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Selection for Increased 12-Day Litter Weight in Mice[1]

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Summary. Selection for increased 12-day litter weight of standard litters of eight mice was practiced for nine generations in a replicated experiment with controls. The two selection lines followed very similar patterns of response. The pooled realized heritability was 0.08 ± 0.04 and the observed genetic gain was 0.57 ± 0.19 g per generation. The replicated controls showed a negative trend in 12-day litter weight which was likely due to the effects of inbreeding and possibly some detrimental environmental fluctuation. Derivations of the components of variance affecting 12-day body weight indicated that direct additive genetic variance arising from genes controlling growth from birth to 12 days of age accounted for 37.0% of the total variation, while maternal additive genetic variance and postnatal maternal variance accounted for 16.4% and 49.6% of the variance, respectively. The direct additive genetic-maternal genetic covariance was negative but small. Significant positive correlated responses were observed for 12, 21, 42 and 56-day body weight, but no correlated responses were observed for postweaning body weight gain or for reproductive efficiency measured as number born and percent fertile matings.

Introduction

Preweaning growth in the laboratory mouse is influenced to a large degree by the postnatal maternal ability of the dam (Cox, Legates and Cockerham 1959; El Oksh, Sutherland and Williams 1967; White, Legates and Eisen 1968 and Young, Legates and Farthing 1965). These studies showed that postnatal maternal influences accounted for 70–80% of the variance on 12-day litter weight of six mice, and that 12-day litter weight may be a useful phenotypic indicator of postnatal maternal performance. Others (Eisen, Legates and Robison 1970; Jara-Almonte and White, 1973 and Young and Legates 1965) have shown that the heritability of postnatal maternal ability measured as the 12-day weight of a standard sized litter averages about 0.25 and should therefore respond to selection. However, selection for increased preweaning litter weight has shown limited success in previous studies (Falconer 1955; Eisen *et al.* 1970; Legates and Farthing 1962). In addition only one previous study (Eisen *et al.* 1970) examined, in detail, correlated responses in other growth and reproductive traits. The purpose of this investigation was to evaluate selection response for increased 12-day litter weight of eight suckling young in a replicated experiment with controls and to assess correlated responses in other growth and reproductive traits.

Experimental Procedure

The base population (ICR-Albino) was obtained from the large, non-inbred colony at the Institute for Cancer Research, Philadelphia, Pa. After two generations of random mating to allow for acclimation to this laboratory and to expand the original base population of 100 females and 50 males, individuals were randomly divided into four lines. Within-family selection for increased 12-day weight of a litter of eight mice was initiated in two replicate lines (S-1 and S-2), while two lines (C-1 and C-2) were maintained as unselected controls. Each of the selection lines ideally consisted of 18 full-sib families, each generation, with each family containing six females and two males. Each control line consisted of 30 paired matings each generation. Generations were contemporary in all four lines throughout the experiment. Results are presented for the first nine generations of selection.

The selection procedure was based on the deviation of the 12-day litter weight from the family mean. The litter within a full-sib family of litters which had the largest positive deviation from its full-sib family 12-day litter weight mean was selected, along with a single litter from 17 other families, to serve as parents for the next generation (Fig. 1). The only exception to this procedure occurred when the litter with the largest deviation did not contain at least one male or three females. In such a case, the litter with the second largest deviation was selected.

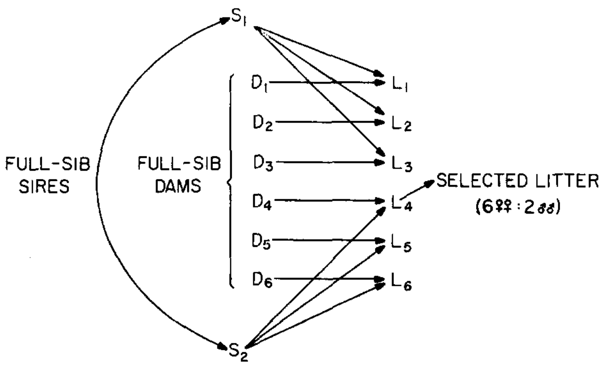

Fig. 1. Mating design for within-family selection scheme

Although 12-day litter weight has been shown to be largely a trait of the dam (Young *et al.* 1965 and El Oksh *et al.* 1967), the additive genotype of the young must also be considered since it also contributes to the preweaning growth of the offspring (Eisen *et al.* 1970 and Bateman 1954). The variation due to the genotype of the suckling young may be minimized by mating all full sisters to

