text{Var}(\sigma_s^2(y))}{4(\sigma_s^2(y))^2} \\ & - \frac{\text{Cov}(\sigma_s^2(x), \text{Cov}_{xy}(s))}{\sigma_s^2(x) \text{Cov}_{xy}(s)} - \frac{\text{Cov}(\sigma_s^2(y), \text{Cov}_{xy}(s))}{\sigma_s^2(y) \text{Cov}_{xy}(s)} \\ & + \frac{\text{Cov}(\sigma_s^2(x), \sigma_s^2(y))}{2 \sigma_s^2(x) \sigma_s^2(y)} \end{aligned}$$

and,  $\text{S.E.}(r_G) = \sqrt{\text{Var}(r_G)}$

## RESULTS AND DISCUSSION

RESPONSE TO SELECTION

The phenotypic means for six-week body weight and six-week tail length for each of the five groups are presented in Tables 5 and 6 for all seven generations of selection and are presented graphically in Figures 1 and 2. Deviations of generation means of Groups A, B, C and D from the control Group E for all seven generations for both six-week body weight and tail length, are presented in Tables 7 and 8.

Response in Six-Week Body Weight. Means for six-week body weight in Group E showed little or no change during the seven generations. Group A showed the most marked increase in six-week body weight which agreed with the fact that Group A was under the most intense selection for six-week body weight (30 percent mass selection). The response of Group B, which was under 60 percent selection for six-week body weight, was less than that of Group A as was expected. The correlated response of six-week body weight in Group C, which was under 30 percent selection for six-week tail length, was comparable to the direct response in six-week body weight of Group B. It seemed that a 30 percent selection for six-week tail length can move the correlated trait (six-week body weight) upwards as fast as direct selection for six-week body weight at the 60 per cent selection level. Group D, which was under 60 percent

Table 5. Generation means and standard deviations for six-week body weight (gm.) of all five groups for each of seven generations of selection

GENERATION	GROUP A	GROUP B	GROUP C	GROUP D	GROUP E
1	23.05 ± 3.15	22.89 ± 3.06	23.34 ± 3.21	22.40 ± 3.32	22.30 ± 3.18
2	25.65 ± 3.17	24.90 ± 2.97	24.20 ± 3.03	23.20 ± 2.91	22.90 ± 3.49
3	26.09 ± 3.41	25.50 ± 2.87	25.40 ± 3.25	24.72 ± 3.23	24.34 ± 3.71
4	24.95 ± 3.57	23.90 ± 3.59	23.67 ± 2.99	22.02 ± 3.22	22.01 ± 3.06
5	26.20 ± 3.01	24.67 ± 3.11	24.76 ± 3.41	23.54 ± 3.53	22.65 ± 2.82
6	28.25 ± 3.60	26.01 ± 3.12	26.50 ± 3.52	24.72 ± 3.90	24.25 ± 2.99
7	26.31 ± 3.14	24.05 ± 3.71	27.00 ± 4.05	24.36 ± 3.38	22.76 ± 2.33

Table 6. Generation means and standard deviations for six-week tail length (cm.) of all five groups for each of seven generations of selection

GENERATION	GROUP A	GROUP B	GROUP C	GROUP D	GROUP E
1	8.81 ± 0.46	8.84 ± 0.42	8.78 ± 0.47	8.79 ± 0.39	8.63 ± 0.45
2	8.73 ± 0.55	8.69 ± 0.47	8.82 ± 0.44	8.60 ± 0.46	8.51 ± 0.53
3	8.67 ± 0.37	8.51 ± 0.43	8.95 ± 0.38	8.69 ± 0.40	8.47 ± 0.71
4	8.86 ± 0.45	8.88 ± 0.41	9.34 ± 0.50	9.14 ± 0.49	8.69 ± 0.56
5	8.91 ± 0.41	9.02 ± 0.49	9.64 ± 0.48	9.44 ± 0.43	8.71 ± 0.38
6	8.86 ± 0.44	8.89 ± 0.40	9.84 ± 0.43	9.49 ± 0.43	8.75 ± 0.36
7	8.94 ± 0.44	8.77 ± 0.56	9.65 ± 0.53	9.51 ± 0.35	8.66 ± 0.41



Figure 1. Generation means for six-week body weight (gm.) of Groups A, B, C, D and E for each of seven generations of selection

