THE EFFECTS OF LONG-TERM SELECTION ON GENETIC CORRELATION AND RESPONSE TO SELECTION IN TWO QUANTITATIVE TRAITS IN MICE

BY

ROBERT MICHAEL McKAY

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ABSTRACT

This study examined the effects of long-term selection over 40 generations on genetic correlation and response to selection in two quantitative traits in mice. The two traits were six-week body weight and six-week tail length, both of which are easily measured and expressed in both sexes. Selection was unidirectional for large six-week body weight and long six-week tail length. Initially the mice were subdivided into five groups (A, B, C, D and E) but two groups (B and D) were phased out in generation 21. The three remaining groups, A - 30% selection for six-week body weight, C - 30% selection for six-week tail length, and E - the control, provided the data for this study.

Response to selection, both direct and indirect, for both six-week body weight and six-week tail length, showed significant linear trends, indicating that the selection limits were not reached after 40 generations of selection. Long-term selection had no apparent effect on the relative efficiency of direct selection to indirect selection, i.e. the ratio of direct selection to indirect selection, for six-week body weight, but suggested a decline in relative efficiency for six-week tail length. Direct selection for six-week tail length was the most effective means of improving both six-week body weight and six-week tail length.

Selection had no apparent effect on the genetic correlation but it did result in marked declines in the heritabilities of both traits. The stability of the genetic correlation could have been due to the genetic covariance declining proportional to the square root of the product of the additive variances of both traits. Heritabilities showed greater declines in the correlated traits than in the directly selected traits.

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INTRODUCTION

Genetic correlation is an integral part of selection methods for the improvement of economic traits in livestock. An understanding of the genetic correlation among traits is necessary to predict the response from indirect selection and to combine measurements on different traits into selection indexes to maximize genetic improvement.

Few experiments have been performed to determine the effects of long-term selection on genetic correlation, direct response to selection and correlated response to selection. As a result there is little experimental evidence to provide answers to the following questions:

1) How is genetic correlation affected by selection?
2) How long does a correlated response persist?
3) What is the total correlated response and when is a selection limit reached?

This study examined the effects of long-term selection on the genetic correlation and response to selection in two quantitative traits in mice. The two traits were six-week body weight and six-week tail length, selection was unidirectional upwards, and all matings were random. The heritabilities of the two traits were also of interest in order to determine how selection affects the additive variance of a trait, whether selection was direct or indirect.

REVIEW OF LITERATURE

A genetic correlation between two traits may be defined as the correlation between the genes affecting the traits (Pirchner, 1969), or the ratio of the genetic covariance to the square root of the product of the genetic variances of the two traits. The magnitude of a genetic correlation indicates how well the traits are additively related (Rahnefeld, 1973).

The primary cause of a genetic correlation is pleiotropy, the ability of genes to affect more than one trait. When such genes segregate, simultaneous variation occurs in both traits (Parker *et al*., 1969). The size of a pleiotropic correlation is a result of the net effect of all segregating genes that affect the traits (Falconer, 1960).

Linkage is considered a minor or transient cause of genetic correlation. For it to be a factor, the coupling-repulsion equilibrium must not exist. Lush (1954) summarized the circumstances that would produce such a state of disequilibrium:

1) recent emergence of the population from a cross of divergent strains,
2) increase in the proportion of repulsion combinations due to selection (especially selection for a genetic intermediate), and
3) excess coupling combinations due to positive assortative mating.

However, in the absence of such instances, a correlation arising from linkage would disappear after a few generations of random mating.

Rendel (1963) pointed out that genetic correlations appear if two different characters measure the same thing and when two traits share the same resources of development, whatever these may be, generated by a given group of genes. He speculated that the distribution of these resources might be under genetic control, such that an increase in the portion received by one character would result in a decreased allotment for the second trait, producing a negative correlation. A selection program designed to exaggerate one of the characters may instead act on the total available resources and their distribution. The resultant genetic correlation would be the net effect of two processes:

1) increase in the total resources, generating a positive correlation, and
2) changes in distribution, producing a negative correlation.

Thus, the effect of selection on genetic correlation would depend on whether selection exerted a greater effect on the total resources or the distribution of these resources.

Lush (1954) suggested that an apparent genetic correlation could be produced by different directions and intensities of selection in non-interbreeding sub-groups of a population. Within the sub-groups no genetic correlation would exist but the population as a whole would possess a genetic correlation due to the differences between groups.

Random drift and previous selection are minor factors that tend to affect the magnitude of genetic correlations. Only when the population size is small do the effects of random drift become significant. Lush (1948) observed that for small populations genes drift into fixation or elimination almost equally, whether selection is for them or against them. Previous selection raises the gene frequencies of the selected traits towards unity. Thus, the net effect of random drift and previous selection is the reduction of the genetic covariance between two traits.

Artificial selection applied to one trait generally results in changes in related traits not under selection (Bohren et al., 1966). Such correlated responses can be of the two forms: obligate or facultative (Lerner, 1958). The first type is important when the response results in a decrease in fitness, while the latter type may affect certain characters under one selection program and entirely different traits in another. Knowledge of the genetic correlation and of the heritabilities of the traits allows for a prediction of the correlated response. The reliability of such predictions is affected by (a) small genetic correlations, (b) random drift, which confounds the estimate, and (c) if the genetic correlation is caused, to any large degree, by linkage, this results in the magnitude decreasing due to recombination (Falconer, 1960).

Indirect selection, the selection for some trait other than the desired trait, is perhaps the easiest way of visualizing the use of a genetic correlation. Factors favouring indirect selection over direct selection are:

1) the secondary trait, the trait being directly selected for, has a higher heritability than the desired trait,

2) the genetic correlation between the traits is large,
3) the desired trait is difficult to measure and the secondary trait can be measured precisely, and
4) the desired trait appears in one sex while the secondary character is expressed in both sexes, thus, a higher selection intensity is possible.

Though indirect selection utilizes the genetic correlation, and improvement can be rapid, it is not one of the most common selection methods. Economic performance is affected by many traits and, in order for selection to be effective, several traits must be selected for simultaneously.

The three methods of simultaneous selection are tandem selection, independent culling levels, and the selection index. Tandem selection is the method whereby one trait is selected at a time until it is improved, then the second trait, the third, and so on. This method is the most inefficient (Hazel and Lush, 1943), while the selected trait is making rapid improvement the other traits, at best, would make substantial gains only if the genetic correlations were high and of the appropriate sign. The second process is to cull simultaneously for a variety of traits, but independently of one another. Hazel and Lush (1943) mentioned two problems with this method:

1) heavy culling for one trait limits the amount of culling that can be practiced on the other traits, and

2) a culling level set too high for a trait of low heritability or economic importance, reduces the selection intensity.

To maximize gain the culling levels should be determined by the heritability and the economic importance of the traits and by the proportion required for breeding. Genetic correlations add to the efficiency of this method in that they add to selection intensity by indirect selection. The selection index, however, uses genetic correlations in the most effective way and is the most efficient means of multi-trait selection. The main advantage of the selection index over independent culling levels is that the index provides a total score of the individual's performance for the desired traits and selection is based on these scores. Hence, an individual inferior in one trait but superior in another can still be selected. For uncorrelated traits, the appropriate weights for each trait is proportional to the product of its economic value and heritability (Hazel and Lush, 1943). For correlated traits, the calculation for the "weights" is more complex and is analogous to the problem of multicollinearity in multiple regression. The presence of correlated traits increases the accuracy of the index (Falconer, 1960) and allows for the greatest genetic improvement per unit of time.

In a simple theoretical model, Lerner (1958) demonstrated that simultaneous selection for two correlated traits will eventually result in a negative genetic correlation. The pleiotropic genes affecting both traits in the desired direction will become fixed, thus contributing very little to the genetic covariance or variances of the two traits. Only those pleiotropic genes that affect one trait favourably and the other adversely would be left to contribute to the covariance, hence, a negative genetic correlation would result (Falconer, 1960). The effect of such a correlation is that even though the two traits possess significant additive genetic variance, simultaneous selection results in no response, which is similar to the combined effects of artificial and natural selection (Falconer, 1960).

Falconer (1953) found that the correlated response of tail length to selection for body weight in mice became irregular after the fifth generation. In a related experiment, he selected for both large and small size in mice. The response was asymmetric and ceased after 20 generations (Falconer, 1955). Selection for heavy body weight was less effective than for lighter body weight while the realized heritability remained constant. In a two-way selection experiment designed to test the validity of genetic correlation theory, Falconer (1954) found estimates of the genetic correlation, calculated separately for the two pairs of lines, to be 0.62 and 0.57. His conclusion was that the theoretical treatment of the genetic relationship between the two characters adequately accounted for the correlated responses to selection actually observed.

Reeve and Robertson (1953) studied the genetic correlation between wing and thorax length in *Drosophila melanogaster*. Their findings suggested an agreement between the genetic correlation in the base population and the correlated response from either of the two selected lines over 50 generations. In a similar experiment Clayton *et al*. (1957) examined the genetic correlation between abdominal bristle number and sternopleural bristle number. Reasonable agreement with expected response was observed in the early generations but as selection and the level of inbreeding increased and since the genetic correlation was low, the correlated response became unpredictable.

In a population of Dominant White Rock chickens under multiple objective selection, Friars _et al._ (1962) found no time trend with respect to the heritabilities of the traits but genetic correlations decreased over the 9 years of the study.

On the other hand Rahnefeld _et al._ (1963) found no appreciable decrease in the genetic correlation between growth and litter size in mice over 17 generations of selection.

Rendel (1963) conducted an experiment with _Drosophila melanogaster_ to examine the genetic correlation between the number of scutellar and abdominal bristles. He suggested that a genetic correlation could be either positive or negative depending on the level of expression of the selected trait. Selection for scutellar bristles provides more developmental resources and at low levels of expression the total amount of resources is most important and a positive correlation exists. At high levels of expression the proportion of the resources available to the two bristles types is most important, producing a negative correlation. Selection was expected initially to produce a negative correlation that would become positive with further selection. Total resources for making bristles can be varied and the proportion allocated to the two types of bristles can be varied, the former results in a positive correlation, the latter a negative correlation. The results of his experiment confirmed the hypothesis. In a follow-up study, Young and Sheldon (1965) selected for abdominal bristles, as opposed to Rendel who had selected for scutellar bristles. The results differed from those of Rendel (1963) who had found that the realized genetic correlation between the two types of bristles were consistently positive for scute males and sometimes positive and sometimes negative in the other genotypes, that is, the genetic correlation was negative in scute flies and absent in wild-type flies. Rendel (1963) observed that selection for scutellar bristles led to great changes in total make, the net effect of certain influences (i.e. time of the initiation of the process, rate of bristle growth, etc.) that result in a certain tendency for bristles to be formed, but small changes in the competitive ability of scutellars versus abdominals. Young and Sheldon (1965) noted that selection for abdominal bristles led to little change in make but large differences in competitive ability. In comparing the two experiments Young and Sheldon (1965) stated that their experiment provided more evidence that the effect of selection for one character did not necessarily mirror the effects of selection on a correlated character, and the difference in observed responses might be due to different pathways.

Rasmuson (1964) and Sen and Robertson (1964) both conducted experiments dealing with simultaneous selection for two traits in Drosophila melanogaster. Rasmuson (1964) observed no effect of selection on genetic correlation over 14 generations, but found significant declines in the heritabilities of the two traits, sternopleural and abdominal bristle numbers. Sen and Robertson (1964) found no significant change in either the genetic correlation or the heritabilities of the two traits they studied, the number of bristles on the fifth abdominal sternite and the number of sternopleural bristles on a single side of the fly.

The time taken to exhaust the genetic variance of six-week body weight has been estimated to be between ten and thirty generations in mice (Roberts, 1966). By definition, genetic variance is exhausted when the alleles become fixed. Roberts also noted that there was a pattern of response with artificial selection, that being that progress is made at an ever decreasing rate. He further pointed out that selection for large six-week body weight reached a limit in the region of 30 grams.

In a study that dealt with the genetic correlation between body weight and egg weight in chickens, Festing and Nordskog (1967) found declines in the genetic correlation over six generations of selection. In the downward selected lines, groups C and E selected for low body weight and low egg weight respectively, the decrease was from 0.6 to 0.4-0.5, while in the upward lines, groups B and D, selected for high body weight and high egg weight respectively, the decrease was from 0.6 to 0.2-0.3. Rahnefeld _et al_. (1966) found no significant change in the genetic correlation between growth rate and litter size over 29 generations of selection in mice.

Parker (1966) performed a computer simulation to theoretically evaluate the effect of selection on genetic correlation. The experiment dealt with an additive model, a complete dominance model, and correlated response to selection.

Under the additive model, Parker found that selection would only affect the magnitude of the genetic correlation if the heritability of the selected trait was high (70%). The reduction in the genetic correlation was due to the decrease in the genetic covariance which was not accompanied by a corresponding decrease in genetic variance. More specifically, at low selection levels the genetic covariance and variances were maintained over the 30 generations. At intermediate selection levels, the covariance and the variances decreased proportionately, hence, the genetic correlation remained relatively constant. Only at high levels of selection and heritability was there a distinct decrease in the genetic covariance and variances. Truncation selection of one trait reduced the observed genetic correlation between two traits, a fact that should be considered in any selection scheme, and the amount of reduction was dependent on the heritability.