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a single, unrelated male. However, mating all full-sib females to a single male is rather risky since one infertile male would result in the loss of an entire family. Therefore, the mating scheme shown in Figure 1 was used in the selected lines. Ideally, six daughters from a litter selected to serve as parents for the next generation were paired randomly with two full-sib sons from an unrelated litter. Each male was then mated to three of the females. This mating design was similar to the one outlined by Eisen *et al.* (1970).

Dams were eight to ten weeks of age at mating. Only first litters were used. At parturition, the number of young born alive, hereafter expressed as the number born, was recorded. At five days of age the litters were standardized to eight mice, including six females and two males in the selection lines and four females and four males in the controls. Litters with five to seven mice were augmented to eight with foster mice from other litters. These fostered mice were discarded at weaning.

At 12 days of age, each mouse was permanently identified by toe clipping and weighed. Total litter weights were also recorded at 12 days, and selection decisions were made at this point. At weaning (21 days) each mouse was again weighed and four unrelated mice of the same sex and age were caged together in polypropylene cages. Only selected litters were weaned. All other mice were discarded. The mice were individually weighted at 42 and 56 days of age. All weights were recorded to the nearest tenth of a gram.

Old Guilford Breeder Pellets were fed ad libitum from mating until weaning and Purina Lab Chow was fed ad libitum after weaning. The laboratory was maintained at approximately 22 °C with a continuous light to darkness ratio of one (12 hr. light to 12 hr. darkness).

Estimates of Genetic and Environmental Variances

The total genetic variance associated with 12-day litter weight was partitioned into three components. These included the direct additive genetic variance $(\sigma^2_{A_0})$ for growth in the offspring, the maternal additive genetic variance $(\sigma^2_{A_m})$ for postnatal maternal ability in the dam and the direct-maternal additive genetic covariance $(\sigma_{A_0A_m})$. These three components were estimated from covariances among various sets of relatives following the procedures of Willham (1963) and Eisen *et al.* (1970). The relative magnitudes of these three parameters indicate their importance in determining 12-day litter weight and are helpful in predicting selection response.

In deriving the covariances among relatives for this design, it was assumed that prenatal genetic and permanent environmental effects; postnatal maternal dominance and epistatic effects; and direct genetic dominance and interaction effects were of minor importance. Although these basic assumptions may not be totally justified (Jara-Almonte and White 1973), biases resulting from the failure of these assumptions to be completely valid should be minimal (Young and Legates 1965).

From the mating design shown in Fig. 1, hierarchical analyses of variance were conducted utilizing the following model:

$$Y_{ijkm} = \mu + g_i + f_{j(i)} + s_{k(ij)} + w_{m(ijk)}$$

where Y_{ijkm} = 12-day litter weight of a litter from the m^{th} dam mated to the k^{th} full-sib sire within the j^{th} family of full-sib dams within the i^{th} generation.

μ = general mean
g_i = the effect of the i^{th} generation ($i = 1, 2, \ldots, 9$)
$f_{j(i)}$ = the effect of the j^{th} full-sib family of dams within the i^{th} generation ($j = 1, 2, \ldots, 18$).
$s_{k(ij)}$ = the effect of the k^{th} full-sib sire within the j^{th} family of full-sib dams ($k = 1, 2$).
$w_{m(ijk)}$ = the effect of the litter from the m^{th} dam.