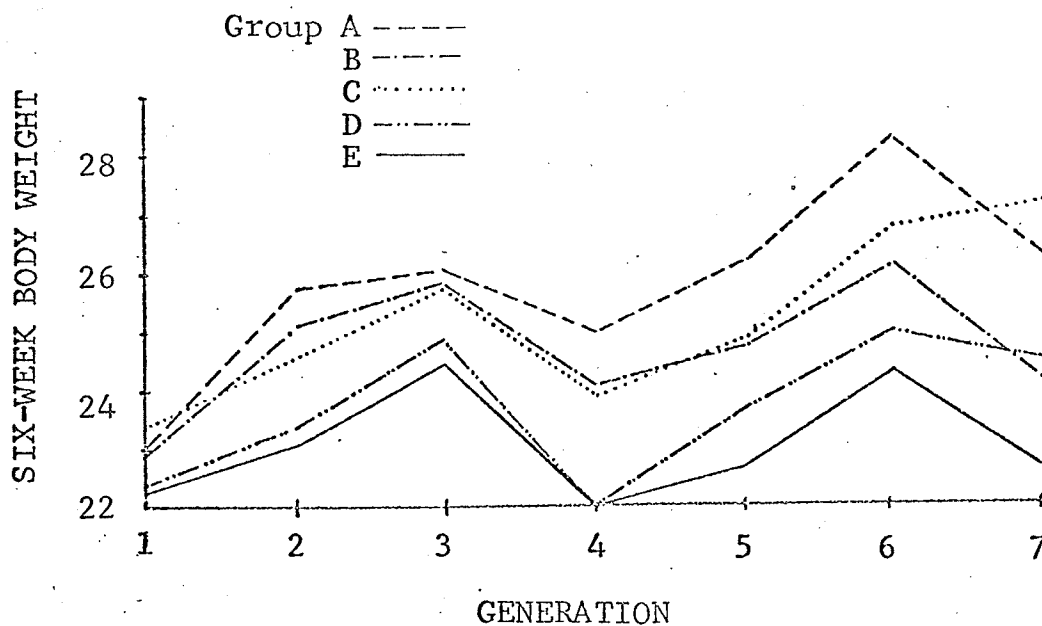


Figure 2. Generation means for six-week tail length (cm.) of Groups A, B, C, D and E for each of seven generations of selection

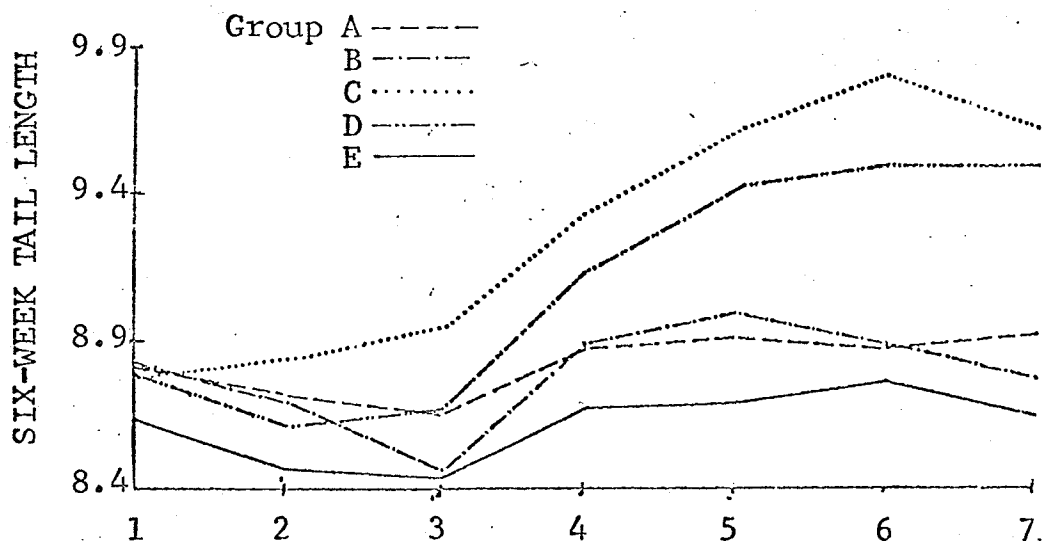


Table 7. Deviation of generation means (gm.) for six-week body weight of group A, B, C and D from the control group E for each of seven generations of selection

GENERATION	GROUP A	GROUP B	GROUP C	GROUP D
1	0.75	0.59	1.04	0.10
2	2.75	2.00	1.30	0.30
3	1.75	1.16	1.06	0.38
4	2.94	1.89	1.66	0.01
5	3.55	2.02	2.11	0.89
6	4.00	1.76	2.25	0.47
7	3.55	1.29	4.24	1.60

Table 8. Deviation of generation means (cm.) for six-week tail length of group A, B, C and D from the control group E for each of seven generations of selection

GENERATION	GROUP A	GROUP B	GROUP C	GROUP D
1	0.18	0.21	0.15	0.16
2	0.22	0.18	0.31	0.09
3	0.20	0.04	0.48	0.22
4	0.17	0.19	0.65	0.45
5	0.20	0.31	0.93	0.73
6	0.11	0.14	1.09	0.74
7	0.28	0.11	0.99	0.85

selection for six-week tail length, also showed correlated increase in six-week body weight though less marked than in Group C.