In the complete dominance model the results were similar to those obtained for the additive model, though in some instances the results were less pronounced. Under this model, the selection had to be intense before it had an effect on genetic correlation. Thus, with more complex genetic arrangements, selection effects would be reduced further.

With respect to correlated response, under the additive model the correlated response was dependent on the genetic correlation between the traits. In the complete dominance model the correlated response was influenced by the selection intensity and the genetic correlation. The same population mechanisms and mode of gene action which affect direct selection response also apply to correlated responses. In the same way change becomes more difficult in selecting a dominant allele as the recessive allele becomes rare, a correlated response in an unselected trait is also difficult to achieve.

Bohren et al. (1966) studied the asymmetry of correlated responses both algebraically and by computer simulation. They found that the greatest asymmetry occurred when the traits were half-way to their selection limit. The length of time required to reach a selection limit and hence display asymmetry depends on the number of genes present. The greater the number of genes present, the longer it takes for asymmetry to develop. Siegal (1962) and Nordskog and Festing (1962) offered explanations for the asymmetry of correlated response. Siegel (1962) suggested the different heritabilities of the two characters while Nordskog and Festing (1962) proposed a differential control of the genetic variance of the two traits. Under certain circumstances Bohren et al. (1966) admitted that these factors may cause asymmetry, but by themselves they would not. They also noted that the genetic covariance between two traits may be even more sensitive to the changes in gene frequency brought about by selection, and to changes due to random sampling when population size was small.

Baker and Cockrem (1970) observed that selection for body weight in mice resulted in a correlated increase in tail length in hot and medium temperatures, while no appreciable correlated response was evident in a cold environment. The genetic correlation between six-week body weight and six-week tail length followed the same pattern, present in the lines selected in the hot and medium temperatures and absent in those selected in the cold environment.

Cheung (1971) found no changes in the genetic correlation and the heritabilities of two traits, six-week body weight and six-week tail length during seven generations of selection for either trait.

Rutledge *et al*. (1973) noted that the genetic correlation may be more powerful than predicted from theory in impeding response during antagonistic selection. They also found no indication of cessation of the linear response in aggregate genotype, and over the short duration of the experiment (7 generations) they observed no change in the genetic correlation.

In an experiment dealing with simultaneous selection for two correlated traits in *Tribolium castaneum*, Bell and Burris (1973) observed declines in the heritabilities of the selected traits due to selection, but no changes were evident in the genetic correlation. They pointed out, that, intuitively, simultaneous selection for two correlated traits would alter the genetic correlation quicker than single trait selection. Current genetic correlation theory relates only to additive gene effects and assumes a linear relationship between them. By changing the frequencies of genes affecting growth and development, their pleiotropic effects become non-linear by switch or modifier genes which maintain some "norm" within the developmental or physiological limits of the organism. The authors contend that the concept of developmental balance via non-linear action appears to be a better explanation for the "stabilized" genetic correlation than the assumption that the declines in genetic variances are due to the change in the frequency of the non-pleiotropic genes.

Falconer (1973) pointed out that the limit to selection for large mice was almost reached after 23 generations of selection. In a later paper Falconer (1976), listed the factors that influence selection limits. These are the number of segregating genes, the magnitude of their effects, and their initial frequencies.

Sheridan and Barker (1974) studied the effects of two-way selection in *Drosophila melanogaster*. Their findings indicated that changes in the genetic correlation between the third coxal and sternopleural bristle numbers were variable and unpredictable. Nonetheless, they concluded that the average realized genetic correlations did not decrease with simultaneous selection for both traits in the same direction.

To assess the relationship between the theory of genetic correlation and the effects of selection with known experimental evidence, it is evident that more research is required. Discrepancies exist between experiments, possibly indicating some underlying factors are not being considered, and there have been few long-term selection experiments conducted. To improve upon the existing knowledge of genetic correlation a total re-evaluation of the concept is required. More specifically, research is required to determine whether or not the genetic correlation provides an accurate estimate of the genetic covariance. To accomplish this, possibly *Drosophila melanogaster* can provide the answers regarding the mechanism behind pleiotropic genes. With respect to the effects of long-term selection on genetic covariance, more comprehensive experiments are required with sufficient numbers to ensure accurate measurements of traits that are closely related and can be precisely measured.

MATERIALS AND METHODS

Breeding Stock

The data for this thesis were generated from a long-term experiment designed to examine the effect of selection on heritability and genetic correlation. The initial seven generations of selection were analyzed and reported by Cheung (1971). This thesis will report on the analysis of the data from generations nine to 40, inclusive.

The mice originated from the Agriculture Canada Research Station at Lacombe, Alberta and were based on eight inbred strains which had been combined through crossing and random mating without selection as a random mating population for 20 generations (Cheung and Parker, 1974).

Initially the mice were separated into five groups: A- 30% selection for increased six-week body weight, B- 60% selection for increased six-week body weight, C- 30% selection for increased six-week tail length, D- 60% selection for increased six-week tail length, and E- no selection, the control group. At generation 21 groups B and D were phased out and this thesis deals with groups A, C, and E. The two traits, six-week body weight and six-week tail length, are both quantitative, easily measured, and expressed in both sexes. Falconer (1960) reported that the genetic correlation between the two traits is 0.59 with heritabilities of 0.35 and 0.60 for six-week body weight and six-week tail length, respectively.

Mating and Selection Scheme

Parent population size was kept constant at 15 males and 30 females each generation, except in group C from generation 36 to generation 40 where parent population size was increased to 20 males and 40 females.[1] This increase resulted in a decrease in intensity of selection in group C from generation 36 to generation 40. The mating ratio was two females per male and the breeding period lasted 10 days. The females were then placed in separate cages and upon littering the number of offspring born were counted. The mice were weaned at four weeks and body weight, to the nearest hundredth of a gram, and tail length, to the nearest tenth of a centimeter, were measured at six weeks of age.

For the two groups under selection 75 males and 75 females were randomly selected from each group and ranked according to individual performance for the specific trait. Of these, the top 15 males and 30 females were selected to be the parents of the next generation. Where 75 males and/or females were not available, the number of individuals available was used. The effect was to reduce the intensity of selection applied to the traits. The proportion saved and the intensity of selection achieved in each generation are listed in Tables I and II in the Appendix. In the control group (E), 15 males and 30 females were chosen at random and mated at random to produce the next generation. Throughout the experiment the mice were housed in an airconditioned laboratory, with a temperature range of $20^{\circ}C$ to $21^{\circ}C$, and fed standard laboratory rodent feed.[2] The data were collected by one technician.

The data were pooled into blocks of eight generations to provide sufficient numbers (greater than 1000) for reliable estimates of

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[1] The numbers of females and males were increased to offset declining litter size.

[2] Purina Laboratory Chow, Ralston Purina Company. Approximate analyses and ingredients are listed in Appendix Table III.

Table 1. Block size and weighted mean selection intensity for each block in each group

Group	Block	Generation Cycles	Number of observations	Weighted mean selection intensity[1]
A	1	9-16	1605	1.169
	2	17-24	1593	1.093
	3	25-32	1374	1.169
	4	33-40	1269	1.150
C	1	9-16	1842	1.169
	2	17-24	1891	1.140
	3	25-32	1425	1.159
	4	33-40	1175	0.981
E	1	9-12,14,15 [2]	1291	---
	2	19-24 [2]	1363	---
	3	25-32	1394	---
	4	33-40	1336	---

[1] In standard deviations for six-week body weight (gm) or six-week tail length (cm) respectively.

[2] Data from generations 13, 16, 17, 18 in group E were unavailable for analysis.

genetic parameters. The number of observations per block and the weighted mean selection intensity are shown in Table 1 for each of the three groups.

Statistical Analysis

The analyses of variance and covariance were performed separately for both sexes, but since the error variances were homogenous the results were pooled and only results from both sexes are reported. Analyses were conducted on all blocks and on all generations in the three groups. Heritabilities, genetic and phenotypic correlations were estimated by the following methods:

a) Regression Analysis

Heritability estimates were obtained by regressing the litter mean on the midparent value for both six-week body weight and six-week tail length. Realized heritabilities were estimated from the regression of cumulative response on cumulative selection differential. The analysis may be generalized by the following:

$$b = \frac{\Sigma xy}{\Sigma x^2}$$

where, b is the heritability

Σxy is the corrected sum of cross products for midparent value (X) and litter mean value (Y)

Σx^2 is the corrected sum of squares for the midparent values (X)

The standard error of the heritability estimate, from Becker (1967), was determined by:

$$\text{S.E. (b)} = \sqrt{\frac{\text{MS(DEV)}}{\Sigma x^2}}$$

where, MS(DEV) is the estimate of the variance of the regression.

Σx^2 is the corrected sum of squares for the midparent values (X)

For realized heritability:

$$b = \frac{\Sigma xy}{\Sigma x^2}$$

where, b is the realized heritability

Σxy is the corrected sum of cross products for cumulative selection differential values (X) and cumulative response values (Y)

Σx^2 is the corrected sum of squares for the cumulative selection differential values (X)

The standard error of the realized heritability estimate was determined by:

$$\text{S.E. (b)} = \sqrt{\frac{\text{MS(DEV)}}{x^2}}$$

where, MS(DEV) is the estimate of the variance of the regression

Σx^2 is the corrected sum of squares of the cumulative selection differential values (X)

b) Analysis of variance and covariance

Components of variance and covariance were estimated from the analyses of variance and covariance by procedures outlined in Becker (1967). Heritability was estimated by:

$$h^2 = \frac{4\,\hat{\sigma}^2_S}{\hat{\sigma}^2_P}$$

where, h^2 is the heritability

$\hat{\sigma}^2_s$ is the estimate of the sire component of variance and is equivalent to one quarter of the additive genetic variance.

$\hat{\sigma}^2_p$ is the total phenotypic variance

The standard error of the heritability estimate is given by the following formula (Becker, 1967):

$$\text{S.E. } (h^2) = \frac{4\sqrt{\text{var } (\hat{\sigma}^2_s)}}{\hat{\sigma}^2_p}$$

where, $\hat{\sigma}^2_p$ is the phenotypic variance

$$\text{var } (\hat{\sigma}_s) = \frac{2}{k_3^2}\left[\frac{\text{M.S. sire}}{\text{d.f. sire} + 2} + \frac{\text{M.S. dam}}{\text{d.f. dam} + 2}\right]$$

k_3 is the coefficient for the sire component of variance

M.S. sire is the mean square for the sire line in the analysis of variance.

M.S. dam is the mean square for the dam line in the analysis of variance.

d.f. sire are the degrees of freedom for the sire line in the analysis of variance.

d.f. dam are the degrees of freedom for the dam line in the analysis of variance.

The genetic correlation was calculated by a product-moment correlation, using the sire component of covariance and the sire component of variance for both traits, in the following generalized form:

$$r_G = \frac{\mathrm{cov}_{xy}}{\sqrt{\hat{\sigma}_x^2 \, \hat{\sigma}_y^2}}$$

where, r_G is the genetic correlation

cov_{xy} is the estimate of sire component of covariance for six-week body weight (X) and six-week tail length (Y)

$\hat{\sigma}_x^2$ is the estimate of sire component of variance for six-week body weight

$\hat{\sigma}_y^2$ is the estimate of sire component of variance for six-week tail length

The standard error of the genetic correlation was determined by the following formula (Mode and Robinson, 1959):

$$\mathrm{S.E.}\ (r_G) = \sqrt{\mathrm{var}\ (r_G)}$$

where, $$\mathrm{var}\ (r_G) \simeq r_G^2 \left[\frac{\mathrm{var}\ (\mathrm{cov}_s)}{\mathrm{cov}_s^2} + \frac{\mathrm{var}\ (\hat{\sigma}^2_{s(x)})}{4\ (\hat{\sigma}^2_{s(x)})^2} + \frac{\mathrm{var}\ (\hat{\sigma}^2_{s(y)})}{4\ (\hat{\sigma}^2_{s(y)})^2} - \right.$$

$$\frac{\mathrm{cov}\ (\hat{\sigma}^2_{s(x)},\ \mathrm{cov}_s)}{\hat{\sigma}^2_{s(x)}\ \mathrm{cov}_s} - \frac{\mathrm{cov}\ (\hat{\sigma}^2_{s(y)},\ \mathrm{cov}_s)}{\hat{\sigma}^2_{x(y)}\ \mathrm{cov}_s} +$$

$$\left. \frac{\mathrm{cov}\ (\hat{\sigma}^2_{s(x)},\ \hat{\sigma}^2_{s(y)})}{2\hat{\sigma}^2_{s(x)}\ \hat{\sigma}^2_{s(y)}} \right]$$

where, r_G is the estimate of the genetic correlation coefficient

cov_s is the estimate of the sire component of covariance

$\hat{\sigma}^2_{s(x)}$ is the estimate of the sire component of variance for six-week body weight

$\hat{\sigma}^2_{s(y)}$ the estimate of sire component variance for six-week tail length

The phenotypic correlation was calculated using the following formula modified from Becker (1967):

$$r_p = \frac{\mathrm{cov}_w + \mathrm{cov}_s + \mathrm{cov}_d}{\sqrt{\hat{\sigma}^2_{p(x)}\ \hat{\sigma}^2_{p(y)}}}$$

where, r_p is the estimate of the phenotypic correlation

cov_w is the estimate of the covariance between six-week body weight and six-week tail length for full sibs

cov_s is the estimate of the sire component of covariance for six-week body weight and six-week tail length

cov_d is the estimate of dam component of covariance for six-week body weight and six-week tail length

$\hat{\sigma}^2_{p(x)}$ is the estimate of the phenotypic variance for six-week body weight

$\hat{\sigma}^2_{p(y)}$ is the estimate of the phenotypic variance for six-week tail length

c) The Arithmetic and Geometric Methods

These methods were modified from Becker (1967) in that midparent and litter mean values were used instead of sire and offspring values.

