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Direct and correlated responses to selection for weaning weight, post-weaning weight gain and six-week weight in mice

R. L. Baker, E. H. Cox and A. H. Carter

Genetics Section, Ruakura Agricultural Research Centre, Private Bag, Hamilton, New Zealand

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Summary. Four lines of mice were formed from a common base population and selected for 37 generations for either increased 3-week weight (weaning weight), 6-week weight, 3–6 week gain, or maintained as a randomly bred control line. Realised heritability estimates for short-term (long-term) responses were 0.33 ± 0.20 (0.07 ± 0.10), 0.46 ± 0.14 (0.26 ± 0.09), 0.36 ± 0.14 (0.24 ± 0.11) for 3-week weight, 6-week weight and 3–6 week gain, respectively. Realised genetic correlations estimated from short-term (long-term) responses were 0.23 ± 0.08 (0.35 ± 0.10) between 3-week weight and 3–6 week gain; 0.82 ± 0.04 (0.58 ± 0.08) between 3-week weight and 6-week weight; and 0.81 ± 0.04 (0.97 ± 0.04) between 3–6 week gain and 6-week weight. The genetic correlation between 3-week weight and 6-week weight was asymmetric with a greater correlated response for 3-week weight when selecting for 6-week weight (1.06) than vice versa (0.63).

Key words: Mice – Selection – Growth – Genetic correlation

Introduction

Because of its predominant influence on profitability of meat production, growth rate has been widely studied in all livestock species. A basic problem is choice among alternative measures of growth performance, such as gains over specified periods of the growth curve, or live weights at specified ages. In New Zealand studies have been undertaken to address this problem by selecting for different measures of growth both in beef cattle (Carter 1971; Baker et al. 1980) and in Southdown sheep (Carter, unpublished).

The selection experiment with mice reported here was designed to be comparable to those being undertaken in New Zealand with sheep and beef cattle. The objective was to compare the effectiveness in terms of improving 6-week liveweight, of selection based on weaning (3-week) weight, post-weaning (3–6 week) gain and 6-week weight itself. By studying direct and correlated responses to selection in each selection line it was also possible to obtain independent estimates of realised genetic correlations among the three growth traits. This permits experimental evaluation of the validity of the genetic correlation theory as first tested by Falconer (1954).

Some results from this study have been reported by Baker et al. (1979a) who investigated the effect of selection in the different lines on patterns of fat deposition.

Materials and methods

The base population for this study was a four-way cross of four inbred lines: Aw, C57, CBA and an albino strain (called Ruakura Whites) of unknown origin. This population was initially split into three lines, one selected for large 6-week weight, one selected for small 6-week weight and a randombred control line. After 12 generations of selection and then 5 generations of relaxed selection, these 3 lines were recombined in a balanced diallel crossing program. From this foundation stock (39 litters), four genetically similar lines were then constituted to initiate the present study.

Four lines were established: S – Selected for increased 6-week weight, G – Selected for increased 3–6 week gain, W – Selected for increased weaning (3-week) weight, Co – Unselected control line. In the Co line, selection was aimed at maintaining a minimum selection differential for 6-week weight; the male and female chosen from each litter were those closest to the litter-sex mean. Each line comprised eight pair matings, and one male and one female were selected from each litter (i.e., within-litter selection). The variance in family size was, therefore, zero, thus doubling the effective population size. Selection was in first parity litters only. A cyclical mating plan was used to minimize inbreeding. Litter size was not standardized. The study lasted 37 generations. Line S was lost in generation 32 due to poor reproduction and to a disease outbreak.

Mice were mated between 7 and 10 weeks of age. Males were removed after the females were palpated as pregnant and mating could continue for up to about a month in duration. At birth, the number of young born (alive plus dead), sex ratio and birth weights were recorded. Mice were weaned at 3 weeks of age, weighed, and placed in plastic boxes separately by sexes, with 4 to 6 mice in each box. At 6 weeks of age all mice were weighed, and 3–6 week gain was calculated. A standard laboratory chow and water were available ad libitum and room temperature varied from 21 to 23 °C.

Direct and correlated responses to selection were first investigated separately for each sex. Because sexes did not show differential responses, results were pooled across sexes. Direct and correlated responses to selection were estimated as the linear regression of the deviations of the selection line generation means from the control line on generation number. All regression equations had an intercept in the model (i.e. $y=a+b\,x$) and statistical analysis included the first 30 generations. To accomodate curvilinear responses, analyses were done over 10 generation intervals, i.e., generations 1–10, 11–20 and 21–30; generation 1 was the first generation of offspring from selected parents. Curvilinear selection response was investigated using the method of Bennett (1981).

Selection differentials were the mean differences in 6-week weight, 3–6 week gain or 3-week weight between the selected individuals and the mean of their sex in their litter. Parents without offspring surviving to 6 weeks were excluded. Falconer (1973) points out this is the only weighting of selection differentials needed in the case of within-family selection. Realised heritabilities were calculated as the regression of response (measured as a deviation from the control) on cumulated selection differential. Standard errors of realised heritability estimates were calculated as in Hill (1972), and modified for within-family selection (Hill 1980). These standard errors take into account the positive correlation among generations due to cumulative genetic drift, which if ignored can result in standard errors which are biased downwards.