Response in Six-Week Tail Length. Means for six-week tail length in Group E remained more or less the same during the seven generations. Group C, which was under 30 percent selection for six-week tail length, showed a marked increase in six-week tail length over the seven generations. Group D, which was under 60 percent selection for six-week tail length, also showed an increase in six-week tail length though less than the response in Group C as was expected. Groups A and B, which were under selection for six-week body weight at the level of 30 and 60 percent respectively, showed little or no correlated response in six-week tail length. It seemed that direct selection for six-week body weight contributed little or no increase in the correlated trait (six-week tail length). It may be concluded that both six-week body weight and six-week tail length respond to direct selection. But, when not directly selected, the correlated response in six-week tail length when six-week body weight is directly selected is less than the correlated response in six-week body weight when six-week tail length is selected for directly. It may be recalled that Falconer (1953) reported the cessation of the correlated response of tail length in mice selected for large body weight after five generations of selection. He suggested the genetic correlation

of tail length with body weight may have been broken down. The same suggestion might explain the failure of response in six-week tail length in groups under selection for six-week body weight in this experiment. It is interesting, however, that whereas six-week tail length failed to respond in groups under selection for six-week body weight, there was an obvious response in six-week body weight in groups under selection for six-week tail length.

Correlated Response in Litter Size. The means for litter size, in terms of number of offspring born alive, for all groups in every generation are presented in Table 9. The mean for litter size in Group E showed great fluctuation with a surprisingly high average in the first generation. The litter size of Groups A and C were comparable and were generally larger than that of Group E except for the first generation. The litter size of Groups B and D also remained more or less the same as in Group E, except for the first generation. It seemed that mass selection at the 30 percent level either for six-week body weight or for six-week tail length resulted in an increase in litter size, though the large fluctuation and the large litter size in Group E in the first generation rendered the interpretation uncertain.

Table 9. Generation means for litter size of all groups for each of seven generations of selection

	GENERATION						
	1	2	3	4	5	6	7
GROUP A	9.3	9.1	10.4	8.8	9.4	10.3	10.6
B	9.4	8.9	9.6	9.1	9.0	9.8	9.4
C	8.6	10.0	10.0	8.8	9.9	11.6	10.6
D	9.6	9.5	8.9	7.7	8.7	9.5	9.3
E	11.5	8.4	9.5	7.8	9.0	9.9	9.3

#### ESTIMATES OF HERITABILITY

The estimates of heritability for both traits in all groups were obtained by two different methods. One set of estimates was furnished by components of variance and the other set by regression of offspring on mid-parent. For Groups A, B, C and D the realized heritability of the trait under direct selection was also calculated.

As can be seen from Tables 10 and 11, the estimates of heritability for both traits obtained from components of variance were rather erratic and difficult to interpret. This may be due to the rather small sample size. For each group, with data from generation 2 to generation 7 pooled, an analysis of variance was performed in which generation effect was removed and a test for significance of each source of variation made (Appendix 1). The F - test showed that all groups behaved

Table 10. Estimates of heritability of six-week body weight obtained from sire components of variance for all groups from cycle 2 to cycle 7

	GROUP A	GROUP B	GROUP C	GROUP D	GROUP E
CYCLE 2	1.10	0.53	-0.08	0.08	1.00
3	0.61	0.10	0.41	-0.07	0.05
4	1.30	0.14	-0.26	0.88	1.45
5	0.31	-0.25	-0.09	0.58	0.04
6	-1.01	-0.31	0.50	0.38	0.46
7	0.01	0.32	-0.74	0.92	-0.80

Table 11. Estimates of heritability of six-week tail length obtained from sire components of variance for all groups from cycle 2 to cycle 7

	GROUP A	GROUP B	GROUP C	GROUP D	GROUP E
CYCLE 2	1.82	0.59	0.45	0.22	1.43
3	0.35	-1.14	0.52	0.64	-0.13
4	0.54	0.75	-0.06	1.34	2.09
5	-0.18	0.61	0.75	0.87	-0.31
6	-1.64	-0.82	0.42	0.85	1.07
7	1.10	-0.45	-0.39	-0.07	0.12

the same in that differences between generations and between dams within sires were significant. In each group, an estimate of heritability for both traits was obtained from components of variance and are presented in Table 12. These heritability estimates were less erratic (perhaps due to an increase in sample size) and showed that the heritability of six-week tail length was higher than the heritability of six-week body weight.

The heritability estimates for both traits obtained by mid-parent offspring regression are presented in Tables 13 and 14. Again, these heritability estimates were quite erratic and fluctuated over wide ranges with large standard errors, but still it was rather obvious that the heritability of six-week tail length was higher than the heritability of six-week body weight.

Realized Heritabilities. The realized heritabilities of six-week body weight for Groups A and B and of six-week tail length for Groups C and D were calculated by regression of generation means on the cumulated selection differentials (Falconer, 1960). The cumulated selection differential of six-week body weight in Groups A and B and of six-week tail length in Groups C and D over the seven generations are shown in Table 15.

The estimates of realized heritability of six-week body weight in Groups A and B and of six-week tail length in Groups C and D are presented in Table 16.

Table 12. Estimates of heritability for both traits for all five groups by method of pooled analysis of variance

GROUP	Heritability of Body Weight	Heritability of Tail Length
A	0.37 $\pm$ 0.26	0.51 $\pm$ 0.82
B	0.10 $\pm$ 0.24	0.74 $\pm$ 0.35
C	0.00 $\pm$ 0.30	0.19 $\pm$ 0.29
D	0.31 $\pm$ 0.25	0.62 $\pm$ 0.25
E	0.29 $\pm$ 0.26	0.56 $\pm$ 0.28



Table 13. Estimates of heritability of six-week body weights obtained from the regression of offspring on mid-parent for all groups from generation two to generation seven.