The effects of $f_{j(i)}$, $s_{k(ij)}$ and $w_{m(ijk)}$ were assumed to be normally and independently distributed random variables with means zero and variances σ^2_f, σ^2_s and σ^2_w, respectively. Based upon the relationships developed from the mating design (Fig. 1), these variance components have the following expected values (Willham 1963 and Eisen *et al.* 1970):

$$\sigma^2_f = Cov\,(L_1, L_4) = .25\sigma^2_{A_0} + .50\sigma^2_{A_m} + .50\sigma_{A_0A_m}\,, \quad (1)$$

$$\begin{aligned}\sigma^2_s &= Cov\,(L_1, L_2) - Cov\,(L_1, L_4)\\ &= \left(.375\sigma^2_{A_0} + .50\sigma^2_{A_m} + .50\sigma_{A_0A_m}\right) - \left(.25\sigma^2_{A_0} + \right.\\ &\quad \left. + .50\sigma^2_{A_m} + .50\sigma_{A_0A_m}\right) = .125\sigma^2_{A_0}\,, \qquad (2)\end{aligned}$$

$$\begin{aligned}\sigma^2_w &= .125\sigma^2_{A_0} + .5\sigma^2_{A_m} + .5\sigma_{A_0A_m} + \sigma^2_c + \\ &\quad + \left(.5\sigma^2_{A_0} + \sigma^2_e\right)/8\\ &= .1875\sigma^2_{A_0} + .5\sigma^2_{A_m} + .5\sigma_{A_0A_m} + \sigma^2_c + .125\sigma^2_e\,, \qquad (3)\end{aligned}$$

where σ^2_c = permanent (common) environmental variance
σ^2_e = random environmental variance.

The phenotypic variance for 12-day litter weight then is:

$$\begin{aligned}\sigma^2_{p'} &= \sigma^2_f + \sigma^2_s + \sigma^2_w = .5625\sigma^2_{A_0} + \sigma^2_{A_m} + \sigma_{A_0A_m} + \sigma^2_c + \\ &\quad + .125\sigma^2_e\,. \qquad (4)\end{aligned}$$

The phenotypic variance of 12-day individual weight is given by the sum of the phenotypic variance for 12-day litter weight explained by the model and the portion not explained by the model as a result of not considering 12-day individual weight. Hence:

$$\sigma^2_p = \sigma^2_{p'} + .43\sigma^2_{A_0} + .875\sigma^2_e\,. \quad (5)$$

Offspring-parent relationships were determined from the regression of daughter 12-day litter weight on dam 12-day litter weight for each line pooled over the nine generations. Since selection was practiced on the dam's record, the parent-offspring covariance was computed as the product of the regression coefficient and the phenotypic variance $(\sigma^2_{p'})$ estimated from the analysis of variance. The regression coefficient was calculated by randomly choosing a daughter from each litter then regressing these random daughters on their dams.

The expected covariance, $Cov(L_1', L_1)$, between dams and daughters, was computed as the weighted mean of all possible covariances between individuals in the dam's litter (L_1') and individuals in the daughter's litter (L_1). $Cov(L_1', L_1) = 8Cov$ (daughter, dam) + 56 Cov (maternal aunt, niece)/64

$$= .281\sigma^2_{A_0} + .500\sigma^2_{A_m} + .813\sigma_{A_0A_m}\,. \quad (6)$$

Estimates of the variance components $\sigma^2_{A_0}$, $\sigma^2_{A_m}$ and $\sigma_{A_0A_m}$ were obtained from the simultaneous solutions of equations (1, 2 and 6). The σ^2_e was obtained by adjusting the variance for 12-day individual weight to a litter total basis by multiplying it by 64, the square of the number of mice per litter, then equating the adjusted variance to the expectation of the within fullsib family variance $\left(.5\sigma^2_{A_0} + \sigma^2_e\right)$ and solving. The σ^2_c was derived by solving equation (3).

Selection Response: The direct response to selection for increased 12-day litter weight was measured as the regression of the deviation of the selection lines from the pooled control on generation number.

The expected selection differential was calculated as the deviation of the selected daughter's 12-day litter weight from the mean of her full-sib family and summing over all families. The realized selection differential which was a weighted selection differential was calculated in a manner similar to the expected selection differential, except that each deviation was weighted by the number of daughters from the selected litter which actually produced a litter. These procedures were performed for each line per generation for males and females and the sexes were subsequently averaged.

Both the expected and realized heritabilities were computed for the nine generations of selection in each selected line. Realized heritability for each selected line was calculated as the regression of the sum of the deviation of selected lines generation mean from the control line mean on the realized cumulative selection differential.