Realised genetic correlations among 3-week weight, 3–6 week gain and 6-week weight were estimated (Falconer 1954) as

$$\hat{r}_G = \frac{C_y}{R_x} \cdot \frac{\hat{h}_x}{\hat{h}_y} \cdot \frac{\hat{\sigma}_x}{\hat{\sigma}_y} \qquad (1)$$

where R_x and C_y are the direct and correlated responses for X and Y respectively, $\hat{h}_x$ and $\hat{h}_y$ are the square roots of the realised heritability estimates and $\hat{\sigma}_x$ and $\hat{\sigma}_y$ are the within-litter estimates of phenotypic standard deviations. Two estimates of each genetic correlation were obtained; from the correlated response of Y when selecting for X, and from the correlated response of X when selecting for Y. Estimates of the joint realised genetic correlation were also obtained (Falconer, 1981) as

$$\hat{r}_G = \left[\frac{C_y}{R_x} \cdot \frac{C_x}{R_y}\right]^{1/2} . \qquad (2)$$

Approximate standard errors of this estimate were calculated from formulae given by Hill (1971).

These realised genetic correlations were estimated for both early and long term response to selection. Early direct and correlated responses to selection were expressed as change per generation (regression coefficients), comprising generations 1–9 for the W line and generations 1–10 for the S and G lines. A marked decline in response between generation 9 and 10 in the W line (from +2 g to zero) was the reason for evaluating early response in this line over generations 1–9. Long term responses were in terms of average deviations from the control for generations 20–28. Realised heritabilities from generations 1–10 (1–9 for the W line) and generations 1–20 (long term) were used in (1). Within-litter variances were estimated separately for each line and period (generations 1–10, 11–20 and 21–30). The estimates were homogenous and were pooled across generations 1–30, sexes and lines. The standard deviation estimates used in (1), based on 5,586 d.f., were 0.8, 1.6 and 1.9 for 3-week weight, 3–6 week gain and 6-week weight respectively. These same values were used for early or long term calculations.

Phenotypic correlations were obtained from the analyses where within-litter variances were estimated; they were not heterogeneous across generations or lines. The values presented were estimated within generations (1–30), lines, sexes and litters. Environmental correlations were then calculated (Falconer 1954) from the phenotypic correlations, realised heritabilities and realised genetic correlations (from eq. (2)).

Correlated responses in some fitness traits were studied as in Falconer (1973). The numerical 'productivity' of mated pairs was defined as the mean number of mice weaned per mating made. This can be partitioned into components including (a) fertility – the proportion of fertile matings (with one or more live young at birth); (b) litter size at birth – the number of live young at birth in litters with at least one live young; and (c) survival from birth to weaning – the proportion surviving to weaning of those born alive. Mice born dead were ignored because they were a very low proportion of the total mice born. 'Productivity' was the product of the above three components and was calculated from first parity litters only.

Results

Direct and correlated responses for the growth traits

Results of selection in the W, G and S lines and trends in the Co line are shown in Fig. 1. The Co line, while fluctuating somewhat from generation to generation (particularly in the case of 3-week weight), did not show any significant trend over the 37 generations of the experiment. Regressions of generation means on generation number (1–30) for the Co line were 0.03 ± 0.02, -0.01 ± 0.01 and 0.02 ± 0.02 for 3-week weight, 3–6 week gain and 6-week weight, respectively. For all three traits, variations from generation to generation were parallel in the four lines suggesting unidentified environmental effects peculiar to each generation. This is shown more clearly for 6-week weight in Fig. 2 where the trends for all four lines are plotted through generation 32.

Regressions of line means as a deviation from the control line on generation number are given in Table 1. Direct and correlated responses to selection for both 3–6 week gain and 6-week weight declined after the first 10 generations of selection and plateaued, with the exception of direct and correlated response for 3-week

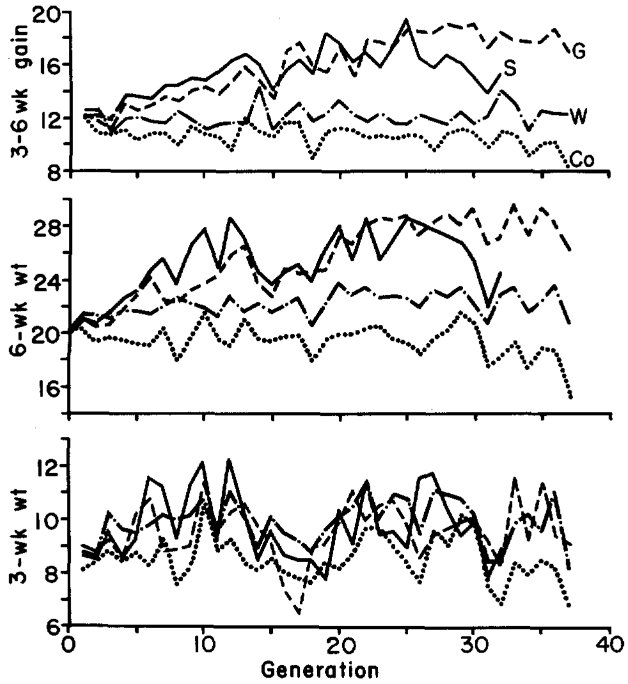

Fig. 1. Direct and correlated responses to selection (g) for 3-week weight (*W*), 6-week weight (*S*) and 3–6 week gain (*G*)