GENERATION	GROUP A	GROUP B	GROUP C	GROUP D	GROUP E
2	0.66 ± 0.74	1.05 ± 0.38	0.55 ± 0.25	0.31 ± 0.28	0.55 ± 0.28
3	0.42 ± 0.17	0.56 ± 0.33	0.39 ± 0.26	0.92 ± 0.03	0.42 ± 0.25
4	1.31 ± 0.52	0.03 ± 0.40	0.03 ± 0.25	0.50 ± 0.20	0.17 ± 0.29
5	0.68 ± 0.33	0.27 ± 0.37	0.40 ± 0.30	0.50 ± 0.32	0.74 ± 0.26
6	0.24 ± 0.52	0.43 ± 0.21	0.05 ± 0.25	0.55 ± 0.52	-0.02 ± 0.28
7	0.15 ± 0.65	---	0.41 ± 0.39	0.24 ± 0.20	-0.34 ± 0.33
Mean*	0.59 ± 0.49	0.47 ± 0.34	0.30 ± 0.29	0.50 ± 0.31	0.25 ± 0.28

\*The average of the six heritability estimates in each group.

Table 14. Estimates of heritability of six-week tail length obtained from the regression of offspring on mid-parent for all groups from generation two to generation seven

GENERATION	GROUP A	GROUP B	GROUP C	GROUP D	GROUP E
2	0.28 ± 0.37	0.94 ± 0.20	0.00 ± 0.68	0.43 ± 0.34	0.13 ± 0.16
3	0.53 ± 0.24	0.33 ± 0.25	0.28 ± 0.40	0.84 ± 0.16	0.46 ± 0.36
4	0.60 ± 0.18	0.54 ± 0.19	0.48 ± 0.73	1.01 ± 0.30	0.43 ± 0.34
5	0.38 ± 0.15	0.33 ± 0.21	0.69 ± 0.48	0.25 ± 0.37	0.59 ± 0.17
6	0.52 ± 0.26	0.61 ± 0.18	0.48 ± 0.40	0.98 ± 0.21	0.25 ± 0.24
7	0.69 ± 0.27	---	0.43 ± 0.39	0.12 ± 0.14	0.11 ± 0.25
Mean*	0.50 ± 0.24	0.55 ± 0.20	0.39 ± 0.51	0.60 ± 0.25	0.33 ± 0.25

\*The average of the six heritability estimates in each group

Table 15. Cumulated selection differentials of six-week body weight (gm.) in Groups A and B and of six-week tail length (cm.) in Groups C and D over the seven generations.

	A	B	C	D
GENERATION 1	0	0	0	0
2	2.88	1.54	0.50	0.27
3	5.89	3.15	1.00	0.66
4	9.30	4.10	1.47	0.98
5	12.67	5.54	2.07	1.27
6	15.53	6.68	2.62	1.64
7	18.71	8.92	3.15	2.10

Table 16. Estimates of realized heritability for six-week body weight in Groups A and B and realized heritability for six-week tail length in Groups C and D.

GROUP	$h^2$ (Body Weight)	$h^2$ (Tail Length)
A	$0.17 \pm 0.08$	-
B	$0.11 \pm 0.12$	-
C	-	$0.36 \pm 0.05$
D	-	$0.48 \pm 0.09$

Again, the realized heritability of six-week tail length is higher than the heritability of six-week body weight.

In six-week body weight, the estimates of heritability obtained from the regression of offspring on mid-parent are consistently higher than the heritability estimates obtained from pooled analysis of variance with estimates of realized heritability the lowest of the three. In six-week tail length, the estimates of heritability obtained from the regression of offspring on mid-parent and from pooled analysis of variance are comparable and are higher than the estimates of realized heritability.

The estimates of heritability of six-week body weight ranged from  $0.00 \pm 0.30$  to  $0.59 \pm 0.49$ . While estimates of heritability of six-week tail length ranged from  $0.19 \pm 0.29$  to  $0.74 \pm 0.35$ . Due to the large standard errors of these heritability estimates, there was no indication that the heritability of six-week body weight or heritability of six-week tail length in the five groups had changed significantly over the seven generations.

GENETIC CORRELATION

Genetic correlation estimates were measured in each generation in each group as the product-moment correlation,  $r_G = \text{Cov}_{xy(s)} / \sqrt{[\sigma^2_{s(x)} \cdot \sigma^2_{s(y)}]}$ , where  $r_G$  is the estimate of genetic correlation,  $\text{Cov}_{xy(s)}$  is the sire component of covariance between genotypic values of the two traits and  $\sigma^2_{s(x)}$ ,  $\sigma^2_{s(y)}$  are the sire component of variance of the two traits respectively. These estimates are presented in Table 17.