(i) The Arithmetic Method:

$$r_G = \frac{cov_{x_1z_2} + cov_{x_2z_1}}{2\sqrt{cov_{x_1z_1} \quad cov_{x_2z_2}}}$$

where, r_G is the estimate of the genetic correlation

$cov_{x_1z_2}$ is the estimate of covariance of midparent six-week weight and litter mean six-week tail length

$cov_{x_2z_1}$ is the estimate of covariance of midparent six-week tail length and litter mean six-week body weight

$\mathrm{cov}_{x_1z_1}$ is the estimate of covariance of midparent six-week body weight and litter mean six-week body weight

$\mathrm{cov}_{x_2z_2}$ is the estimate of covariance of midparent six-week tail length and litter mean six-week tail length

The standard error of the genetic correlation by the arithmetic method was determined by (Becker, 1967):

$$\mathrm{S.E.}\ (r_G) = \frac{1 - r_G^2}{\sqrt{2}} \sqrt{\frac{\mathrm{S.E.}\ (h_1^2)\ \mathrm{S.E.}\ (h_2^2)}{h_1^2\ h_2^2}}$$

where, r_G is the estimate of genetic correlation

S.E. (h_1^2) is the standard error of the heritability estimate for six-week body weight

h_1^2 is the heritability of six-week body weight from midparent regression

S.E. (h_2^2) is the standard error of the heritability estimate for six-week tail length

h_2^2 is the heritability of six-week tail length from midparent regression

(ii) Geometric Method

$$r_G = \sqrt{\frac{\mathrm{cov}_{x_1z_2}\ \ \mathrm{cov}_{x_2z_1}}{\mathrm{cov}_{x_1z_1}\ \ \mathrm{cov}_{x_2z_2}}}$$

all terms as previously defined.

d) Realized Genetic Correlation

It was assumed that the two selected groups experienced the same level of selection intensity, hence the following formula was used (Falconer, 1960):

$$r_G^2 = \frac{CR_x \; CR_y}{R_x \; R_y}$$

where, r_G is the estimate realized genetic correlation

CR_x is the correlated response in six-week body weight in group C

CR_y is the correlated response in six-week tail length in group A

R_x is the direct response in six-week body weight in group A

R_y is the direct response in six-week tail length in group C

Estimations were made in consecutive eight generation groups, i.e. generations 9-16, generations 10-17, and so on to generations 33-40. This was done to more precisely determine the effect of selection on genetic correlation.

RESULTS AND DISCUSSION

Response to Selection

a) Six-week body weight

Midparent and offspring phenotypic means and standard errors are contained in Table 2, deviations from the control group (for the offspring values only) are in Table 4. The regression analyses for offspring mean on generation number and for the deviations from the control on generation number are presented in Tables 3 and 5, respectively. The graphs of offspring means and deviations from the control mean are presented in Figures 1 and 2, respectively.

The results indicate that group A, directly selected for six-week body weight, showed the greatest upwards response; group C, indirectly selected for six-week body weight, displayed a lower but significant upward response; group E, the control, showed a significant decline in performance. The rates of gain in six-week body weight, indicated by the slope of the regression line for generation mean response on generation number, for the three groups suggest that the response in group A is twice that in group C (0.35 ± 0.06 gm/generation in group A and 0.18 ± 0.05 gm/generation in group C) while in group E inbreeding depression and random drift probably accounts for the -0.14 ± 0.05 gm/generation decline. The results in the two selected groups agree with the results of Cheung (1971), who noted that the response in group C was comparable to the response in group B (under 60% selection for large six-week body weight). Though Cheung (1971) did not observe a decline in group E, it should be noted that he dealt with only seven

Table 2. Means and standard errors for six-week body weight (gm) for generations 9-40

Generation	Group A		Group C		Group E	
	Midparent	Offspring	Midparent	Offspring	Midparent	Offspring
9	28.23±0.18	27.99±0.21	28.42±0.22	26.64±0.26	23.55±0.65	24.29±0.23
10	30.88±0.22	29.26±0.26	28.80±0.38	29.17±0.25	25.71±0.28	24.84±0.24
11	32.93±0.35	26.92±0.24	30.57±0.31	24.68±0.26	25.00±0.38	21.91±0.26
12	30.12±0.18	28.49±0.23	27.77±0.36	26.61±0.25	---	24.17±0.24
13	31.88±0.32	29.77±0.29	28.87±0.59	27.48±0.29	---	---
14	34.23±0.46	33.00±0.31	30.32±0.68	28.07±0.27	---	22.61±0.26
15	35.42±0.25	27.67±0.35	30.20±0.23	27.67±0.25	---	24.19±0.22
16	32.46±0.26	28.75±0.30	29.61±0.38	25.21±0.24	---	---
17	33.11±0.30	28.16±0.43	27.95±0.44	25.87±0.28	---	---
18	33.48±0.34	28.25±0.78	29.73±0.41	26.87±0.31	---	---
19	33.56±0.47	28.11±0.39	30.93±0.41	25.02±0.33	---	19.01±0.32
20	33.69±0.19	25.64±0.40	29.13±0.36	24.92±0.35	20.43±0.88	16.71±0.26
21	32.21±0.23	24.57±0.31	28.25±0.30	29.60±0.22	17.46±0.36	21.03±0.17
22	35.63±0.43	30.62±0.49	31.55±0.35	29.84±0.31	20.73±0.37	20.36±0.26
23	34.41±0.59	30.55±0.52	32.01±0.50	27.02±0.37	21.27±0.36	18.51±0.36
24	35.02±0.41	35.45±0.48	31.02±0.40	30.45±0.28	20.23±0.36	23.25±0.16
25	41.57±0.36	34.69±0.41	34.09±0.42	30.35±0.33	23.05±0.29	20.78±0.23
26	34.02±0.16	29.88±0.38	33.67±0.39	25.92±0.42	21.00±0.46	15.65±0.40
27	35.56±0.28	32.36±0.40	31.62±0.45	27.40±0.35	17.81±0.46	18.21±0.41
28	35.98±0.18	35.93±0.33	31.33±0.44	33.51±0.37	19.02±0.41	24.61±0.24
29	41.54±0.38	32.34±0.39	36.28±0.38	28.42±0.39	24.64±0.44	18.99±0.34
30	37.18±0.30	30.00±0.47	33.40±0.37	26.59±0.44	19.86±0.44	17.06±0.39
31	35.48±0.34	34.29±0.35	30.97±0.32	30.40±0.56	18.78±0.32	19.81±0.26
32	39.14±0.24	39.99±0.44	34.63±0.61	32.38±0.57	20.34±0.25	23.53±0.28
33	44.72±0.27	33.14±0.42	37.21±0.41	28.72±0.37	23.39±0.32	18.94±0.32
34	39.24±0.28	28.60±0.45	33.68±0.64	24.26±0.44	20.29±0.32	17.22±0.35
35	34.59±0.34	34.60±0.42	28.96±0.48	29.76±0.33	17.92±0.35	19.29±0.24
36	39.44±0.27	39.97±0.49	32.05±0.34	33.46±0.33	19.72±0.36	21.86±0.26
37	43.65±0.30	39.46±0.42	35.71±0.41	32.75±0.36	22.79±0.29	19.76±0.28
38	44.49±0.33	35.52±0.48	35.45±0.30	29.90±0.40	21.30±0.42	17.05±0.37
39	41.74±0.31	35.96±0.45	31.66±0.57	30.64±0.45	18.61±0.32	17.68±0.23
40	41.41±0.29	42.92±0.47	33.95±0.42	36.15±0.37	18.64±0.32	23.02±0.32
b[1]		0.35±0.06		0.18±0.05		-0.14±0.05

[1] Regression of offspring mean on generation number.

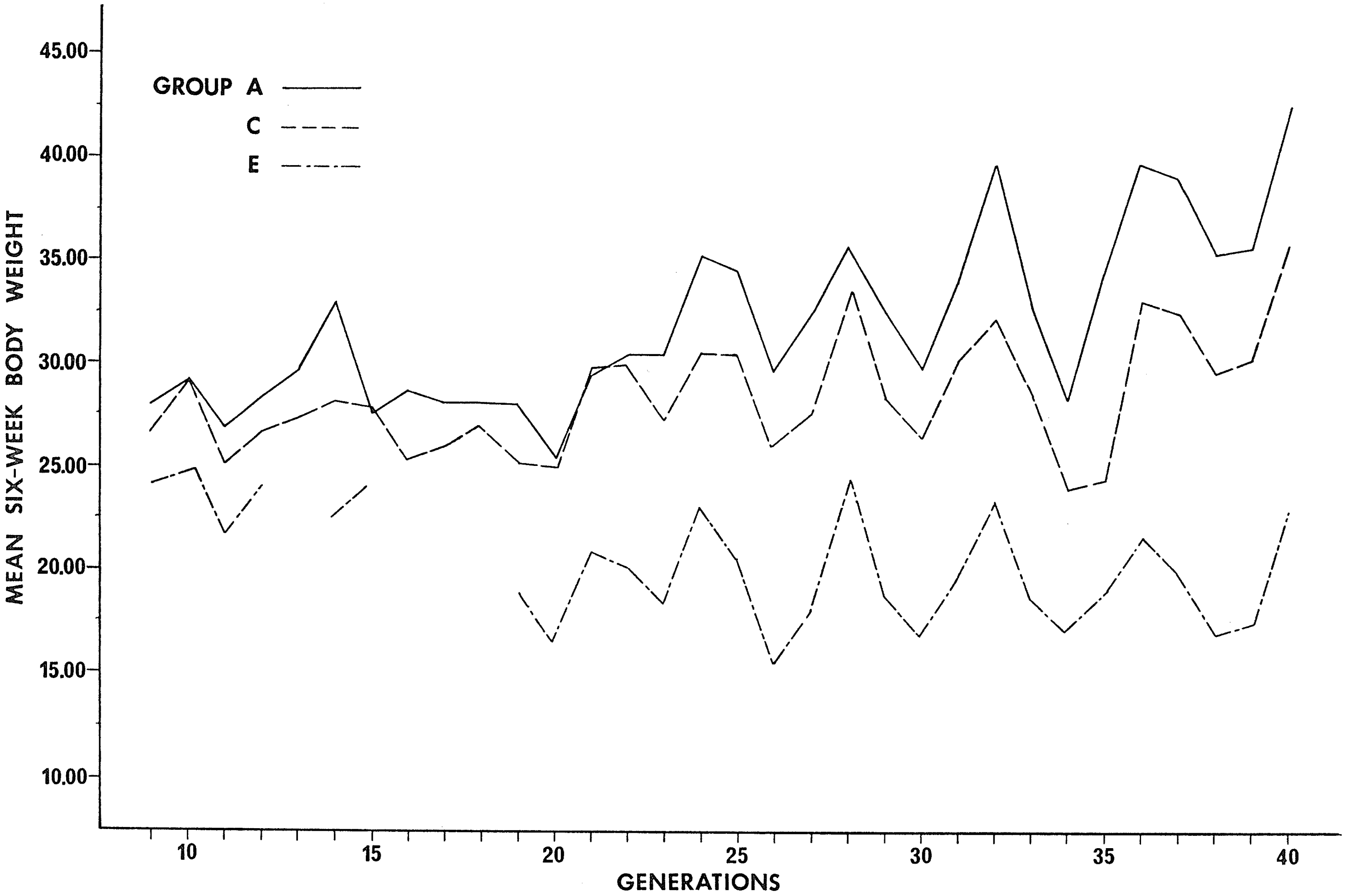

Figure 1. Generation means for six-week body weight (gm) for groups A, C and E.

generations of selection, hardly enough time for inbreeding depression and/or random drift to become evident.

With respect to the midparent values, they appear to be parallel to the offspring values in groups A and E, suggesting that the selection applied in group A and lack of it in group E remained constant throughout the 40 generations of selection. In group C the midparent and offspring values appear to be converging, probably due to the decrease in selection intensity from generations 36 through 40 (Appendix Table II).

The regression analysis performed on offspring mean and generation number showed that only the linear components were significant ($\alpha = 0.01$) but the coefficients of determination (R^2) were relatively low, thus reducing the predictive value of these regressions.