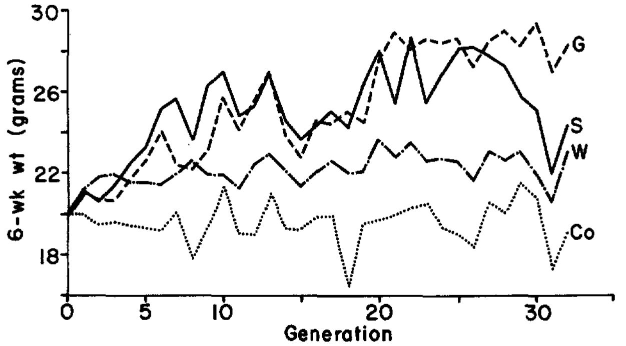

Fig. 2. Direct and correlated responses to selection for 6-week weight

Table 1. Regression of direct (underlined) and correlated responses to selection expressed as deviations from the control line on generation number ± SE[a] in g.

Generations	Line	Traits		
		3-week wt	3–6 week gain	6-week wt
1– 9	W	0.18±0.06	0.07±0.10	0.32±0.11
1–10	W	0.07±0.06	0.03±0.08	0.10±0.11
	G	0.05±0.07	0.36±0.06	0.38±0.09
	S	0.24±0.07	0.40±0.06	0.64±0.08
11–20	W	0.01±0.06	0.11±0.09	0.14±0.11
	G	−0.07±0.08	−0.26±0.09	0.19±0.12
	S	−0.06±0.05	0.19±0.09	0.21±0.10
21–30	W	−0.08±0.06	−0.07±0.08	−0.15±0.10
	G	−0.32±0.08	0.16±0.06	−0.06±0.10
	S	−0.04±0.12	−0.09±0.07	−0.16±0.15

[a] SE of least squares estimates

weight in the G line, between generations 20 and 30. There were no clear responses to selection in the W line. However, it appeared that some reponse to selection occurred in the W line from generations 1–9 (Table 1).

Direct selection was more effective than indirect selection for increasing either 6-week weight or 3–6 week gain. In the short term (generations 1–10), indirect selection for 6-week weight gave a larger response in 3–6 week gain than direct selection for this trait. In the case of increasing 3-week weight, the best strategy in the short-term (generations 1–10) was to select for 6-week weight. In the long term this trait did not respond to direct or indirect selection.

Realised heritabilities

Average selection differentials per generation from generation 1 to 30 are presented in Table 2. Selection differentials applied in each line were consistent over generations as shown in Fig. 3. Selection differentials in standard deviation units (Table 2) were similar in lines G and S and somewhat higher in the W line. Selection differentials actually applied (0.64 to 0.78 σ) were a little lower than their expectations from a table of order statistics (Becker 1967), where selecting one individual out of 3 (i.e., within-sex, within-litter, selection) gives an expected selection differential of 0.85 σ.

Realised heritabilities (Table 3) estimated for the first 20 generations of selection and trends were similar to direct responses in Table 1. Realised heritabilities for 3–6 week gain and 6-week weight tended to decline in later generations. However, curvilinear response was not significant in any of the three lines when fitting a quadratic term in the regression model and taking into account the effect of errors correlated among generations (Bennett 1981). Realised heritability for 3-week weight was not significant either in the early or later generations of selection.

Selection response in the W, G and S lines is depicted in Figs. 4–6 respectively. Figure 4 shows clearly that a maximum response of just over 2 g in 3-week weight occurred in generation 8. The marked decline in response between generation 9 and 10 (from +2 g to zero), was the reason for the difference between a realised heritability of 0.33 (generations 1–9) and 0.09 (generations 1–10). No further response to selection for 3-week weight was found after generation 9. In contrast, response to selection for 3–6 week gain (Fig. 5) continued but the rate of response decreased after generation 10. Selection response for 6-week weight (Fig. 6) was marked and linear over generations 1–10, then plateaued for seven generations and resumed thereafter. The response was extremely variable between generations 20 and 30.

Table 2. Per generation average selection differential (generations 1 to 30) in absolute and standardised units

Line	Selection differential	
	g	$\sigma_W{}^1$
W	0.6	0.78
G	1.1	0.64
S	1.3	0.65

[a] σ_W – within-litter SD

Table 3. Estimates of realised heritabilities ± SE[a]

Line	Trait	Generations		
		1–10	11–20	1–20
W	3-week wt	0.09±0.16 (0.33±0.20)[b]	0.03±0.14	0.07±0.10
G	3–6 week gain	0.36±0.14*	0.21±0.12	0.24±0.11*
S	6-week wt	0.46±0.10**	0.15±0.10	0.26±0.09**