Table 17. Genetic correlation estimates from product-moment correlation of genotypic values for all groups in every generation

GENERATION	GROUP A	GROUP B	GROUP C	GROUP D	GROUP E
2	0.98±0.28	0.95±0.71	0.50±1.12	1.00±3.22	1.03±0.34
3	0.75±0.82	1.07±2.83	0.54±0.74	0.98±4.81	0.83±4.58
4	1.26±0.38	1.03±1.14	*	0.97±0.32	0.91±0.22
5	0.63±0.78	-0.19±0.52	0.63±2.95	0.33±0.32	0.71±2.26
6	-1.05±0.76	1.38±1.09	1.18±0.75	0.98±0.74	0.63±0.35
7	*	0.09±0.37	0.92±1.61	*	0.93±3.24
POOLED	0.76±0.32	0.78±0.60	> 1.00	0.81±0.59	1.00±0.49

Except for Group E, the generation by generation genetic correlation estimates were extremely erratic and were almost impossible to interpret. The pooled estimates showed that the genetic correlation of Group C was higher than that of Groups A, B and D, which provided similar estimates of genetic correlation, but the difference is not significant.

Genetic correlation was also estimated each generation

\* Genetic correlation < -2.00 or > + 10.00

by two variations of the method proposed by Hazel (1943) as outlined in Materials and Methods section and these estimates are presented in Tables 18 and 19.

Table 18. Estimates of genetic correlation for all groups in each generation by arithmetic method

GENERATION	GROUP A	GROUP B	GROUP C	GROUP D	GROUP E
2	0.04±0.86	0.32±0.18	---	0.18±0.58	1.05±0.06
3	0.24±0.29	0.44±0.38	0.41±0.57	0.73±0.03	1.61±0.78
4	0.49±0.19	0.96±0.13	---	0.43±0.20	0.14±0.80
5	-0.15±0.31	0.48±0.50	0.46±0.40	0.30±0.63	0.69±0.12
6	1.31±0.53	0.73±0.12	2.00±4.43	0.64±0.19	1.20±1.07
7	1.19±0.39	---	0.04±0.66	0.87±0.17	-0.91±0.18

Table 19. Estimates of genetic correlation for all groups in each generation by geometric method

GENERATION	GROUP A	GROUP B	GROUP C	GROUP D	GROUP E
2	-0.72	0.28	---	-0.09	1.03
3	0.18	0.44	0.40	0.72	0.43
4	1.42	0.62	---	0.41	-0.41
5	-0.11	-0.53	-0.17	-0.49	0.64
6	0.77	0.72	-1.07	-0.10	-1.20
7	1.13	---	0.71	0.84	0.69

Estimates obtained by both methods were difficult to interpret with estimates obtained by the geometric method more erratic than those obtained by the arithmetic method. Only oc-

asionally did the estimates obtained by the two methods agree with each other in magnitude.

The estimates of genetic correlation obtained by all methods had large standard errors and there was no indication that the genetic correlations in the five groups differed significantly.

There were four groups under selection. Group A was under 30 percent selection for large six-week body weight and Group C was under 30 percent selection for long six-week tail length. Group B was under 60 percent selection for large six-week body and Group D was under 60 percent selection for long six-week tail length. In each group, the cumulative correlated response of the trait not directly selected for as well as the cumulative response of the trait directly selected for were measured in each generation as the deviation of generation mean from the control Group E in the same generation. These results are presented in Table 20.

Since Groups A and C were under the same intensity of selection, one estimate of realized genetic correlation can be obtained by the following equation, Falconer (1960):

$$r_g = \sqrt{\frac{CR_x \cdot CR_y}{R_x \cdot R_y}}$$

where

$r_g$  = genetic correlation

$CR_x$  = cumulative correlated response of six-week body weight in Group C through generations 2, 3, 4.....and 7

$CR_y$  = cumulative correlated response of six-week tail length in Group A through generations 2, 3, 4.....and 7

$R_x$  = cumulative response of six-week body weight in Group A through generations 2, 3, 4..... and 7

$R_y$  = cumulative response of six-week tail length in Group C through generations 2, 3, 4..... and 7

Likewise, for Groups B and D, one estimate of realized genetic correlation in each generation was obtained using the same equation. The estimates of realized genetic correlation for the two group pairs are presented in Table 21.

In addition, by using the same formula, realized genetic correlation in each Group Pair was estimated from the rate of gain in direct response and rate of gain in correlated response from the regression of generation means on generations of selection. The rate of gain in direct response and rate of gain in correlated response in Groups A, B, C and D are presented in Table 22.