Deviations from the control group were used to eliminate the effects of common environment and inbreeding (assuming that the rate of inbreeding was the same in all groups). The adjusted rates of change, from the regression of deviations from the control on generation number, were 0.48 ± 0.04 gm/generation and 0.31 ± 0.03 gm/generation for groups A and C, respectively. Instead of direct selection for six-week body weight being twice as effective as indirect selection, as indicated previously by the offspring values, it is actually only 1.55 times more effective. These results were quite similar to those of Cheung and Parker (1974), who dealt with the first 14 generations of selection in this experiment. They found that direct selection was 1.51 times more effective than indirect selection for six-week body weight. This could suggest that selection has little effect on the effectiveness of direct

Table 3. Partitioning of the sums of squares due to regression into linear and quadratic components - six-week body weight

Group A

Source	d.f.	M.S.	F		R^2
Linear	1	335.05	42.14	**	56.82
Quadratic	1	23.96	3.01	N.S.	
Deviations	29	7.95			

Group C

Source	d.f.	M.S.	F		R^2
Linear	1	92.35	16.70	**	34.99
Quadratic	1	11.14	2.01	N.S.	
Deviations	29	5.53			

Group E

Source	d.f.	M.S.	F		R^2
Linear	1	45.35	8.00	**	21.81
Quadratic	1	20.67	3.65	N.S.	
Deviations	25	5.67			

N.S. - Not significant

* - Significant at = 0.05

** - Significant at = 0.01

Table 4. Deviations from the control group for six-week body weight (gm) for groups A and C

Cycle	Group A	Group C
9	3.70	2.35
10	4.42	4.33
11	5.01	2.77
12	4.32	2.44
13	-	-
14	10.39	5.46
15	3.48	3.48
16	-	-
17	-	-
18	-	-
19	9.10	6.01
20	8.93	8.21
21	8.49	8.57
22	10.26	9.48
23	12.04	8.51
24	12.20	7.20
25	13.91	9.57
26	14.23	10.27
27	14.15	9.19
28	11.32	8.90
29	13.35	9.43
30	12.94	9.53
31	14.48	10.59
32	16.46	8.85
33	14.20	9.78
34	11.38	7.04
35	15.31	10.47
36	18.11	11.60
37	19.70	12.99
38	18.47	12.85
39	18.28	12.96
40	19.90	13.13
b[1]	0.48±0.04	0.31±0.03

[1] The regression of deviations from the control group on generation number.

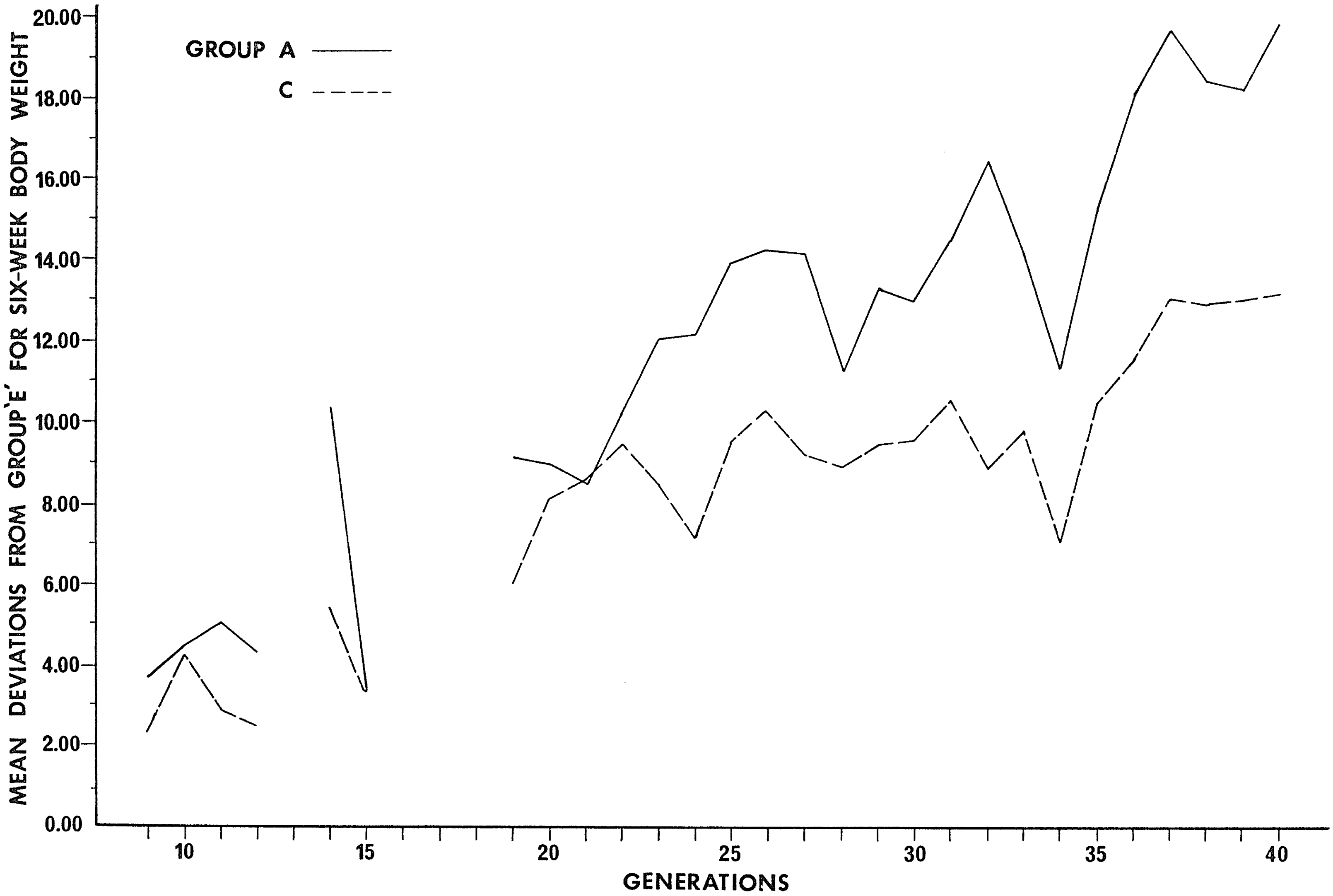

Figure 2. Mean deviations from the control group for six-week body weight (gm) for groups A and C.

Table 5. Partitioning of the sums of squares due to regression into linear and quadratic components for deviations from the control group - six-week body weight

		Group A				Group C			
Source	d.f.	M.S.	F		R^2	M.S.	F		R^2
Linear	1	557.69	166.97	**	86.96	230.30	130.85	**	83.14
Quadratic	1	0.04	0.01	N.S.		2.66	1.51	N.S.	
Deviations	25	3.34				1.76			

selection to indirect selection for six-week body weight.

The results of the regression analysis performed on deviations from the control and generation number indicated that only the linear component was significant ($\alpha = 0.01$) for both selected groups. The coefficients of determination were very large (greater than 80%), indicating the predictive value of these regressions.

These results suggest that the selection limit for large six-week body weight has not been reached after 40 generations of selection in either group A or C. These results are contrary to the conclusions of Roberts (1966), who suggested that selection limits for upward selection for six-week body weight would be reached by 30 generations of selection and mice at the selection limit would weigh approximately 30 grams (the average six-week body weight in generation 40 was 42.92 grams).

b) Six-week tail length

Midparent and offspring phenotypic means and standard errors are contained in Table 6 and deviations from the control group (for the offspring values only) are in Table 8. The regression analyses for offspring mean on generation number and for the deviations from the control on generation number are presented in Tables 7 and 9, respectively. The graphs of offspring means and deviations from the control are presented in Figures 3 and 4, respectively.

The offspring results indicated that group C, directly selected for six-week tail length, showed the greatest upwards response; group A, indirectly selected for six-week tail length, displayed a marginal, but non-significant, upwards response; group E, the control,

Table 6. Means and standard errors for six-week tail length (cm) for generations 9-40

Generation	Group A		Group C		Group E	
	Midparent	Offspring	Midparent	Offspring	Midparent	Offspring
9	9.10±0.01	8.91±0.03	9.92±0.03	9.90±0.05	9.02±0.04	8.63±0.03
10	9.20±0.05	8.71±0.03	10.49±0.05	9.97±0.06	8.91±0.06	8.35±0.04
11	8.83±0.05	8.63±0.03	10.64±0.05	9.87±0.05	8.36±0.09	8.31±0.03
12	8.90±0.05	8.57±0.03	10.59±0.04	10.23±0.04	---	8.64±0.03
13	8.86±0.05	9.27±0.10	11.32±0.40	11.03±0.05	---	---
14	9.86±0.04	9.27±0.03	11.81±0.07	11.50±0.04	---	8.74±0.03
15	9.93±0.05	8.96±0.06	11.72±0.06	11.00±0.04	---	8.76±0.04
16	9.50±0.04	8.80±0.05	11.61±0.04	10.78±0.04	---	---
17	9.19±0.04	8.78±0.06	11.37±0.07	11.10±0.05	---	---
18	9.28±0.04	8.83±0.05	11.92±0.03	11.24±0.08	---	---
19	9.34±0.07	8.92±0.07	12.13±0.03	11.08±0.07	---	8.53±0.05
20	9.49±0.06	8.17±0.05	12.12±0.05	10.95±0.05	8.71±0.09	7.84±0.04
21	8.80±0.04	8.45±0.06	11.62±0.03	11.93±0.22	7.91±0.05	8.34±0.01
22	9.09±0.06	8.51±0.08	12.22±0.04	11.52±0.08	8.29±0.06	8.45±0.06
23	8.77±0.08	8.05±0.07	12.15±0.06	11.14±0.06	8.54±0.05	7.57±0.12
24	8.56±0.07	9.17±0.07	11.85±0.04	12.14±0.06	7.98±0.07	8.92±0.02
25	9.67±0.05	8.76±0.06	12.97±0.04	12.09±0.05	8.93±0.05	8.42±0.06
26	9.12±0.05	8.40±0.04	12.81±0.03	11.51±0.17	8.45±0.08	7.02±0.11
27	8.90±0.03	9.25±0.06	12.97±0.03	12.34±0.09	7.64±0.07	8.16±0.13
28	9.48±0.07	9.58±0.03	13.21±0.04	13.26±0.12	8.48±0.08	9.19±0.08
29	9.95±0.06	8.82±0.06	14.07±0.04	12.42±0.07	9.26±0.05	8.00±0.11
30	9.27±0.06	8.68±0.09	13.41±0.04	12.25±0.09	8.35±0.11	7.66±0.14
31	9.27±0.06	9.26±0.04	13.24±0.02	12.46±0.25	8.16±0.06	8.36±0.03
32	9.68±0.05	9.07±0.07	13.78±0.03	12.71±0.17	8.37±0.05	8.41±0.06
33	9.43±0.03	9.27±0.07	13.62±0.03	12.76±0.16	8.45±0.06	8.18±0.11
34	9.71±0.05	8.55±0.10	13.89±0.04	12.02±0.20	8.54±0.05	7.70±0.12
35	9.22±0.06	9.34±0.09	13.29±0.05	13.35±0.05	8.04±0.07	8.33±0.04
36	4.76±0.04	8.82±0.08	13.83±0.03	12.85±0.15	8.37±0.05	7.85±0.04
37	9.06±0.05	9.16±0.04	13.65±0.05	13.44±0.14	7.97±0.04	7.90±0.07
38	9.38±0.04	8.95±0.09	14.10±0.06	12.92±0.22	8.11±0.06	7.49±0.11
39	9.61±0.05	9.24±0.06	13.83±0.04	13.26±0.21	7.87±0.05	7.89±0.07
40	9.69±0.04	9.59±0.22	14.23±0.04	13.96±0.10	8.06±0.05	8.23±0.09
b[1]		0.01±0.01		0.11±0.01		-0.02±0.01

[1] Regression of offspring mean on generation number.