The expected heritability calculated from the data pooled over generations was based on considerations involving the covariances between litters which were both single first cousins and half-sibs and litters which were double first cousins.

$$\begin{aligned} Cov\,(L_1, L_2) &= Cov\,(L_1, L_3) = Cov\,(L_2, L_3) = (L_4, L_5) \\ &= Cov\,(L_4, L_6) = Cov\,(L_5, L_6) \\ &= Cov\ \text{(single first cousins)} + Cov \\ &\quad \text{(paternal half-sibs)} \\ &= .375\sigma^2_{A_0} + .5\sigma^2_{A_m} + .5\sigma_{A_0A_m}\,, \end{aligned} \tag{7}$$

$$\begin{aligned} Cov\,(L_1, L_4) &= Cov\,(L_1, L_5) = Cov\,(L_1, L_6) = Cov\,(L_2, L_4) \\ &= Cov\,(L_2, L_5) = Cov\,(L_2, L_6) = Cov\,(L_3, L_4) \\ &= Cov\,(L_3, L_5) = Cov\,(L_3, L_6) \\ &= Cov\ \text{(double first cousins)} \\ &= .25\sigma^2_{A_0} + .5\sigma^2_{A_m} + .5\sigma_{A_0A_m}\,. \end{aligned} \tag{8}$$

The weighted average of all 15 covariances then becomes:

$$\begin{aligned} Cov_{A_v} &= \left[6\left(.375\sigma^2_{A_0} + .5\sigma^2_{A_m} + .5\sigma_{A_0A_m}\right) + 9\left(.25\sigma^2_{A_0} + \right.\right. \\ &\quad \left.\left. + .5\sigma^2_{A_m} + .5\sigma_{A_0A_m}\right)\right]/15 \\ &= .30\sigma^2_{A_0} + .50\sigma^2_{A_m} + .50\sigma_{A_0A_m}\,. \end{aligned} \tag{9}$$

The value of the weighted average must be subtracted from the total genotypic variance available for selection $\left(\sigma^2_G\right)$ using within family heritability:

$$\begin{aligned} h^2_A &= \left(\sigma^2_G - Cov_{A_v}\right)/\sigma^2_{p'}(1-t) \\ &= \frac{.2625\sigma^2_{A_0} + .5\sigma^2_{A_m} + .5\sigma_{A_0A_m}}{\left(.5625\sigma^2_{A_0} + \sigma^2_{A_m} + \sigma_{A_0A_m} + \sigma^2_C + .125\sigma^2_e\right)(1-t)}\,. \end{aligned} \tag{10}$$

Where:

t = intraclass correlation among 12-day litter weights of females from the same dam.

The intraclass correlation among 12-day litter weights of females from the same dam was obtained from the ratio of the family component of variance to the sum of the components of variance for family, sire and litter. These components were those obtained from the analysis of variance for 12-day litter weight.

Correlated Responses: The correlated responses to selection for increased 12-day litter weight were measured as a regression of the deviation of the trait in the selection lines from the pooled control lines on generation number. The correlated traits examined were individual body weight at 12, 21, 42, and 56 days; growth from 21 to 42 and 42 to 56 days; reproductive fitness measured as litter size and percent fertile matings.

Results and Discussion

Estimates of Genetic and Environmental Parameters

Estimates of variance components derived from analyses of variance and daughter-dam regression coefficients are shown in Table 1. Although there are many degrees of freedom available for each effect, sizable fluctuations occurred in the estimates of the two lines. Similar results were reported by Eisen *et al.* (1970). The trends observed between the family component and sire component of variance for line S-1 were reversed when compared to those for line S-2. Logically, one would expect a greater variability between families than between sires. The estimates obtained from line S-1 were nearly equal indicating as much variation between sires as between families. Estimates from line S-2 followed more closely the expectation. The two lines were tested for homogeneity of error variances and found to be significantly different. However, due to the rather small actual differences in the error variances, the two lines were pooled. The family and sire components contributed 14.2% and 5.7% to the phenotypic variance for 12-day litter weight while the major contribution (80.1%) was made by the litter component. The estimates from Eisen *et al.* (1970) when calculated as a percentage agreed very closely with the percentage contribution found in the present study.