The estimate of realized genetic correlation for Group Pair AC was found to be 0.41 and that for Group Pair BD was 0.44. These estimates agree quite closely with the mean estimates of 0.44 and 0.35 shown in Table 21, and there appears to be no difference between the estimates obtained from the



Table 20. Cumulative direct response (R) and cumulative correlated response (CR) in Groups A, B, C and D from generation 2 to 7 as deviation from Group E

		GENERATION					
		2	3	4	5	6	7
GROUP A	Rx	2.75 gm.	1.75 gm.	2.94 gm.	3.55 gm.	4.00 gm.	3.55 gm.
	CRy	0.22 cm.	0.20 cm.	0.17 cm.	0.20 cm.	0.11 cm.	0.28 cm.
GROUP B	Rx	2.00 gm.	1.16 gm.	1.89 gm.	2.02 gm.	1.76 gm.	1.29 gm.
	CRy	0.18 cm.	0.04 cm.	0.19 cm.	0.31 cm.	0.14 cm.	0.11 cm.
GROUP C	Ry	0.31 cm.	0.48 cm.	0.65 cm.	0.93 cm.	1.09 cm.	0.99 cm.
	CRx	1.30 gm.	1.06 gm.	1.66 gm.	2.11 gm.	2.25 gm.	4.24 gm.
GROUP D	Ry	0.09 cm.	0.22 cm.	0.45 cm.	0.73 cm.	0.74 cm.	0.85 cm.
	CRx	0.30 gm.	0.38 gm.	0.01 gm.	0.89 gm.	0.47 gm.	1.60 gm.

Table 21. Realized genetic correlation in the two group pairs

GENERATION	Group Pair AC	Group Pair BD
2	0.57	0.55
3	0.51	0.24
4	0.39	0.05
5	0.36	0.42
6	0.23	0.22
7	0.57	0.40
Mean*	0.44	0.35

\*Average of the six estimates in each Group Pair

two group pairs representing two different intensities of selection. Also, the individual estimates obtained in each of the six generations of selection, also shown in Table 21, although showing more variability, provide no indication that the genetic correlation between the two traits has changed over the six generations of selection at either level of selection.

Table 22. Rate of gain in direct response and rate of gain in correlated response in Groups A, B, C and D

	Rate of Gain in Direct Response (R)	Rate of Gain in Correlated Response (CR)
GROUP A	0.53 gm./generation	0.03 cm./generation
GROUP B	0.17 gm./generation	0.02 cm./generation
GROUP C	0.19 cm./generation	0.53 gm./generation
GROUP D	0.16 cm./generation	0.27 gm./generation

## SUMMARY AND CONCLUSION

The effect of different levels of mass selection on the heritability of a primary and correlated trait, and the genetic correlation between the two traits was examined in a random mating population of mice. The selection applied was directional for large six-week body weight or for long six-week tail length. Two levels of selection were applied to each trait. Group A was under 30 percent mass selection for six-week body weight and Group B was under 60 percent mass selection for six-week body weight. Group C and Group D were under 30 percent and 60 percent mass selection for six-week tail length respectively. Group E was a control group with no selection applied. Mating was random over the period of the experiment.

It was found that direct selection has no apparent effect on heritability of the trait selected for, and there was no indication that the heritability of the correlated trait changed to any appreciable extent. The heritability of six-week tail length was found to be higher than the heritability of six-week body weight. It was also found that selection has no apparent effect on genetic correlation between the two traits.

## LITERATURE CITED

- Anderson, R. L. and T. A. Bancroft. 1952. Statistical theory in research. McGraw-Hill Book Co., New York.
- Becker, W. A. 1967. Manual of Procedures in Quantitative Genetics. 2nd Ed. Washington State University Press, Pullman.
- Clayton, G. A., G. R. Knight, J. A. Morris and A. Robertson. 1957. An Experimental Check on Quantitative Genetic Theory III. Correlated Responses. J. Genetics. 55:171.
- Darwin, C. 1875. The Variation of Animals and Plants Under Domestication. 2nd Ed. Murray.
- Dickerson, G. E. 1960. Techniques for research in quantitative animal genetics. Techniques and procedures in animal production research. pp. 56-105. American Society of Animal Production publication.
- Falconer, D. S. 1953. Selection for large and small size in mice. J. Genetics. 51:470.
- Falconer, D. S. 1955. Patterns of response in selection experiments with mice. Cold Spring Harbor Symp. Quant. Biol. 20:178.
- Falconer, D. S. 1960. Introduction to Quantitative Genetics. The Ronald Press Company, New York, N.Y.
- Festing, M. F. and A. W. Nordskog. 1967. Response to selection for body weight and egg weight in chickens. Genetics 55:219.
- Hazel, L. N. 1943. A Genetic Basis for Constructing Selection Indexes. Genetics 28:476.

- Lerrer, L. M. 1958. The Genetic Basis of Selection. John Wiley and Sons Inc., New York, N.Y.
- Lush, J. L. 1948. The Genetic of Populations. (Mimeo).  
Dept. of Animal Science, Iowa State University  
Ames, Iowa.
- MacArthur, J. W. 1949. Selection for small and large body size in the house mouse. *Genetics* 34:194.
- Mode, C. J. and H. F. Robinson. 1959. Pleiotropism and the genetic variance and covariance. *Biometrics* 15:51.
- Parker, R. J., L. D. McGilliard and J. L. Gill. 1969. Genetic Correlation and Response to Selection in Simulated Populations. I. The additive model. *Theoretical and Applied Genetics* 39:365.
- Parker, R. J., L. D. McGilliard and J. L. Gill. 1970a. Genetic Correlation and Response to Selection in Simulated Populations. II. Model of complete dominance. *Theoretical and Applied Genetics* 40:106.
- Parker, R. J., L. D. McGilliard and J. L. Gill. 1970b. Genetic Correlation and Response to Selection in Simulated Populations. III. Correlated response to selection. *Theoretical and Applied Genetics* 40:157.
- Rahnefeld, G. W., R. E. Comstock, M. Singh and S. R. NaPuket. 1966. Genetic Correlation between Growth Rate and Litter Size in Mice. *Genetics* 54:1423.
- Reeve, E. C. R. 1955. The variance of the genetic correlation coefficient. *Biometrics* 11:357.
- Robertson, A. 1959. The sampling variance of the genetic correlation coefficient. *Biometrics* 15:469.