[a] * $P < 0.05$; ** $P < 0.01$

[b] From generations 1–9

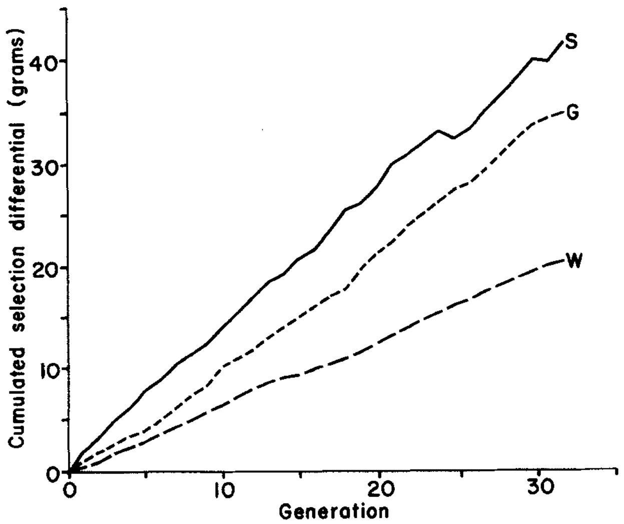

Fig. 3. Cumulated selection differentials plotted against generations

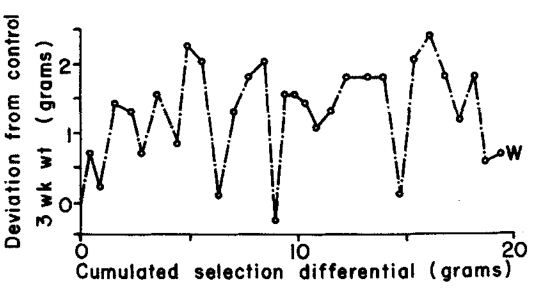

Fig. 4. Response as a deviation from control plotted against cumulated selection differential for 3-week weight

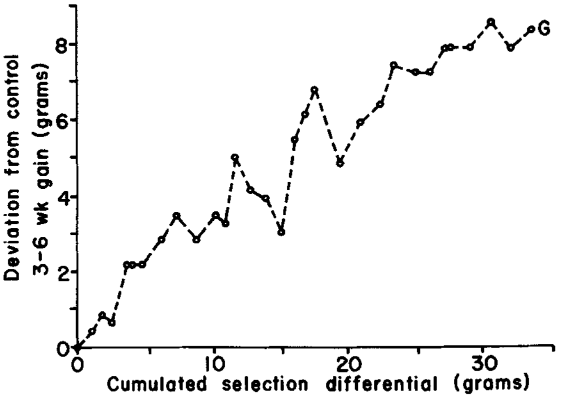

Fig. 5. Response as a deviation from control plotted against cumulated selection differential for 3–6 week gain

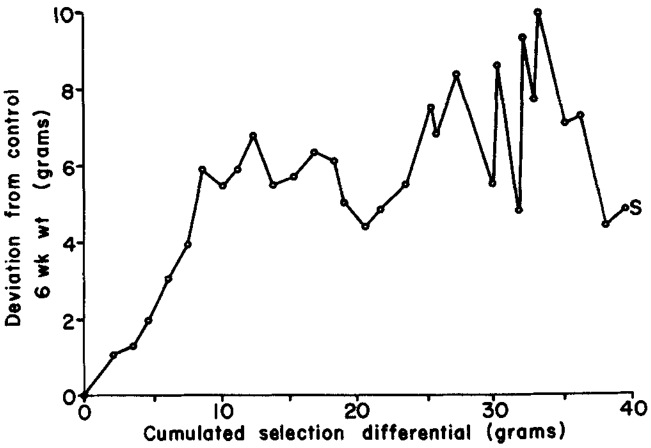

Fig. 6. Response as a deviation from control plotted against cumulated selection differential for 6-week weight

Long-term response

Curvilinearity of long-term direct and correlated response was further investigated by regression equations including both linear and quadratic terms over generations 1 to 30. The only significant curvilinearity was for 6-week weight and 3–6 week gain in the S line.

Long-term response was estimated by averaging the deviations from control over the generations when responses had either ceased or shown evidence of declining. This has been done in Table 4 for generations 20–28. Generations 29 and 30 were not included, since the S line had already started to show evidence of a decline in performance which resulted in its loss in generation 32 (Figs. 1 and 2).

The effect of long-term selection on growth curves at generation 24 (second litters) in the selected and control lines is depicted in Fig. 7. Both Table 4 and Fig. 7 show clearly that both 3–6 week gain, 6-week weight and all subsequent weights up to 12 weeks of age were larger in the G and S lines than in the W or

Table 4. Long-term direct (underlined) and correlated responses. Deviation from control (SD units) averaged over generations 20–28 and control line averages (g)

Line	Traits		
	3-week wt	3–6 week gain	6-week wt
W	2.1	0.9	1.6
G	1.4	4.5	4.8
S	1.8	3.9	4.0
Co	8.9	10.7	19.6