Table 1. *Estimates of variance components from analysis of variance and regression coefficients of daughter on dam for 12-day litter weight*

	Degrees of Freedom for Mean Squares			Variance Components†				Regression of Daughter on Dam
Line	f	s	w	σ^2_f	σ^2_s	σ^2_w	$\sigma^2_{p'}$	
S-1	146	137	389	3.6	4.1	45.6	53.3	−0.041 ± .107
S-2	133	134	324	7.7	2.1	34.9	44.7	0.156 ± .118
Pooled	288	271	713	7.2	2.9	40.7	50.8	0.110 ± .080
Percent				14.2	5.7	80.1	100.0	

† σ^2_f = variance among families of full sib dams, σ^2_s = variance among full-sib sires mated to full-sib dams, σ^2_e = variance among full-sib dams mated to the same sire, $\sigma^2_{p'} = \sigma^2_f + \sigma^2_s + \sigma^2_e$.

The regression coefficients of daughter on dam also presented in Table 1 showed great diversity. The negative regression for line S-1 can only be explained on the basis of sampling error associated with regressing a randomly drawn daughter on each dam. The estimates for line S-2 and the pooled value of the two lines were both positive but relatively small.

The genetic and environmental variances and covariances for 12-day individual weight are shown in Table 2. The individual weight at 12 days of age was utilized to enable the division of the environmental variation into the components between and within litters. The direct additive genetic variance for growth of the offspring represented 37.0% of the phenotypic variance for 12-day individual weight. This estimate of $\sigma^2_{A_0}$ was slightly larger than those reported by Eisen *et al.* (1970), Young *et al.* (1965), and El Oksh *et al.* (1967).

Table 2. *Genetic and environmental components of variance and covariance for individual 12-day weight**

Component	$\sigma^2_{A_0}$	$\sigma^2_{A_m}$	$\sigma_{A_0A_m}$	σ^2_c	σ^2_E	σ^2_p
Estimate	23.2	10.3	− 7.5	31.1	5.6	62.7
Percent	37.0	16.4	−12.0	49.6	8.9	100

* $\sigma^2_{A_0}$ = direct additive genetic variance, $\sigma^2_{A_m}$ = maternal additive genetic variance, $\sigma_{A_0A_m}$ = direct-maternal additive genetic covariance, σ^2_c = maternal environmental variance, σ^2_E = random environmental variance, σ^2_p = phenotypic variance.

The direct maternal genetic variance was smaller, contributing 16.4% of the variation in 12-day individual weight. Eisen *et al.* (1970) reported that the component for the genetic maternal variation represented 6.1% of the total variance. Therefore, based upon these estimates of $\sigma^2_{A_0}$ and $\sigma^2_{A_m}$, response to selection for increased 12-day litter weight would be more associated with increased growth from birth to 12 days than with increased postnatal maternal ability.

The direct-maternal genetic covariance estimate was negative (−7.5) and fairly small. However, it is likely that rather large sampling errors were encountered in attempting to develop this covariance through indirect procedures. These results do not agree with those of Eisen *et al.* (1970) who found a small positive value representing 7% of the phenotype variance for 12-day individual weight. If this covariance is in fact negative, selection response would be further restricted since there is a genetic antagonism between two of the factors determining 12-day weight.

The total postnatal maternal variance $(\sigma^2_{A_m} + \sigma^2_c)$ accounted for 66.0% of the phenotypic variance which is similar to that (56.2%) reported by Eisen *et al.* (1970). Young *et al.* (1965); El Oksh *et al.* (1967); and Cox *et al.* (1959) reported values of 63%, 63% and 61.6%, respectively, for the postnatal maternal variance. As a result of the large common environmental effect which is primarily maternal in origin, the within-family selection scheme utilized in this study was probably the only one that could logically have been used.