## APPENDIX

Table 1. Analysis of variance in six-week body weight

GROUP	Source of Variation	d.f.	Mean Square	F
A	G	5	319.21	**
	S	80	52.05	*
	D	61	33.70	**
	W	1242	7.70	
B	G	5	165.01	**
	S	78	41.01	N.S.
	D	60	36.78	**
	W	1162	7.21	
C	G	5	507.94	**
	S	79	53.40	N.S.
	D	65	54.44	**
	W	1306	7.06	
D	G	5	211.08	**
	S	77	49.35	**
	D	61	29.68	**
	W	1128	7.64	
E	G	5	173.02	**
	S	78	45.55	N.S.
	D	56	32.98	**
	W	1108	6.78	

G = variance due to differences between generations

S = variance due to differences between sires within generations

D = variance due to differences between dams within sires within generations

W = variance due to differences between full sibs within dams within sires within generations

\*\* (P < 0.01); \* (P < 0.05)

N.S. Not significant

Table 2. Analysis of variance in six-week tail length

GROUP	Source of Variation	d.f.	Mean Square	F
A	G	5	9.11	**
	S	80	1.27	*
	D	61	0.83	**
	W	1242	0.09	
B	G	5	11.70	**
	S	78	2.01	*
	D	60	1.23	**
	W	1162	0.09	
C	G	5	47.33	**
	S	79	1.31	N.S.
	D	65	1.07	**
	W	1306	0.10	
D	G	5	39.50	**
	S	77	0.98	**
	D	61	0.53	**
	W	1128	0.10	
E	G	5	6.77	**
	S	78	1.35	*
	D	56	0.79	**
	W	1108	0.15	

G = variance due to differences between generations

S = variance due to differences between sires within generations

D = variance due to differences between dams within sires within generations

W = variance due to differences between full sibs within dams within sires within generations

\*\* (P < 0.01); \* (P < 0.05)

N.S. Not significant

Table 3. Analysis of covariance in six-week body weight and six-week tail length

GROUP	Source of Variation	d.f.	Mean Cross Product	F
A	G	5	10.20	N.S.
	S	80	5.58	*
	D	61	3.51	**
	W	1242	0.38	
B	G	5	-2.36	N.S.
	S	78	5.10	N.S.
	D	60	4.78	**
	W	1162	0.35	
C	G	5	108.80	**
	S	79	4.45	N.S.
	D	65	5.95	**
	G	1306	0.40	
D	G	5	27.90	**
	S	77	4.35	**
	D	61	2.35	**
	W	1128	0.47	
E	G	5	2.04	N.S.
	S	78	5.99	*
	D	56	3.52	**
	W	1108	0.47	

G = variance due to differences between generations

S = variance due to differences between sires within generations

D = variance due to differences between dams within sires within generations

W = variance due to differences between full sibs within dams within sires within generations

\*\* ( $P < 0.01$ ); \* ( $P < 0.05$ )

N.S. Not significant



Table 4. Analysis of variance in six-week body weight and six-week tail length in Group A.

Generation		d.f.	Body Weight (M.S.)	Tail Length (M.S.)	
2	S	13	67.20	2.95	$k_1 = 8.99$
	D	10	21.36	0.62	$k_2^1 = 9.50$
	W	199	5.78	0.12	$k_3^2 = 15.83$
3	S	13	71.29	0.84	$k_1 = 9.41$
	D	12	35.65	0.57	$k_2^1 = 10.29$
	W	231	7.06	0.08	$k_3^2 = 18.32$
4	S	14	62.69	0.96	$k_1 = 8.52$
	D	9	5.56	0.59	$k_2^1 = 8.46$
	W	180	9.26	0.12	$k_3^2 = 13.47$
5	S	14	43.47	0.65	$k_1 = 9.26$
	D	12	27.17	0.75	$k_2^1 = 9.71$
	W	230	8.69	0.11	$k_3^2 = 17.05$
6	S	12	20.33	0.61	$k_1 = 9.22$
	D	9	71.03	1.87	$k_2^1 = 9.28$
	W	182	9.70	0.09	$k_3^2 = 15.52$
7	S	14	45.30	1.71	$k_1 = 10.04$
	D	9	44.42	0.82	$k_2^1 = 10.21$
	W	220	6.21	0.07	$k_3^2 = 16.10$

Table 5. Analysis of variance in six-week body weight and six-week tail length in Group B.