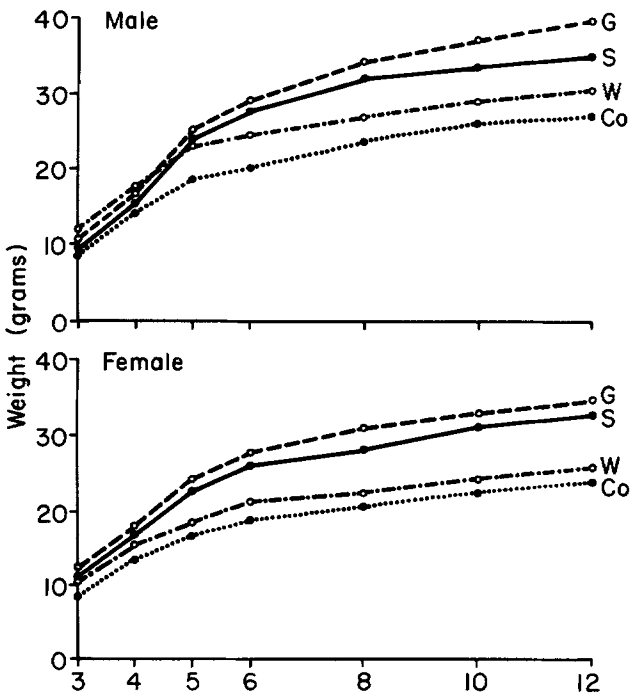

Fig. 7. Growth curves for males and females in the selected lines and the control line in generation 24

Co lines, with a small advantage for the G line over the S line. Direct selection for 3-week weight in the W line resulted in this line being the heaviest at this age. Mice in the W line were heavier than those in the Co line but lighter than G or S animals.

Realised genetic correlations

Estimates of realised correlations are presented in Table 5. Estimates of the genetic correlation between 3-week weight and 6-week weight, depended on the trait selected. Selection for 6-week weight resulted in strong short-term and long-term correlated responses in 3-week weight. However, selection for 3-week weight did not elicit such a strong correlated response in 6-week weight. A similar relationship for 3-week weight and 3–6 week gain occurred and the difference between the estimates of genetic correlation was more marked in the long-term in this particular case. Estimates of the genetic correlation between 3–6 week gain and 6-week weight were consistent and ranged between 0.78 and 1.01.

Table 5. Estimates of realised genetic correlations (r) among growth traits

Generations	Traits		Realised genetic correlations[a]		
	X	Y	r_{yx}	r_{xy}	r ± SE
1–9 or 10	3-week wt	3–6 week gn	0.18	0.29	0.23 ± 0.08
	3-week wt	6-week wt	0.63	1.06	0.82 ± 0.04
	3–6 week gn	6-week wt	0.78	0.89	0.82 ± 0.04
20–28	3-week wt	3–6 week gn	0.22	0.58	0.35 ± 0.10
	3-week wt	6-week wt	0.39	0.86	0.58 ± 0.08
	3–6 week gn	6-week gn	0.93	1.01	0.97 ± 0.04

[a] r_{yx} is the genetic correlation estimated from the correlated response of Y when selecting for X, and vice versa for r_{xy}. The estimate denoted as r was calculated as in eq. (2)

In the case of the genetic correlations between 3-week weight and 3–6 week gain, and between 3–6 week gain and 6-week weight the estimates increased from early to long-term; for the latter case this was perhaps real (0.81 ± 0.04 vs. 0.97 ± 0.04). In the case of the genetic correlation between 3-week weight and 6-week weight the short-term estimate was larger than its long-term counterpart (0.82 ± 0.04 vs. 0.58 ± 0.08).

Phenotypic and environmental correlations

The correlation estimates in Table 6 were similar for early or long-term response. Correlations were positive and large for 3–6 week gain and 6-week weight (0.71–0.90), moderate for 3-week weight and 6-week weight (0.42–0.57) and low for 3-week weight and 3–6 week gain (0.08–0.13).

Correlated responses for some reproductive traits

Fertility was higher in this study than in most other selection studies with mice (e.g. Falconer 1973), due mainly to the extended mating period. Over the first 30 generations 'fertility' was 97.5% in the G line, 94.1% in the S line, 99.6% in the W line, and 95.4% in the Co line. Litter size, survival from birth to weaning and 'productivity', were plotted against 5-generation intervals as shown in Figs. 8–10, respectively. Litter size in the Co line declined over 30 generations from about 8 to 6 mice born per litter (Fig. 8). Inbreeding accumulated over this period is the most likely cause of this decline. With an effective population size of 32, the

Table 6. Estimated phenotypic ($\hat{r}_P$), genetic ($\hat{r}_G$) and environmental ($\hat{r}_E$) correlations among the growth traits

Generations	Traits correlated	$\hat{r}_P$	$\hat{r}_G$	$\hat{r}_E$
1–9 or 10	3-week wt – 3–6 week gn	0.13	0.23	0.08
	3-week wt – 6-week wt	0.57	0.82	0.42
	3–6 week gn – 6-week wt	0.90	0.81	0.71
20–28	3-week wt – 3–6 week gn	0.13	0.35	0.10
	3-week wt – 6-week wt	0.57	0.58	0.57
	3–6 week gn – 6-week wt	0.90	0.97	0.90