Response lo Selection: The mean 12-day litter weights for generations zero through nine are presented in Table 3. The control lines (C-1 and C-2) showed a significant decline in 12-day litter weight over the nine generations studied. Although the two control lines differed to a small extent, the trends were essentially the same since the regression coefficients were homogeneous (Steel and Torrie 1960). Similar trends in the controls were reported by Eisen *et al.* (1970) who used lines that were genetically

Table 3. *Means (g), standard deviations and regressions of 12-day litter weight means on generation number*

	Line			
Gen	C-1 Mean ± SD	C-2 Mean ± SD	S-1 Mean ± SD	S-2 Mean ± SD
0	68.1 ± 5.9	71.1 ± 7.5	68.3 ± 4.9	67.8 ± 6.5
1	71.0 ± 4.9	71.5 ± 4.6	70.8 ± 5.8	72.8 ± 5.7
2	68.1 ± 6.9	70.9 ± 6.6	65.1 ± 8.2	67.2 ± 8.5
3	67.6 ± 5.2	70.6 ± 5.0	69.2 ± 5.3	70.3 ± 6.3
4	66.1 ± 4.7	66.2 ± 5.1	69.2 ± 5.7	72.6 ± 6.1
5	69.7 ± 6.2	70.5 ± 5.8	70.6 ± 6.3	72.2 ± 4.8
6	63.5 ± 5.8	64.1 ± 5.5	66.9 ± 8.2	70.5 ± 5.9
7	59.5 ± 5.9	62.0 ± 4.2	59.4 ± 9.1	64.6 ± 9.0
8	65.1 ± 4.9	64.5 ± 6.2	68.8 ± 5.1	69.5 ± 5.0
9	64.8 ± 5.1	62.8 ± 4.1	65.2 ± 6.6	67.1 ± 7.1
Regression Coefficients	−0.74 ± .29*	−1.11 ± .22**	−0.47 ± .36 0.46 ± .24†	−0.26 ± .30 0.67 ± .27*†

* Statistically significant ($P < .05$)
** Statistically significant ($P < .01$).
† Deviation from the mean of both controls each generation.

quite different from those in the present study and litters that were standardized to six rather than eight.

The negative trends in the controls can be partially explained on the basis of inbreeding depression (White 1972). The average rate of inbreeding was approximately 1% per generation in each line which accumulated to 9% after nine generations. This amount of inbreeding could be expected to account for about a two gram reduction in 12-day litter weight (White 1972). Therefore, it is likely that some unidentified, but consistent environmental trend such as the gradual build-up of subclinical pathogens could also be partially responsible for the decline in the control lines. The control means did not reflect any consistent seasonal trend.

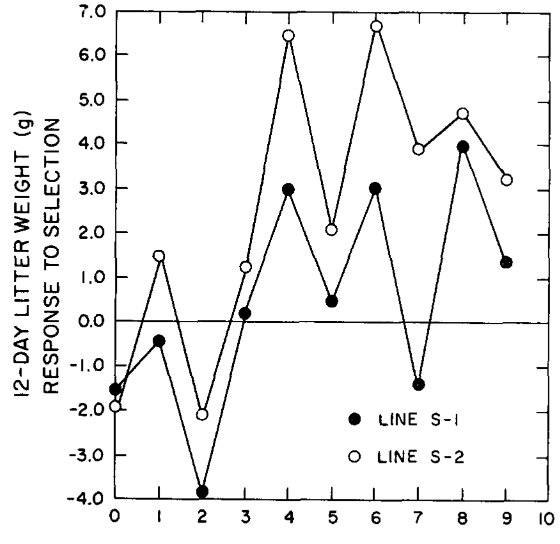

Fig. 2. Response to selection for 12-day litter weight in the two lines expressed as deviations from controls

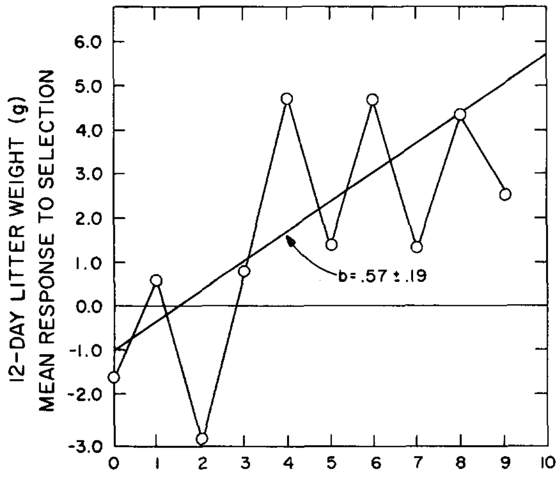

Fig. 3. Response to selection for 12-day litter weight pooled over the two lines as deviations from controls

Response to selection for increased 12-day litter weight, expressed as deviations of generation means from the pooled control, is shown in Fig. 2 and 3. Although wide fluctuations occurred from generations to generation, it is evident that the response was significant (0.57 ± 0.19) and consistent between the two lines (Fig. 2). The individual line regression coefficients were 0.46 ± 0.24 for line S-1 and 0.67 ± 0.27 for line S-2, and these two regressions were homogeneous. Although there was a tendency toward nonlinearity, the quadratic regression coefficients were not significant.