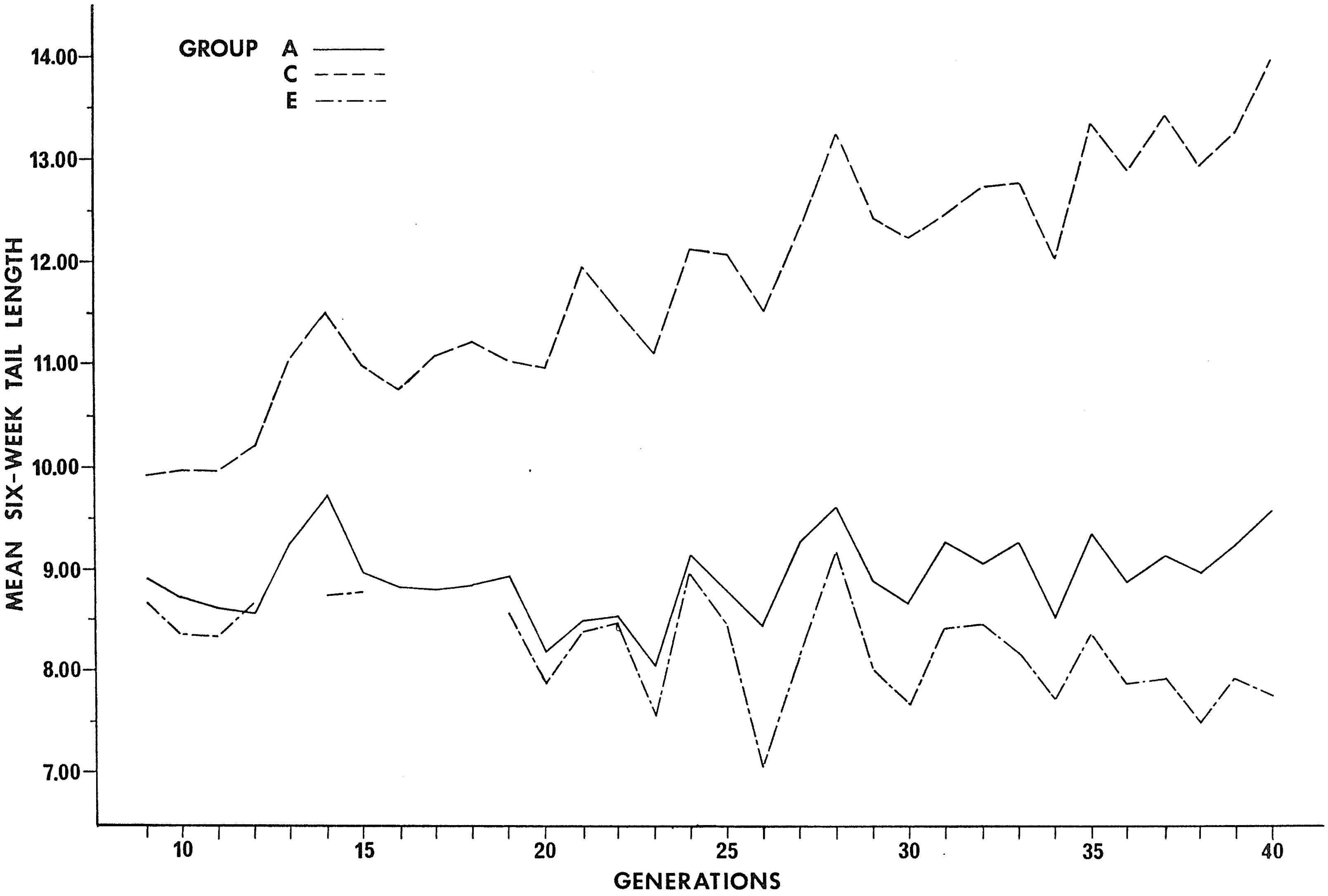

Figure 3. Generation means for six-week tail length (cm) for groups A, C and E.

showed a significant decline in criteria. The rates of gain were 0.11 ± 0.01 cm/generation in group C, 0.01 ± 0.01 cm/generation in group A. The -0.02 ± 0.01 cm/generation decline in group E was probably due to inbreeding depression and random drift. The results suggest that only group C showed an effective response to selection for six-week tail length, while group A seemed unaltered by selection for six-week body weight. These results were similar to those attained by Cheung (1971) who noted a response in group C, little or no response in group A, and no change in group E.

The midparent results indicated that in groups A and E they are parallel to the offspring results. This suggests that the selection applied in group A and the lack of it in group E remained constant over the 40 generations of selection. In group C the midparent and offspring values appear to be converging. This result is probably due to the decrease in selection intensity from generations 36 to 40 (Appendix Table II).

The regression analysis performed on offspring mean and generation number demonstrated that only groups C and E showed significant linear associations between generation means and generation number. However, only group C had a sufficiently large coefficient of determination for the regression to have a predictive value. These results would suggest that the correlated response for tail length in group A had ceased and only the direct response to selection for tail length persisted.

The deviations from the control group showed that the adjusted rates of change were 0.13 ± 0.01 cm/generation for group C and 0.04 ±

Table 7. Partitioning of the sums of squares due to regression into linear and quadratic components - six-week tail length

Group A

Source	d.f.	M.S.	F		R^2
Linear	1	0.41	2.93	N.S.	--
Quadratic	1	0.42	3.00	N.S.	
Deviations	29	0.14			

Group C

Source	d.f.	M.S.	F		R^2
Linear	1	32.77	192.76	**	86.76
Quadratic	1	0.09	0.53	N.S.	
Deviations	29	0.17			

Group E

Source	d.f.	M.S.	F		R^2
Linear	1	1.15	6.05	*	18.67
Deviations	26	0.19			

Table 8. Deviations from the control group for six-week tail length (cm) for groups A and C

Cycle	Group A	Group C
9	0.28	1.27
10	0.36	1.62
11	0.32	1.56
12	-0.07	1.59
13	-	-
14	0.98	2.76
15	0.20	2.24
16	-	-
17	-	-
18	-	-
19	0.39	2.55
20	0.33	3.11
21	0.11	3.59
22	0.06	3.07
23	0.48	3.57
24	0.25	3.22
25	0.34	3.67
26	1.38	4.49
27	1.09	4.18
28	0.39	4.07
29	0.82	4.42
30	1.02	4.59
31	0.90	4.10
32	0.66	4.30
33	1.09	4.58
34	0.85	4.32
35	1.01	5.01
36	0.97	5.00
37	1.26	5.54
38	1.46	5.43
39	1.35	5.37
40	1.36	5.73
b[1]	0.04±0.01	0.13±0.01

[1] Regression of deviations from the control on generation number.

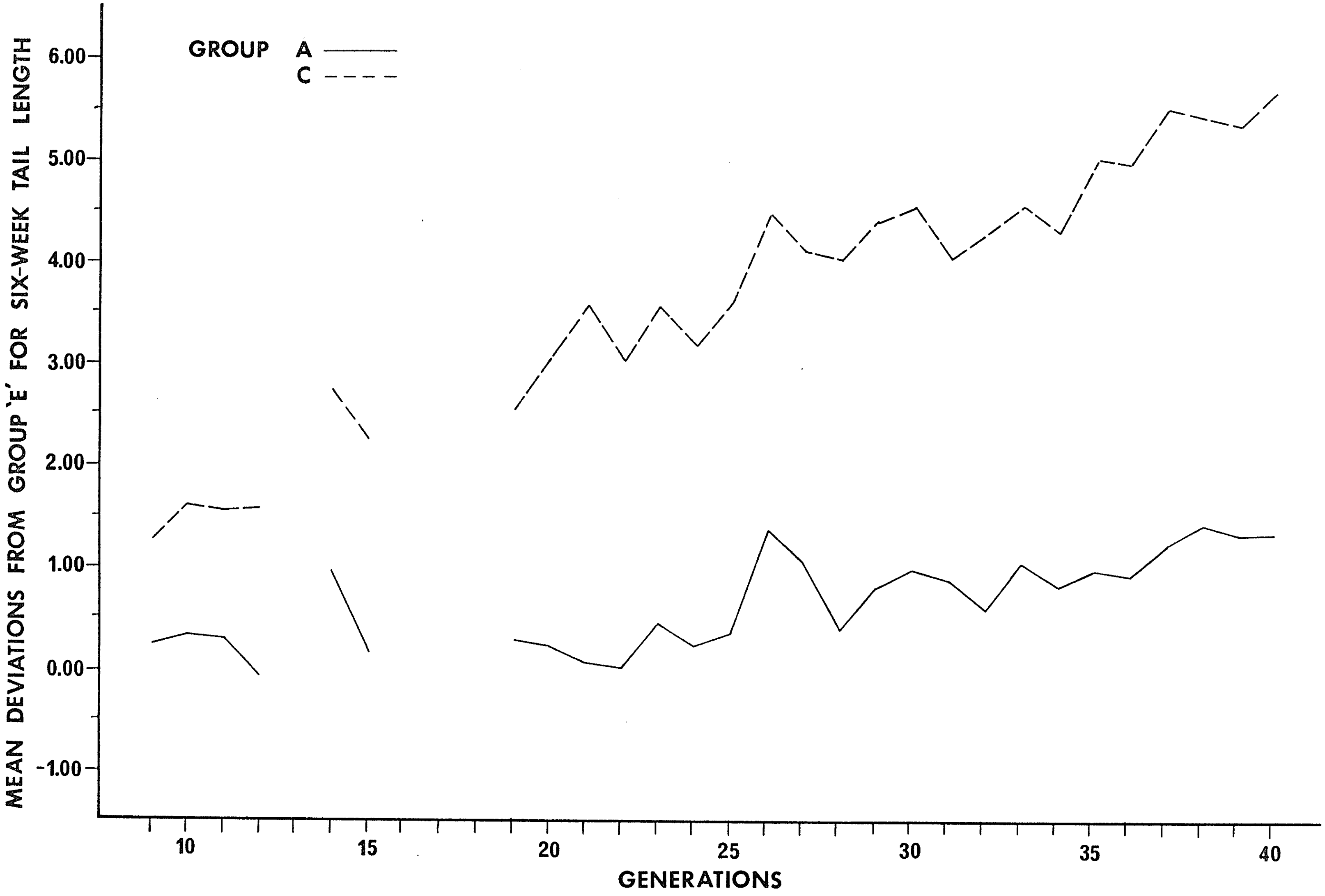

Figure 4. Mean deviations for six-week tail length (cm) for groups A and C.

Table 9. Partitioning of the sums of squares due to regression into linear and quadratic components for deviations from the control group - six-week tail length

		Group A				Group C			
Source	d.f.	M.S.	F		R^2	M.S.	F		R^2
Linear	1	3.22	35.78	**	56.59	42.84	476.00	**	94.74
Quadratic	1	0.34	3.77	N.S.		0.13	1.44	N.S.	
Deviations	25	0.09				0.09			

0.01 cm/generation for group A. These results suggest that direct selection was 3.25 times more effective than indirect selection for six-week tail length. Cheung and Parker (1974) found that direct selection was 7.74 times more effective than indirect for six-week tail length. This could suggest that long-term selection reduces the effectiveness of direct selection to indirect selection for six-week tail length, but since they are ratios with small numbers any change in the numbers results in large changes in the ratio, their reliability is questionable.

The results of the regression analysis performed on deviations from the control and generation number indicated that significant linear associations, with large coefficients of determination, existed for both groups A and C. These results indicate the existence of definite direct and correlated responses to selection for six-week tail length in groups C and A, respectively. These results are contrary to those of Cheung (1971) who noted that the correlated response in tail length in group A ceased after the initial seven generations, while there was a direct response to selection for six-week tail length in group C.

The above conclusions would indicate that a selection limit for long six-week tail length has not been reached in either group, C or A, even though group A, indirectly selected for six-week tail length, has a large, but not significant, quadratic component. The results obtained in group A are contrary to those of Falconer (1953), who noted that the correlated response in tail length to selection for body weight in mice became irregular after five generations.

Of the two methods of selection, direct selection for six-week tail length and indirect selection for six-week body weight was superior to direct selection for six-week body weight and indirect selection for six-week tail length. This observation is consistent with theory, since six-week tail length is a more highly heritable trait than six-week body weight and, according to Falconer (1960), the genetic correlation between the two traits is quite large ($r_G = 0.59$).

In comparison to the results for the first 14 generations (Cheung and Parker, 1974) the relative efficiencies of direct selection to indirect selection remained unchanged for six-week body weight and decreased for six-week tail length. These results suggest that for a highly heritable trait (six-week tail length) the relative efficiency of direct selection to indirect selection decreased with long-term selection. This decrease could be due to a greater reduction in the heritability of six-week tail length relative to the heritability of six-week body weight during long-term selection.

c) Correlated response in six-week litter size

Generation means and standard errors for six-week litter size and fertility, expressed as the percentage of successful matings per generation, are presented in Table 10. Deviations from the control for six-week litter size are in Table 12. The regression analysis for generation mean on generation number is contained in Table 11. Graphs of generation means and deviations from the control are presented in Figures 5 and 6, respectively.