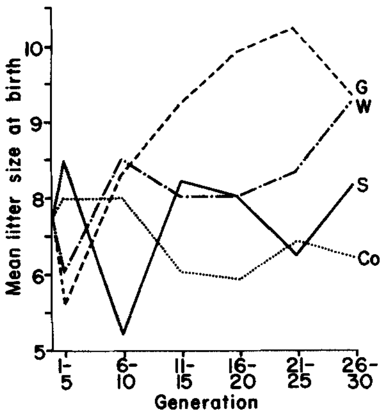

Fig. 8. Mean litter size at birth averaged over 5-generation intervals

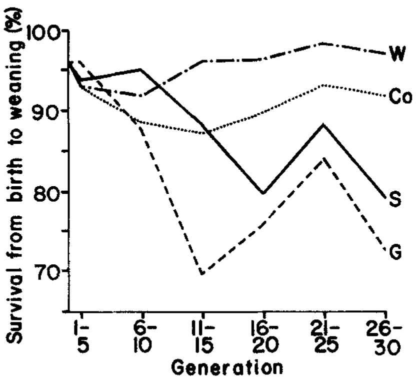

Fig. 9. Per cent survival from birth to weaning averaged over 5-generation intervals

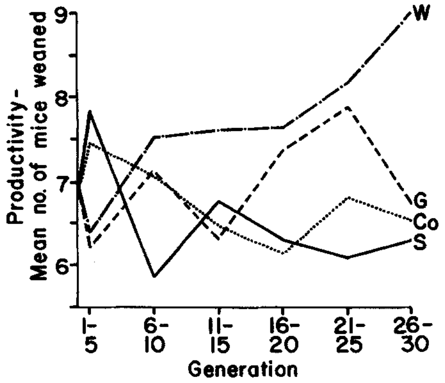

Fig. 10. Productivity, defined as mean number of mice weaned per mating made, averaged over 5-generation intervals

expected rate of increase of inbreeding is 1.6% per generation, i.e., the coefficient of inbreeding (F) would be 48% by generation 30. Inbreeding depression was estimated as 0.42 mice per 10% increase of F. This compares with values of 0.58 obtained by Bowman and Falconer (1950) and 0.50 by Falconer (1973). Litter size increased over generations in the G and W lines but not in the S line. Pre-weaning survival (Fig. 9) remained relatively constant over generations in the W and Co lines but declined in the S and G lines from 95% to about 80%. The net result was a small decline in productivity over generations in the Co line from about 7 to 6.5 mice (Fig. 10). The S and the G lines, had 'productivity' levels similar to the Co line. However, 'productivity' in the G line increased between generations 16 and 25. There was a linear increase in 'productivity' in the W line from 7 to 9 mice over the course of the experiment.

Discussion

Response to selection

The literature on selection for increased body weight growth in mice is large and has been reviewed by Roberts (1965), Eisen (1974) and McCarthy (1982). Studies where the three growth traits considered here were selected simultaneously have not been reported. However, either 3–6 week gain or 6-week weight have been common selection criteria in numerous experiments with mice. The average of 11 realised heritability estimates for 3–6 week gain in 6 different studies was 0.25 (McCarthy 1982). The average of 13 realised heritability estimates for 6-week weight in 6 other experiments was 0.33 (McCarthy 1982). These were estimates based on medium-to long-term responses to selection (8–24 generations) and can be compared with the estimates of 0.24 and 0.26 for 3–6 week gain and 6-week weight respectively, estimated from 20 generations of selection in the present study (Table 3). The evidence would suggest that these two traits have similar, moderate, levels of heritability.

Two other studies selected for 3-week weight in mice. Hull (1960) in an experiment of 5 generations reported a realised heritability estimate of 0.74 ± 0.14. Frahm and Brown (1975) in a replicated selection study of 14 generations obtained estimates of 0.15, 0.16 and 0.19. The estimates in the present study were 0.33 ± 0.20 over the first 9 generations of selection, and 0.07 ± 0.10 over 20 generations. Hull's (1960) estimate of realised heritability for 3-week weight was larger than that for 6-week weight (0.57 ± 0.20) found in the same study. This was surprising because it is well known that 3-week weight in mice is strongly affected by maternal effects (e.g., Monteiro and Falconer 1966; Legates 1972) which often mask expression of additive genetic variance. Hull (1960) suggested that his high estimate of realised heritability could be due to the fact that within-litter selection was used, thus rendering selection more effective presumably because differences in maternal environment were eliminated. In the present study and in that of Frahm and Brown (1975) within-litter selection was practised but estimates of heritability were much lower. Random drift in gene frequencies might be a factor in Hull's results.

The present study was unreplicated and the results were undoubtedly influenced by random genetic drift. Falconer (1973) in a replicated selection experiment for 6-week weight in mice demonstrated the importance of random drift in lines selected with an effective population size (N_e) of 32. Falconer's six replicates gave dissimilar estimates of realised heritability, and evidence of asymmetry of direct and correlated responses. Falconer (1973) concluded that a single experiment of the scale of the present one ($N_e = 32$) can be misleading about the rate of response and the direction of correlated responses. However, as summarised by McCarthy (1982), there have also been studies where there was close agreement among realised heritability estimates in replicate populations with similar or smaller size than Falconer's (i.e., Sutherland et al. 1970; Hanrahan et al. 1973; Rutledge et al. 1973; Frahm and Brown 1975). To the extent that many of the results obtained in the present study can be compared with other experiments which have selected for the same traits, albeit not in the one study, the consistency of results will at least broadly establish the generality or otherwise of particular outcomes.