The genetic advance of 0.57 ± 0.19 g per generation represents a cumulative genetic advance of 5.13 g. Based upon the genetic (3.3 g) and phenotypic (6.1 g) standard deviations reported by Jara-Almonte and White (1973), this represents an increase of 1.55 genetic standard deviations and 0.84 phenotypic standard deviation units. This response is approximately twice the genetic gain reported by Eisen *et al.* (1970) for 10 generations of selection and is much greater than other reports (Bateman, cited by Falconer 1955; Legates and Farthing 1962; Dalton and Bywater 1963) which reported little or no genetic gain from selection for litter weight. One of the basic differences between this experiment and that reported by Eisen *et al.* (1970) was the magnitude of the selection differentials. In the present experiment, with litters standardized to six females and two males, the cumulative realized selection differentials (Table 4) were about double those shown by Eisen *et al.* (1970) whose litters were standardized to four females and two males. Strain differences (ICR-albino vs four-way crosses of inbred lines) may also have contributed to the differences in the results of the two experiments.

Table 4. *Cumulative expected and realized selection differentials (g) and the ratio of realized to expected selection differentials for 12-day litter weight*

Line	Expected	Realized	Realized / Expected
S-1	47.7	47.7	1.00
S-2	46.7	47.5	1.02

The ratio of the cumulative realized to the expected selection differentials shown in Table 4 were near unity. Therefore, it is unlikely that natural selection, which would be reflected in the realized selection differential (Falconer 1960), affected the selection response in either direction.

The expected within-family heritability estimate for 12-day litter weight calculated by substituting the components of variance in Table 2 and the intraclass correlation (.14) into formula (10) was 0.25. This value was slightly larger than the 0.20 reported by Eisen *et al.* (1970). However, realized heritabilities in Table 5 were not significant and were much

Table 6. *Regression of various body weights and body weight gain on generations*

Line	12-Day weight	21-Day weight	42-Day weight	56-Day weight	Gain 21 to 42 days	Gain 42 to 56 days
C-1	−0.08 ± 0.04*	−0.21 ± 0.07*	−0.06 ± 0.10	−0.10 ± 0.12	0.15 ± 0.08	−0.04 ± 0.04
C-2	−0.14 ± 0.03**	−0.26 ± 0.04**	−0.10 ± 0.08	−0.10 ± 0.10	0.14 ± 0.09	0.02 ± 0.05
Pooled	−0.11 ± 0.02**	−0.24 ± 0.02**	−0.08 ± 0.07	−0.10 ± 0.07	0.14 ± 0.07	0.03 ± 0.03
S-1	0.10 ± 0.03*†	0.20 ± 0.07*	0.19 ± 0.06*	0.29 ± 0.07**	−0.02 ± 0.10	0.07 ± 0.06
S-2	0.12 ± 0.04*	0.23 ± 0.10*	0.22 ± 0.09*	0.29 ± 0.11*	−0.01 ± 0.10	0.05 ± 0.09
Pooled	0.11 ± 0.03**	0.22 ± 0.06**	0.20 ± 0.06**	0.29 ± 0.06**	−0.01 ± 0.07	0.06 ± 0.05

† Deviation from the mean of both controls each generation.
* Statistically significant ($P < .05$).
** Statistically significant ($P < .01$).

lower than the expected value. Eisen *et al.* (1970) reported a pooled realized heritability of 0.09 ± 0.02 which is very close to the 0.08 ± 0.04 found in this study. Falconer (1955) reported a realized heritability value of 0.14 for increased 12-day litter weight.