Generation		d.f.	Body Weight (M.S.)	Tail Length (M.S.)	
2	S	13	40.31	1.57	$k_1 = 8.57$
	D	14	19.24	0.96	$k_2 = 8.85$
	W	216	6.27	0.09	$k_3 = 17.41$
3	S	14	22.30	0.69	$k_1 = 9.46$
	D	8	19.95	1.49	$k_2 = 9.09$
	W	190	6.72	0.09	$k_3 = 13.98$
4	S	14	59.03	1.25	$k_1 = 8.68$
	D	14	49.96	0.66	$k_2 = 8.96$
	W	227	7.84	0.08	$k_3 = 17.03$
5	S	14	26.24	1.46	$k_1 = 8.85$
	D	8	33.98	0.91	$k_2 = 9.11$
	W	185	7.44	0.12	$k_3 = 13.70$
6	S	11	18.28	0.56	$k_1 = 9.61$
	D	7	30.41	1.09	$k_2 = 9.25$
	W	160	8.30	0.09	$k_3 = 14.68$
7	S	12	80.71	2.08	$k_1 = 9.66$
	D	9	66.04	2.80	$k_2 = 9.12$
	W	184	6.94	0.07	$k_3 = 15.66$

Table 6. Analysis of variance in six-week body weight and six-week tail length in Group C.

Generation		d.f.	Body Weight (M.S.)	Tail Length (M.S.)	
2	S	14	37.37	1.13	$k_1 = 9.25$
	D	10	40.76	0.81	$k_2 = 9.07$
	W	204	5.77	0.10	$k_3 = 15.13$
3	S	14	52.32	0.82	$k_1 = 9.32$
	D	12	32.72	0.49	$k_2 = 9.60$
	W	229	6.87	0.08	$k_3 = 16.99$
4	S	12	30.29	1.24	$k_1 = 8.61$
	D	12	38.00	1.23	$k_2 = 9.27$
	W	199	5.94	0.14	$k_3 = 17.17$
5	S	11	48.66	1.77	$k_1 = 9.23$
	D	10	49.47	0.89	$k_2 = 10.04$
	W	191	7.57	0.11	$k_3 = 17.66$
6	S	14	65.24	1.13	$k_1 = 9.76$
	D	10	35.95	0.74	$k_2 = 10.61$
	W	232	8.20	0.10	$k_3 = 17.01$
7	S	14	82.23	1.94	$k_1 = 10.21$
	D	11	129.91	2.29	$k_2 = 10.98$
	W	251	7.79	0.11	$k_3 = 18.39$

Table 7. Analysis of variance in six-week body weight and six-week tail length in Group D.

Generation		d.f.	Body Weight (M.S.)	Tail Length (M.S.)	
2	S	13	40.32	1.17	$k_1 = 9.22$
	D	14	36.61	0.93	$k_2 = 9.41$
	W	233	5.06	0.12	$k_3 = 18.63$
3	S	14	32.45	0.97	$k_1 = 8.35$
	D	10	33.47	0.57	$k_2 = 8.82$
	W	191	7.63	0.08	$k_3 = 14.29$
4	S	14	42.38	1.42	$k_1 = 7.65$
	D	9	13.21	0.39	$k_2 = 7.92$
	W	164	7.53	0.13	$k_3 = 12.43$
5	S	11	62.20	1.00	$k_1 = 8.15$
	D	12	29.88	0.31	$k_2 = 8.57$
	W	177	8.27	0.13	$k_3 = 16.69$
6	S	11	72.39	1.17	$k_1 = 9.90$
	D	7	51.49	0.59	$k_2 = 9.52$
	W	165	9.93	0.10	$k_3 = 15.12$
7	S	14	53.55	0.27	$k_1 = 9.14$
	D	9	13.98	0.30	$k_2 = 9.28$
	W	198	8.38	0.10	$k_3 = 14.66$

Table 8. Analysis of variance in six-week body weight and six-week tail length in Group E.

Generation		d.f.	Body Weight (M.S.)	Tail Length (M.S.)	
2	S	14	80.21	1.94	$k_1 = 8.46$
	D	10	34.32	0.44	$k_2 = 8.73$
	W	191	6.11	0.15	$k_3 = 14.28$
3	S	13	49.36	1.55	$k_1 = 8.56$
	D	12	44.37	1.74	$k_2 = 9.02$
	W	203	9.74	0.36	$k_3 = 16.30$
4	S	12	65.13	2.60	$k_1 = 7.83$
	D	7	17.29	0.35	$k_2 = 8.86$
	W	150	4.46	0.13	$k_3 = 12.99$
5	S	14	28.58	0.63	$k_1 = 8.56$
	D	11	25.86	0.76	$k_2 = 9.18$
	W	206	5.63	0.08	$k_3 = 15.37$
6	S	13	22.61	0.71	$k_1 = 9.75$
	D	7	7.98	0.22	$k_2 = 9.22$
	W	177	8.04	0.08	$k_3 = 13.94$
7	S	12	26.14	0.82	$k_1 = 9.27$
	D	9	56.63	0.75	$k_2 = 9.17$
	W	181	6.11	0.10	$k_3 = 15.47$