Mean litter size in all groups showed significant declines from generations 9 through 40. The regression analysis indicated that the

Table 10. Means and standard errors for some reproductive traits

	Group A		Group C		Group E	
Generation	Fertility[1]	Litter size[2]	Fertility	Litter size	Fertility	Litter size
9	0.767	8.87±0.64	0.933	10.11±0.48	0.933	8.39±0.42
10	0.733	9.36±0.70	0.767	9.96±0.60	0.767	10.17±0.33
11	0.700	9.19±0.50	0.833	9.92±0.48	0.667	9.15±0.51
12	0.767	9.87±0.41	0.866	9.42±0.39	1.000	7.86±0.40
13	0.767	9.22±0.44	0.767	9.30±0.35	--	---
14	0.767	6.57±0.46	0.667	8.35±0.76	0.733	7.23±0.33
15	0.733	8.68±0.51	0.833	8.24±0.57	0.825	7.79±0.14
16	0.900	8.26±0.44	0.933	8.93±0.49	--	---
17	0.767	7.96±0.59	0.933	8.54±0.45	--	---
18	0.867	8.46±0.62	0.867	8.42±0.54	--	---
19	0.733	7.73±0.54	0.867	9.23±0.55	0.800	8.21±0.53
20	0.933	8.11±0.62	0.833	8.00±0.48	0.833	7.86±0.46
21	0.955	8.81±0.46	0.955	8.86±0.38	1.000	8.34±0.33
22	0.567	7.76±0.78	0.767	8.43±0.70	0.933	8.38±0.40
23	0.433	7.08±0.70	0.600	7.72±0.69	0.700	7.76±0.38
24	0.833	8.28±0.42	0.967	9.66±0.47	0.933	8.34±0.30
25	0.700	7.90±0.60	0.767	8.70±0.54	1.000	8.13±0.35
26	0.733	7.95±0.49	0.900	7.85±0.48	0.867	6.38±0.42
27	0.833	6.68±0.34	0.900	8.41±0.47	0.867	5.46±0.31
28	0.733	9.09±0.64	0.733	7.59±0.61	0.800	7.58±0.29
29	0.700	8.14±0.61	0.767	8.26±0.56	0.867	8.42±0.34
30	0.733	8.18±0.41	0.667	7.85±0.63	0.733	7.09±0.26
31	0.633	8.58±0.38	0.733	7.05±0.58	0.700	6.38±0.26
32	0.767	6.87±0.43	0.600	7.56±0.72	0.933	6.54±0.38
33	0.800	8.42±0.41	0.833	7.72±0.48	0.800	7.58±0.37
34	0.733	7.50±0.31	0.700	6.86±0.55	0.800	6.83±0.43
35	0.733	7.23±0.33	0.667	6.80±0.59	0.767	6.26±0.31
36	0.667	6.40±0.46	0.700	5.75±0.46	0.833	6.00±0.41
37	0.733	7.48±0.46	0.600	6.04±0.58	0.900	7.44±0.39
38	0.733	6.82±0.54	0.550	5.73±0.50	0.800	6.25±0.50
39	0.733	7.50±0.45	0.575	5.70±0.50	0.933	6.71±0.24
40	0.800	6.13±0.60	0.650	6.27±0.57	0.867	6.77±0.31
b[3]	-0.002± 0.003	-0.06±0.01	-0.008± 0.002	-0.12±0.01	0.000± 0.002	-0.07±0.02

---

[1] The percentage of successful matings per generation i.e. proportion of females mated which produced a litter.

[2] Litter size at six weeks of age.

[3] Regression ±S.E. of either fertility or litter size on generation number.

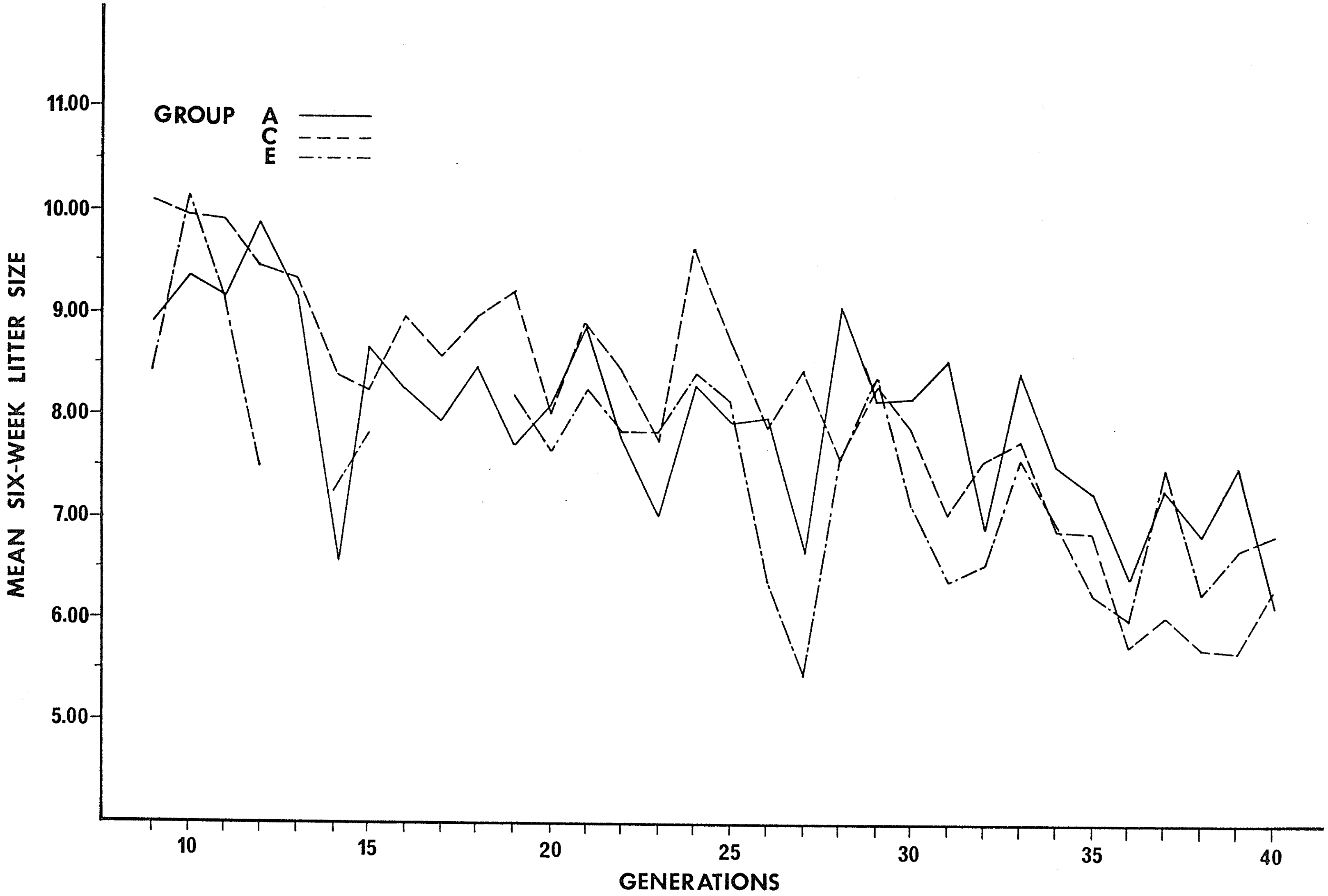

Figure 5. Generation means for six-week litter size for groups A, C and E.

Table 11. Partitioning of the sums of squares due to regression into linear and quadratic components - six-week litter size

Group A

Source	d.f.	M.S.	F		R^2
Linear	1	10.85	20.09	**	16.05
Deviations	30	0.54			

Group C

Source	d.f.	M.S.	F		R^2
Linear	1	39.45	112.71	**	77.80
Quadratic	1	1.11	3.17	N.S.	
Deviations	29	0.35			

Group E

Source	d.f.	M.S.	F		R^2
Linear	1	14.37	23.18	**	47.93
Quadratic	1	0.11	0.18	N.S.	
Deviations	25	0.62			

Table 12. Deviations from the control group for six-week litter size for groups A and C

Cycle	Group A	Group C
9	0.48	1.72
10	-0.81	-0.21
11	0.04	0.77
12	2.01	1.56
13	-	-
14	-0.66	1.12
15	0.89	0.45
16	-	-
17	-	-
18	-	-
19	-0.48	1.02
20	0.25	0.14
21	0.47	0.52
22	-0.62	0.05
23	-0.68	-0.04
24	-0.11	1.27
25	-0.23	0.57
26	1.57	1.47
27	1.22	2.95
28	1.51	0.01
29	-0.28	-0.16
30	1.09	0.76
31	2.20	0.67
32	0.33	1.02
33	0.84	0.14
34	0.67	0.03
35	0.97	0.54
36	0.40	-0.25
37	0.04	-1.40
38	0.57	-0.52
39	0.79	-1.01
40	-0.64	-0.50

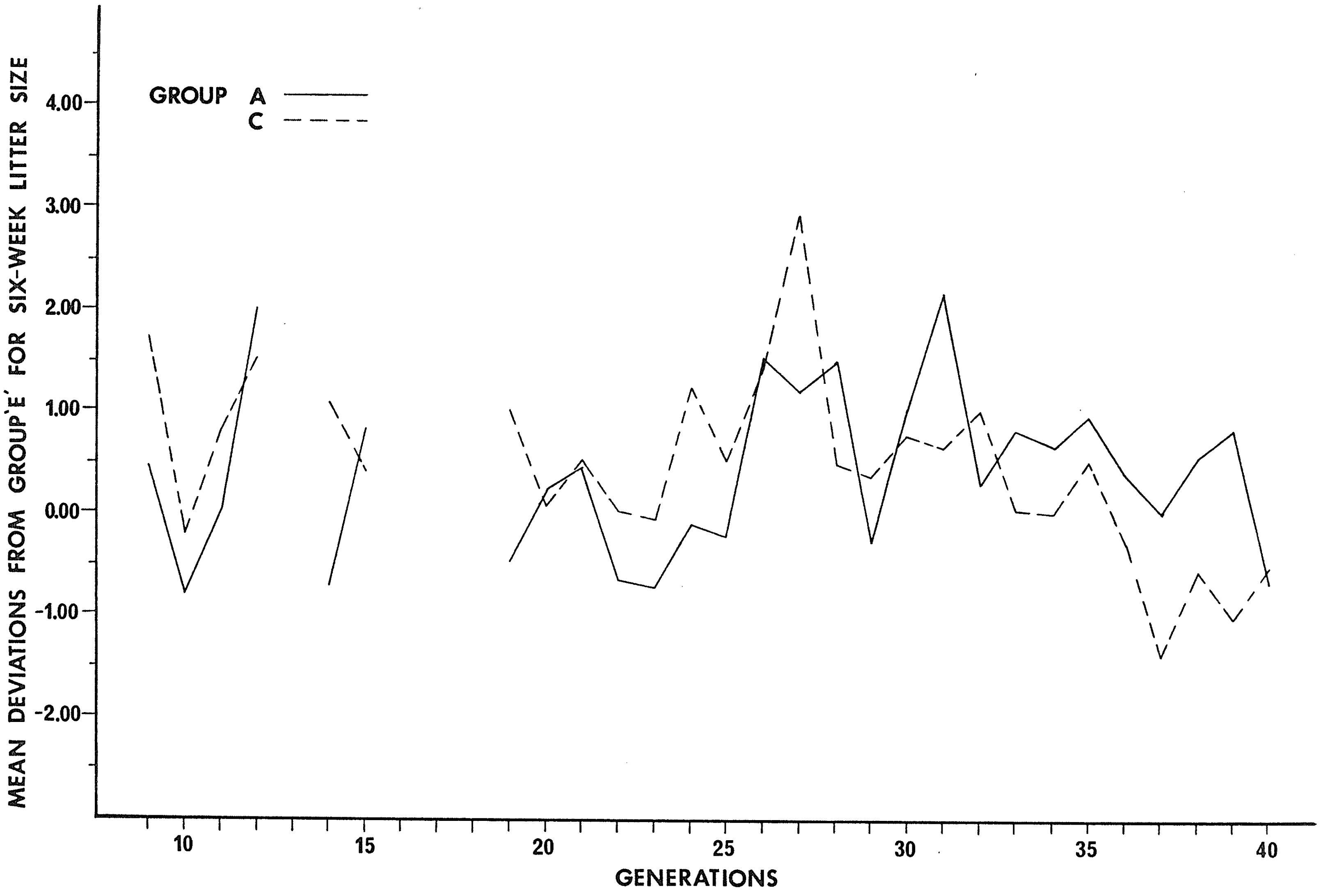

Figure 6. Mean deviations from the control group for six-week litter size for groups A and C.

linear component was significant in all groups, but only group C possessed a sufficiently large coefficient of determination for predictive purposes. These results are consistent with those of Cheung (1971), who noted an increase in litter size in groups A and C, since an increased six-week body weight results in an increase in litter size. This trend continues until an intermediate optimum, for body weight, is reached. Beyond this optimum, litter size decreases with an increase in body weight. Also inbreeding probably began to have a marked effect on litter size in later generations, since the rate of inbreeding in all groups was approximately 1.25% (Appendix Table IV).

The decline in litter size in the control group provided an indication of inbreeding depression. The deviations from the control for six-week litter size, suggest that inbreeding is constant in all groups.

With respect to fertility, group C showed a definite decline in successful matings while groups A and E showed no apparent change in successful matings. These results differ from those obtained for six-week litter size, but this could be due to the criterion used to measure fertility.

Heritability Estimates

Heritability estimates were calculated by two methods, from the sire component of variance and by midparent-litter mean regression. The results from these two methods are in Tables 13 and 14, respectively. Realized heritabilities were calculated from the regression of cumulative response on cumulative selection differential for six-week body weight (group A) and six-week tail length (group C). Table linear component was significant in all groups, but only group C possessed a sufficiently large coefficient of determination for predictive purposes. These results are inconsistent with those of Cheung (1971), who observed an increased litter size in the two selected groups. The declines in litter size were probably the result of inbreeding which causes declines in reproductive traits. More specifically, inbreeding probably caused marked decreases in fertility and ovulation rate which would account for the declines in litter size. Further evidence is that the rate of inbreeding was approximately 1.25% (Appendix Table IV), suggesting that after 40 generations the incidence of inbreeding would be 50%.

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15 contains the values for cumulative selection differential, cumulative response, and realized heritability estimates for groups A and C. Figure 7 shows the plot of cumulative selection differential on generation number for groups A and C.