Correlated responses and genetic correlations

Because of the long-term nature of this study it was possible to investigate changes in realized genetic correlations over time. It was also possible to obtain two estimates of each genetic correlation. Discordance between the two estimates will be referred to as asymmetrical correlated responses (Bohren et al. 1966).

The estimates of the genetic correlation between 3–6 week gain and 6-week weight were large, positive and symmetric. Estimates for long-term response were larger than those from early response. These genetic correlation estimates were in agreement with other estimates with mice, e.g., 1.04 ± 0.05 estimated from two replicate lines selected for 6-week weight (Rutledge et al. 1973) and paternal half-sib estimates of about 0.75 by Hanrahan and Eisen (1973). Falconer (1973) reported correlated responses for 3–6 week gain graphically over the first 8 generations. From his graphs, averaged over the 6 replicates up to generation 8, a direct response (divergence) of 11 g and a correlated response of 7 g were approximately calculated. Using Falconer's realised heritability of 0.37 for divergent response for 6-week weight, and assuming a heritability of 0.35 for 3–6 week gain and within-litter standard deviations of 2.0 and 1.6 for 6-week weight and 3–6 week gain, respectively, an estimate of 0.82 was found for the genetic correlation between these two traits from his study. It appears that the genetic correlation between 3–6 week gain and 6-week weight is in the range of 0.8 to 1.0.

Estimates of the genetic correlation between 3-week weight and 3–6 week gain were positive and low to moderate in value. For early response (0.23 ± 0.08) there was no evidence of asymmetry. However, the long-term genetic correlation was asymmetric (0.22 vs. 0.58). This was due to the low realised heritability estimate for 3-week weight (0.07) used in the calculations. Long-term correlated response in standard deviation units for 3–6 week weight when selecting for 3-week weight was 0.9; that for 3-week weight when selecting for 3–6 week gain was 1.4 (Table 4).

Frahm and Brown (1975) found a realised genetic correlation of 0.47 between 21-day weight and 21 to 42-day average daily gain, over 14 generations of selection and 3 replicates. This estimate, calculated as in (2), is not significantly different from our corresponding long-term value of 0.35 ± 0.10. Frahm and Brown's data do not suggest asymmetry of the genetic correlation. From 8 generations of selection for 3–6 week gain in two replicates, Wilson (1973) reported realised genetic correlations with 3-week weight of 0.20 and 0.32, which compare well with our estimate of 0.29 over 10 generations.

The estimated genetic correlation between 3-week weight and 6-week weight was larger when selecting for 6-week than when selecting for 3-week weight. This was true for both short-term and long-term responses (Table 5). Genetic correlations were smaller for long-term responses than for short-term responses. Hull (1960) reported estimates comparable to the ones estimated here. His estimate calculated as in (2) was 0.82; this is the same as our estimate of 0.82 ± 0.04 over 10 generations of selection.

Hull (1960) found asymmetrical correlated responses opposite to those found here. The correlated response in 6-week weight when selecting for 3-week weight was larger than the direct response to selection for 6-week weight. The only other study where selection was for 3-week weight was that of Frahm and Brown (1975). While these authors did not calculate a realised genetic correlation with 6-week weight, this can be indirectly estimated from correlated responses for 6-week weight they reported. Assuming a heritability of 6-week weight of 0.35, the estimate of the genetic correlation between 3-week and 6-week weight would be 0.59. This is similar to the estimate in this study of 0.63 but not to Hull's estimate of 1.01. Hull's (1960) results, in terms of direct and correlated responses, seem atypical.

Rutledge et al. (1973) reported a genetic correlation with 3-week weight from selection for 6-week weight averaged over two replicates, of 3.24. This estimate was obtained using paternal half-sib heritability estimates from their base population of 0.01 ± 0.16 for 3-week weight, and 0.36 ± 0.10 for 6-week weight. Falconer (1973) graphically portrayed correlated responses for 3-week weight from selection for 6-week weight in each of six replicate lines. The average direct and correlated responses for upwards selection (the deviation of the large line from the control at generation 8) were about 7.5 g and 2 g, respectively. Taking Falconer's realised heritability of 0.4 for 6-week weight and a heritability of 0.17 (Frahm and Brown 1975) for 3-week weight, and appropriate standard deviations, the estimate of genetic correlations derived is 1.02. The comparable value in the present study was 1.06 (Table 5). Hull's (1960) value of 0.63 seems to be the lowest reported.

Correlated responses to selection, are more sensitive to changes in genetic variances and covariances stemming from changes in gene frequencies than direct responses (Bohren et al. 1966). In the absence of mutation (Hill 1982) gene frequencies change in a selection experiment due to selection and to random drift. This was well demonstrated in Falconer's (1973) study where the correlated response for 3-week weight to selection for 6-week weight showed marked variation among the 6 replicates. Bohren et al. (1966) concluded that asymmetry of correlated responses was a more likely event than symmetry in selection programs. We seem to have a case of asymmetry of correlated response in the case of 3-week weight and 6-week weight reported in this paper.