The estimates from the sire component of variance suggest no change due to selection in all groups for six-week body weight and six-week tail length, except for the heritability estimates for six-week tail length in group E. However, due to the large standard errors associated with these estimates their reliability is in doubt. The group estimates, though more reliable, provide little insight into the effects of selection on the heritabilities of six-week body weight and six-week tail length. In both selected groups, A and C, the heritability estimates for six-week tail length were greater than those for six-week body weight. This was expected since six-week tail length is a more highly heritable trait than six-week body weight (Falconer, 1960). Comparing the pooled heritability estimates for six-week body weight and six-week tail length for groups A and C it is evident that the values for group A are almost double those in group C. This would suggest, assuming the heritabilities for six-week body weight and six-week tail length were similar in magnitude when this experiment began, that selection for a more highly heritable trait (six-week tail length in group C) led to a greater reduction in the additive variances of the directly selected trait (six-week tail length) and correlated trait (six-week body weight) than did selection for a less highly heritable trait (six-week body weight). With respect to the pooled estimates in group E, the control, little can be discussed since there was no pooled estimate for six-week body weight. However, the pooled

Table 13. Heritability estimates for six-week body weight and six-week tail length from the sire component of variance

Group	Block	n	h^2(body weight)	h^2(tail length)
A	1	1604	0.15±0.23	0.47±0.27
	2	1593	0.52±0.26	0.52±0.27
	3	1374	0.39±0.29	0.67±0.33
	4	1269	0.64±0.31	0.45±0.24
Pooled		5840	0.45±0.14	0.50±0.14
C	1	1842	0.15±0.22	0.23±0.20
	2	1889	0.23±0.23	0.32±0.28
	3	1425	0.09±0.31	0.25±0.30
	4	1175	0.55±0.28	0.24±0.29
Pooled		6331	0.22±0.13	0.27±0.13
E	1	1293	0.03±0.23	0.93±0.33
	2	1363	***[1]	0.55±0.33
	3	1394	***	***
	4	1336	0.09±0.24	0.09±0.29
Pooled		5386	***	0.36±0.15

[1] Values undefined.

estimate for six-week tail length is lower than expected (0.60 - Falconer, 1960), but this could be due to inbreeding causing fixation of genes, reducing the additive variance of the trait (six-week tail length).

Midparent regression results provided more reliable estimates (i.e. smaller standard errors) and indicated definite declining trends in the heritabilities of six-week body weight and six-week tail length for all groups over the course of the experiment. In the two selected groups, A and C, the declines were more pronounced in the correlated traits (six-week tail length in group A; six-week body weight in group C) than in the directly selected traits (six-week body weight in group A; six-week tail length in group C). The control group results were quite dramatic in both six-week body weight and six-week tail length. These results could have been produced by sampling errors (i.e. the large standard errors relative to the heritability estimates), inbreeding depression, and random drift or combinations of these. The results from the pooled heritability estimates show the same pattern: the heritability estimate of the correlated trait is lower than the estimate of the directly selected trait. This suggests that indirect selection for either six-week body weight or six-week tail length causes a greater reduction in the heritabilities of these traits than direct selection for them. This result contradicts selection theory which states that direct selection would lead to a greater reduction in the heritability of the directly selected trait than the heritability of the correlated trait.

Table 14. Heritability estimates for six-week body weight and six-week tail length by midparent-litter mean regression

Group	Block	n	h^2(body weight)	h^2(tail length)
A	1	182	0.25±0.10	0.52±0.03
	2	195	0.32±0.15	0.08±0.11
	3	175	0.20±0.14	0.10±0.09
	4	178	0.14±0.11	0.06±0.14
Pooled		730	0.59±0.04	0.32±0.04
C	1	198	0.33±0.11	0.76±0.05
	2	216	0.13±0.10	***[1]
	3	182	0.11±0.15	0.51±0.12
	4	189	0.10±0.11	0.48±0.25
Pooled		785	0.39±0.05	0.83±0.02
E	1	79	0.45±0.18	0.58±0.19
	2	144	***	***
	3	203	0.04±0.10	0.08±0.11
	4	201	0.01±0.09	0.10±0.13
Pooled		627	0.25±0.05	0.18±0.06

[1] Values undefined.

Table 15. Cumulative selection differentials and response for six-week body weight (gm) in group A and six-week tail length (cm) in group C

	Group A		Group C	
Generation	Cum. S.D. (gm)	Cum. Resp. (gm)	Cum. S.D. (cm)	Cum. Resp. (cm)
9	---	---	---	---
10	3.00	1.27	0.92	0.07
11	6.85	-1.07	1.58	-0.03
12	9.96	0.50	2.31	0.33
13	13.35	1.78	3.01	1.13
14	16.68	5.01	3.78	1.60
15	19.40	-0.32	3.96	1.10
16	24.22	0.76	4.56	0.88
17	28.66	0.17	5.16	1.20
18	34.14	0.26	6.00	1.34
19	40.23	0.12	6.89	1.18
20	45.58	-2.35	7.95	1.05
21	52.29	1.53	8.63	2.03
22	58.38	2.63	8.91	1.62
23	63.62	2.56	9.57	1.24
24	67.14	7.46	10.31	2.24
25	73.39	6.70	11.14	2.19
26	77.58	1.89	11.83	1.61
27	83.07	4.37	13.09	2.44
28	86.48	7.94	14.00	3.36
29	91.92	4.35	14.81	2.52
30	96.90	2.01	15.84	2.35
31	102.28	6.30	16.83	2.56
32	107.14	12.00	18.18	2.81
33	111.80	5.15	19.08	2.86
34	117.69	0.61	20.22	3.12
35	123.65	6.61	21.50	4.44
36	128.65	11.98	22.02	3.95
37	132.44	11.47	22.82	4.54
38	137.84	7.53	23.53	4.02
39	144.01	7.97	24.45	4.36
40	149.57	14.93	25.41	5.06
Realized h^2 [1]		0.07±0.01		0.17±0.01

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[1] Estimated as the regression of cumulative response on cumulative selection differential.

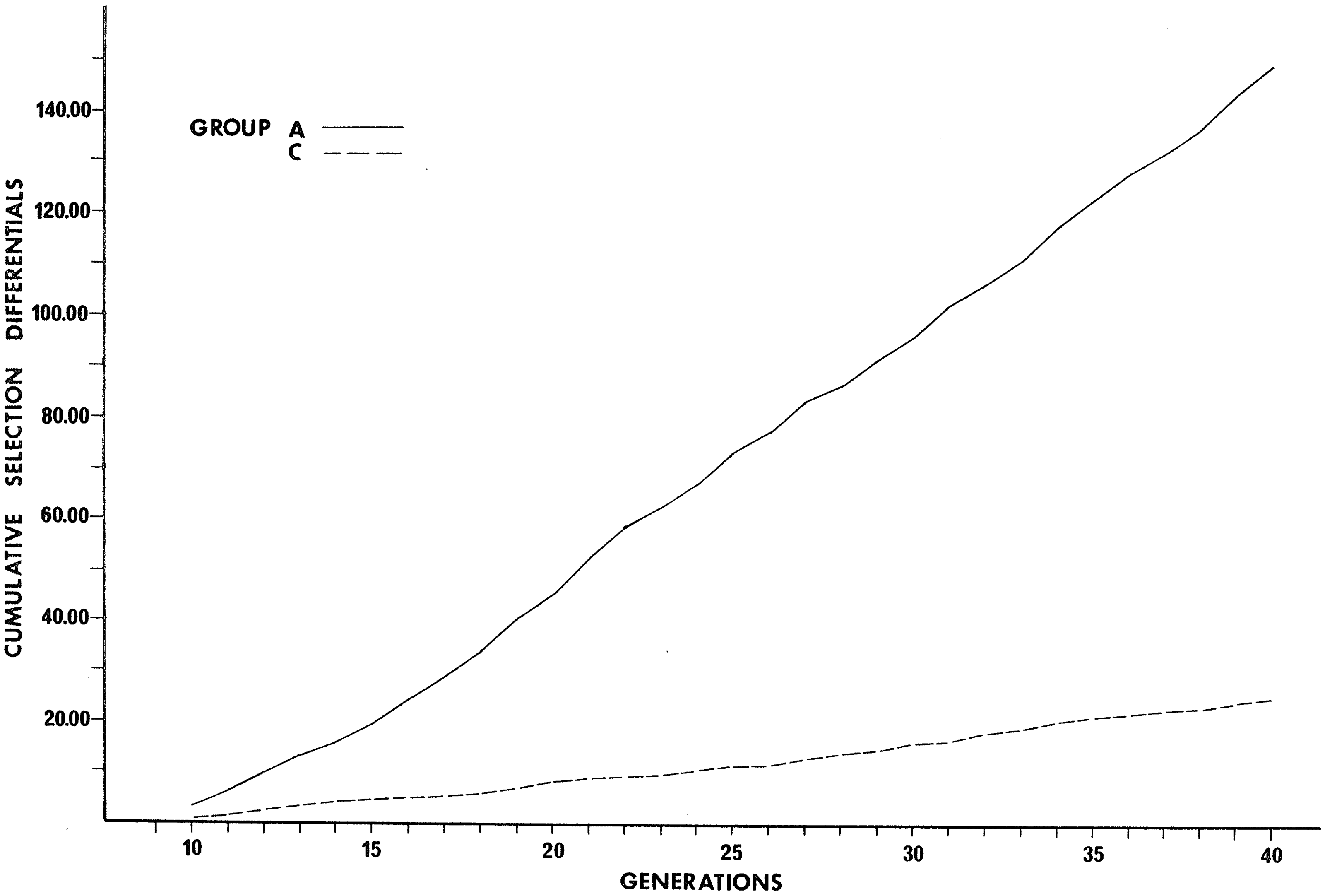

Figure 7. Generation means for cumulative selection differentials for groups A (gm) and C (cm).

Realized heritability estimates demonstrated that there was more actual additive variance present for six-week tail length than for six-week body weight. These results are lower than the estimates of Cheung and Parker (1974) for 14 generations of selection and provide some further evidence that the heritabilities of the two traits are declining as a consequence of long-term selection.

Comparison of the heritability estimates from the sire component of variance and midparent regression with those of Cheung (1971) and Cheung and Parker (1974) provided little insight into the effects of selection on heritability. These workers reported that their estimates were erratic and difficult to interpret.

Phenotypic Correlations

Phenotypic correlations appeared to remain quite constant in group A, and to increase in groups C and E (Table 16). The constancy of the correlations in group A could be attributed to an increase in non-genetic covariance and variance equal to the reduction in genetic covariance and variance (Falconer, 1960). The increase in phenotypic correlations in groups C and E could have been produced by an increase in non-genetic covariance and variance greater than the decline in genetic covariance and variance. Falconer further pointed out that homozygotes are more variable due to environmental variance, and since selection leads to increased homozygosity, this could result in increases in non-genetic covariance and variances.

Table 16. Phenotypic correlation estimates from analyses of covariance and variance

Block	Group A	Group C	Group E
1	0.64	0.56	0.58
2	0.75	0.24	0.77
3	0.70	0.77	0.72
4	0.65	0.78	0.74
Pooled	0.68	0.40	0.77

Genetic Correlations

Of the four methods used to estimate the genetic correlation coefficient only the realized genetic correlation estimates provided an insight into the effect of selection on genetic correlation. The estimates from the sire components of covariance and variance yielded results having very large standard errors or failed to provide any estimates due to negative sire components of variance (Table 17). The arithmetic method also had large standard errors and failed to provide estimates (Table 18) while the geometric method failed to provide sufficient numbers of estimates for interpretation.

The realized genetic correlations (Table 20 and Figure 8), though quite variable (ranging from -2.91 to 2.92) demonstrated that there was no apparent change over the 32 generations of selection. These results are similar to those of Cheung and Parker (1974) in which they noted that there was no change over the initial fourteen generations of this experiment.

However, since the heritabilities of the two traits are declining and the genetic correlation coefficient is remaining constant, a contradiction exists. With reference to the following formula;

$$r_G = \frac{cov_{xy}}{\sqrt{\sigma_x^2 \sigma_y^2}}$$

it is evident that for the genetic correlation coefficient (r_G) to remain constant while the additive variance of the traits is declining ($\sigma_x^2 \sigma_y^2$), the genetic covariance (cov_{xy}) must decrease proportionately to the square root of the product of the sire components of variance for both traits. If such is the case, then the genetic correlation coefficient is not accurately measuring the genetic covariance. Instead of it indicating the decline in the genetic covariance it is indicating, by a constant genetic correlation, that no change is occurring despite the reduction of the heritabilities of the two traits.

Table 17. Genetic correlation estimates from the sire components of covariance and variance

Group	Block	n	r_G
A	1	1604	0.59 ± 0.47
	2	1593	0.87 ± 0.03
	3	1374	***[1]
	4	1269	1.00 ± 0.19
Pooled		5840	0.88 ± 0.11
C	1	1842	0.34 ± 1.26
	2	1889	0.93 ± 0.52
	3	1425	***
	4	1175	0.89 ± 0.12
Pooled		6331	0.91 ± 0.12
E	1	1293	***
	2	1363	***
	3	1394	***
	4	1336	0.90 ± 1.47
Pooled		5386	***

[1] Values undefined.

Table 18. Genetic correlation estimates by the arithmetic method

Block	Group A	Group C	Group E
1	***[1]	0.40±0.09	***
2	***	***	***
3	0.01±0.56	0.50±0.30	0.37±1.13
4	***	0.22±0.51	***

Table 19. Genetic correlation estimates by the geometric method

Block	Group A	Group C	Group E
1	***	0.38	0.99
2	0.41	***	***
3	***	***	***
4	0.91	***	0.64

[1] Values undefined.

Table 20. Realized genetic correlation estimates in groups A and C combined

Generation	R_x	CR_x	R_y	CR_y	r_G
9-16[1]	0.76	-1.43	0.88	-0.11	0.49
10-17	-1.10	-3.30	1.13	0.07	0.43
11-18	1.33	2.19	1.37	0.20	0.49
12-19	-0.38	-1.59	0.85	0.35	1.31
13-20	-4.13	-2.56	-0.08	-1.10	2.92
14-21	-3.48	1.53	0.43	-1.27	1.14
15-22	2.95	2.17	0.52	-0.45	-0.80
16-23	1.80	1.81	0.36	-0.75	-1.45
17-24	7.29	4.58	1.04	0.39	0.49
18-25	6.44	3.48	0.85	-0.07	-0.21
19-26	1.77	0.90	0.43	-0.52	-0.78
20-27	6.72	2.48	1.39	1.08	0.54
21-28	6.41	3.91	1.33	1.13	0.72
22-29	1.72	-1.42	0.90	0.31	-0.53
23-30	-0.55	-0.43	1.11	0.63	0.67
24-31	-1.16	-0.05	0.32	0.09	0.11
25-32	5.30	2.03	0.62	0.31	0.44
26-33	3.26	2.80	1.25	0.87	0.77
27-34	-3.76	-3.24	-0.32	-0.70	1.35
28-35	-1.33	-3.75	0.08	-0.24	-2.91
29-36	7.63	5.04	0.43	0.00	0.00
30-37	9.46	6.16	1.19	0.48	0.51
31-38	1.23	-0.50	0.46	-0.31	0.52
32-39	-4.03	-1.74	0.55	0.17	0.37
33-40	9.78	7.43	1.20	0.32	0.45

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[1] Eight generation blocks.

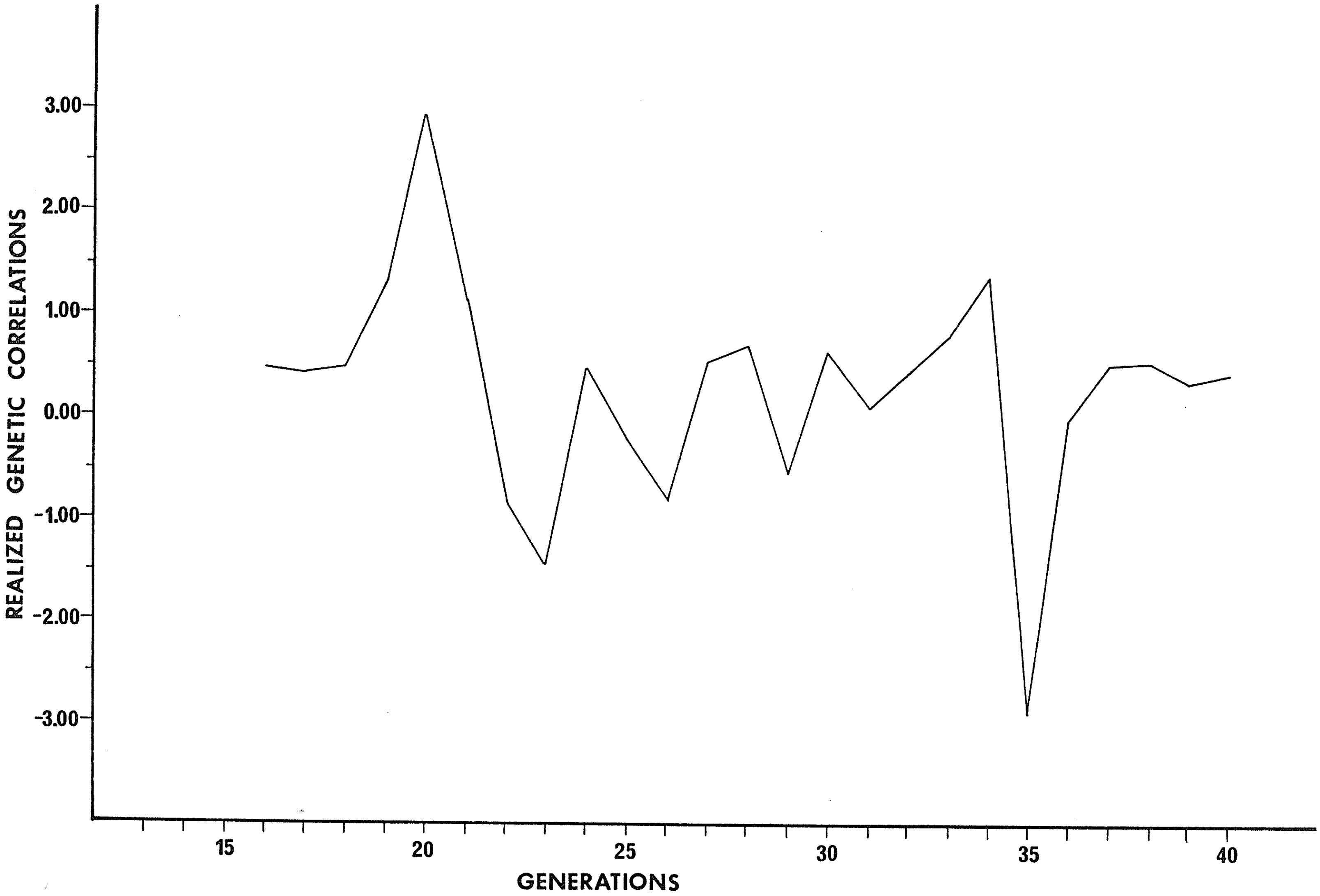

Figure 8. Realized genetic correlation estimates for 8 generation blocks for the 32 generations of selection.

SUMMARY AND CONCLUSIONS

The effect of long-term selection on genetic correlation and response to selection in two quantitative traits was examined in a random mating mouse population. Selection was unidirectional for large six-week body weight and long six-week tail length. The two selected groups, A and C, were under 30% selection for their respective traits, six-week body weight and six-week tail length, while group E was the control, experiencing no selection.

Response to selection, both direct and indirect, for both six-week body weight and six-week tail length showed significant linear trends. These results suggest that the selection limits for the two traits were not reached after 40 generations of selection. Long-term selection had no apparent effect on the relative efficiency of direct selection to indirect selection for six-week body weight, however, it suggests a decline in the relative efficiency of direct selection to indirect selection for six-week tail length. Direct selection for six-week tail length, and indirect selection for six-week body weight, was the most effective means of improving both traits.

Selection appeared to have no apparent effect on the genetic correlation between six-week body weight and six-week tail length. However, with the heritabilities of the two traits declining due to selection, the stability of the genetic correlation seemed unrealistic. A possible explanation for this statility would be that the genetic covariance declined proportional to the square root of the product of the additive variance of the two traits. The declines in the heritabilities of six-week body weight and six-week tail length were greater in the correlated traits than in the directly selected traits. This apparent contradiction to selection theory and the apparent inability of the genetic correlation to estimate the genetic covariance points out the shortcomings of the genetic correlation theory and current theory regarding the effect of selection on single-trait and pleiotropic genes.

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APPENDIX

Table I. The intensities of selection per generation for group A

Generation	Females selected	Selection intensity	Males selected	Selection intensity	Mean selection intensity
9	-	-	-	-	-
10	30/75	0.956	15/75	1.381	1.169
11	30/75	0.956	15/75	1.381	1.169
12	30/75	0.956	15/75	1.381	1.169
13	30/75	0.956	15/75	1.381	1.169
14	30/75	0.956	15/75	1.381	1.169
15	30/75	0.956	15/75	1.381	1.169
16	30/75	0.956	15/75	1.381	1.169
17	30/75	0.956	15/75	1.381	1.169
18	30/75	0.956	15/75	1.381	1.169
19	30/75	0.956	15/75	1.381	1.169
20	30/75	0.956	15/75	1.381	1.169
21	44/75	0.657	15/75	1.381	1.019
22	30/75	0.956	15/75	1.381	1.169
23	30/75	0.956	15/75	1.381	1.169
24	30/50	0.634	15/42	1.024	0.829
25	30/75	0.956	15/75	1.381	1.169
26	30/75	0.956	15/75	1.381	1.169
27	30/75	0.956	15/75	1.381	1.169
28	30/75	0.956	15/75	1.381	1.169
29	30/75	0.956	15/75	1.381	1.169
30	30/75	0.956	15/75	1.381	1.169
31	30/75	0.956	15/75	1.381	1.169
32	30/75	0.956	15/75	1.381	1.169
33	30/75	0.956	15/75	1.381	1.169
34	30/75	0.956	15/75	1.381	1.169
35	30/75	0.956	15/75	1.381	1.169
36	30/69	0.895	15/75	1.381	1.138
37	30/60	0.788	15/67	1.316	1.052
38	30/73	0.936	15/75	1.381	1.159
39	30/75	0.956	15/75	1.381	1.169
40	30/75	0.956	15/75	1.381	1.169

Table II. The intensities of selection per generation for group C

Generation	Females selected	Selection intensity	Males selected	Selection intensity	Mean selection intensity
9	-	-	-	-	-
10	30/75	0.956	15/75	1.381	1.169
11	30/75	0.956	15/75	1.381	1.169
12	30/75	0.956	15/75	1.381	1.169
13	30/75	0.956	15/75	1.381	1.169
14	30/75	0.956	15/75	1.381	1.169
15	30/75	0.956	15/75	1.381	1.169
16	30/75	0.956	15/75	1.381	1.169
17	30/75	0.956	15/75	1.381	1.169
18	30/75	0.956	15/75	1.381	1.169
19	30/75	0.956	15/75	1.381	1.169
20	30/75	0.956	15/75	1.381	1.169
21	44/75	0.657	15/75	1.381	1.019
22	30/75	0.956	15/75	1.381	1.169
23	30/75	0.956	15/75	1.381	1.169
24	30/75	0.956	15/75	1.381	1.169
25	30/68	0.884	15/71	1.350	1.117
26	30/75	0.956	15/75	1.381	1.169
27	30/75	0.956	15/75	1.381	1.169
28	30/75	0.956	15/75	1.381	1.169
29	30/75	0.956	15/75	1.381	1.169
30	30/75	0.956	15/75	1.381	1.169
31	30/75	0.956	15/75	1.381	1.169
32	30/68	0.884	15/75	1.381	1.133
33	30/69	0.895	15/65	1.299	1.097
34	30/75	0.956	15/75	1.381	1.169
35	30/67	0.873	15/75	1.381	1.127
36	40/62	0.482	20/74	1.209	0.847
37	40/75	0.738	20/75	1.217	0.978
38	40/65	0.613	20/75	1.217	0.915
39	40/67	0.639	20/59	1.064	0.852
40	40/66	0.626	20/75	1.217	0.922

Table III. Ingredients in Purina Rodent Laboratory Chow

Guaranteed Analysis	
Crude protein not less than	23.0%
Crude fat not less than	4.5%
Crude fibre not more than	6.0%
Ash not more than	8.0%
Added minerals not more than	2.5%

Ingredients

Ground extruded corn, soybean meal, ground oat groats, dried beet pulp, wheat germ meal, fish meal, brewers' dried yeast, dehydrated alfalfa meal, cane molasses, dried milk products, meat and bone meal, wheat middlings, animal fat preserved with BHA, calcium carbonate, dicalcium phosphate, salt, animal liver meal, calcium iodate, vitamin B_{12} supplement, methionine hydroxy analogue calcium, calcium pantothenate, choline chloride, folic acid, riboflavin supplement, thiamine, niacin, pyridoxine hydrochloride, D activated animal sterol, vitamin E supplement, iron oxide, manganese oxide, cobalt carbonate, copper oxide, zinc oxide.

Table IV. The average rate of inbreeding per generation per block (as a percentage)

Group	Block	Ave. No. of females/generation	Ave. No. of males/generation	Rate of inbreeding (ΔF)[1]
A	1	30.00	15.00	1.25
	2	31.75	15.00	1.23
	3	30.00	15.00	1.25
	4	30.00	15.00	1.25
	Pooled	30.44	15.00	1.24
C	1	30.00	15.00	1.25
	2	31.75	15.00	1.23
	3	70.00	15.00	1.25
	4	36.25	18.13	1.03
	Pooled	32.00	15.78	1.18
E	1	30.00	15.00	1.25
	2	32.33	15.00	1.22
	3	30.00	15.00	1.25
	4	30.00	15.00	1.25
	Pooled	30.50	15.00	1.24

[1] From the formula (Falconer, 1960): $\Delta F = \frac{1}{8N_m} + \frac{1}{8N_f}$

where, ΔF is the rate of inbreeding.

N_m is the number of males per generation.

N_f is the number of females per generation.