Implications of the results

The selection study with mice reported here was initiated in New Zealand in 1965 to answer questions regarding appropriate selection criteria for growth in sheep and beef cattle. In general terms the question asked was: 'What is the relative efficiency of selecting for weight at an early age (i.e., weaning), versus selecting for a weight at an older age prior to first mating, versus selecting for gain in weight between these ages?' If we assume that 6-week weight in mice is equivalent to 'market weight' in domestic species it appears that in the short-term at least (e.g., 10 generations) 'market weight' is the best selection criterion. For long-term response there is little difference between market weight or post-weaning gain as selection criterion to improve market weight. If, however, the objective is to improve weaning weight, the best selection criteria is market weight because of the higher realised heritability of market weight, than weaning weight and a high genetic correlation between them (~ 0.8).

Table 7. Summary of genetic parameter estimates for some growth traits in beef cattle, sheep, pigs, and mice

Species	Heritability			Genetic correlations	
	Weaning wt (WW)	Final wt (FW)[a]	Gain (G)	WW–FW	G–FW
Beef cattle[b]	0.24 (0.21)	0.46 (0.36)	0.34 (0.36)	0.71 –	0.82 –
Sheep[c]	0.20	0.35	0.32	0.70	0.77
Pigs[d]	0.18	(0.47)	0.40	(– 0.80)	(– 0.88)
Mice[e]	0.17	0.33	0.25	0.80	0.80

[a] FW is 12–20 month wt for beef cattle, 6–12 month wt for sheep, and 6-week wt in mice. Since pigs are commonly marketed at a fixed weight (85–100 kg) the measure of growth here is age at a constant weight (in brackets)

[b] From Woldehawariat et al. (1977); bracketed values are a summary of North American realised heritability estimates (Koch et al. 1982)

[c] From Clarke and Rae (1977) and Olson et al. (1976 a)

[d] From Hutchens and Hintz (1981)

[e] FW and G from McCarthy (1982) and WW from Frahm and Brown (1975); genetic correlations-literature summary in this paper (based on eq. (2))

These results are compatible with estimated genetic parameters for similar growth traits in beef cattle, sheep and pigs as summarised in Table 7. Final weight is about twice as heritable as weaning weight and there is a high genetic correlation between them (~ 0.8). Weaning weight in any species is a trait strongly influenced by both direct genetic and maternal effects (both environmental and genetic), and improvement of this trait requires partitioning of these effects and knowing the genetic covariance between direct and maternal genetic effects (e.g., Willham 1972; Legates 1972; Koch 1972; Gianola et al. 1977; Baker 1980; Itulya et al. 1983). However, there is a strong case for indirect selection on final weight to improve weaning or earlier weights in many livestock species (e.g., Baker et al. 1979 b; Kuhlers and Jungst 1983).

The estimates summarised in Table 7 also show a moderate level of heritability for gain but in most cases being a little lower than that for final weight. All parameter estimates for beef cattle in Table 7, and those for gain in sheep, were obtained with high-energy feeding under feedlot situations. Under pasture feeding situations the heritability of post-weaning gain in both sheep and cattle average about half the values shown in Table 7 (e.g., Carter 1971; Baker et al. 1975; Ch'ang and Rae 1970; Baker et al. 1979 b) and range from 0 to 0.25. This has been interpreted in terms of compensatory growth due to both pre- and post-weaning environmental effects which mask genetic variance and accurate estimation of breeding value. For this reason national genetic improvement programs in New Zealand for sheep and beef cattle use weights at a given age (adjusted for known environmental effects) rather than gain as selection criteria for growth. The situation seems different in more controlled environmental conditions, where gain may be an adequate selection criterion for growth. It may be, however, that there is an optimum period over which to measure this gain in terms of predicting breeding value for final market weight (e.g., Olson et al. 1976b).

In this study with mice the significant asymmetrical correlated responses involved weaning weight and 6-week weight. The "joint" estimate (eq. 2) was 0.82 ± 0.04, and the two separate estimates 0.63 and 1.06. The value of 0.82 is similar to estimates in domestic species (Table 7). The value of 0.70 for sheep is the genetic correlation between weaning and yearling weight used in index calculations in the New Zealand sheep improvement program (Clarke and Rae 1977). Selection index theory as presently formulated (Hazel 1943), assumes symmetric genetic correlations. However, theoretical (Bohren et al. 1966) and experimental evidence (e.g., Falconer 1960; Bell and McNary 1963; Yamada and Bell 1963; Baker and Cockrem 1970; Rutledge et al. 1973; Nordskog et al. 1974; Sheridan and Barker 1974; Falconer 1981; Gianola 1982; Kuhlers and Jungst 1983) indicates that correlated responses and genetic correlations may be asymmetric, the differences depending on the trait being selected, the direction of selection, the type of selection (multiple vs. single trait), the system of mating, the environment in which selection takes place, and the number of generations of selection. At our present state of knowledge it seems impossible to predict either the rate or the direction these differences in correlated responses may take. It is, however, an area of importance in animal breeding applications and further theoretical and experimental work is clearly needed to help elucidate the genetic architecture of genetic correlations.

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