Table 5. *Realized heritabilities in the replicated selection lines for increased 12-day litter weight*

Line	h^2 ± S.E.
S-1	.08 ± .06
S-2	.10 ± .06
Pooled	.08 ± .04

The discrepancy between the expected and the realized heritability may be due to overestimated genetic parameters due to nonadditive and intrauterine maternal effects in the numerator of formula (10). Although Miller, Legates, and Cockerham (1963) reported no evidence of nonadditive genetic variance for 12-day litter weight, Jara-Almonte and White (1973), El Oksh *et al.* (1967) and Moore, Eisen, and Ulberg (1970) reported that both nonadditive genetic and intrauterine maternal effects may significantly affect 12-day litter weight.

Correlated Responses in Growth and Reproductive traits: Jara-Almonte and White (1973) utilized the C-1 and C-2 lines in a large population study designed to estimate genetic parameters associated with growth and maternal ability. Their estimated genetic correlations between 12-day litter weight and 12-day individual weight, 21-, 42-, and 56-day body weight and gain from 21 to 42 days and 42 to 56 days were 1.14 ± 0.99, 1.33 ± 0.36, 0.42 ± 0.30, 0.25 ± 0.33, −0.31 ± 0.40 and −0.43 ± 0.40, respectively. Eisen *et al.* (1970) estimated the genetic correlation between number born and 12-day litter weight to be 0.19. From these results, correlated responses would be expected to be sizable for the preweaning body weights, smaller for postweaning weights and negligible for postweaning gain and litter size.

Table. 7 *Regression of number born and % fertile matings on generation number*

Line	Number born	% Fertile matings
C-1	0.04 ± 0.10	−0.9 ± 1.3
C-2	0.15 ± 0.07*	−1.2 ± 1.1
Pooled	0.10 ± 0.06*	−1.1 ± 0.9
S-1	−0.01 ± 0.08	1.5 ± 1.4
S-2	−0.04 ± 0.09	2.5 ± 1.5
Pooled	−0.02 ± 0.06	2.0 ± 0.9*

† Deviation from the mean of both controls each generation.
* Statistically significant ($P < .05$).

Regressions of control mean on generations and the correlated responses (regression of deviations of selection lines from the pooled control) for growth and reproductive traits are shown in Tables 6 and 7, respectively. The regressions for the C-1 and C-2 lines were homogeneous for each trait and there was no significant deviation from linearity. Therefore, generation means for each correlated trait, pooled

Table 8. *Pooled control line means (g) for females for the correlated traits*

Gen	12-Day weight	21-Day weight	42-Day weight	56-Day weight	Gain 21−42 days	Gain 42−56 days	Number born	% Fertile matings
0	8.6	15.2	26.1	28.3	10.8	2.2	12.3	100
1	8.8	15.0	27.6	29.9	12.7	2.3	13.2	89
2	8.6	15.0	26.9	28.4	11.9	1.5	12.9	80
3	8.5	15.1	26.4	28.2	11.9	1.6	13.8	80
4	8.2	14.5	27.2	29.0	12.7	1.9	13.2	80
5	8.6	15.0	27.7	30.0	12.7	2.3	13.8	86
6	7.9	13.4	25.7	27.2	12.3	1.5	15.0	83
7	7.6	13.3	25.4	27.4	12.0	1.9	13.0	80
8	8.1	13.9	25.9	28.2	11.9	2.4	12.9	86
9	7.9	13.3	27.0	28.6	13.7	1.7	13.8	80

over the two control lines, are shown in Table 8 to illustrate the trends in the control lines and to serve as a point of reference for the correlated responses shown in Fig. 4, 5, 6 and 7.

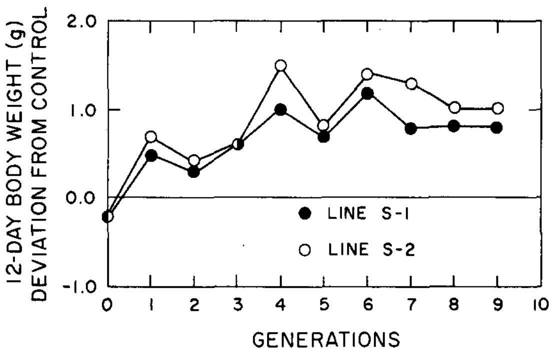

Fig. 4. Correlated response in 12-day individual weight as deviations from the controls

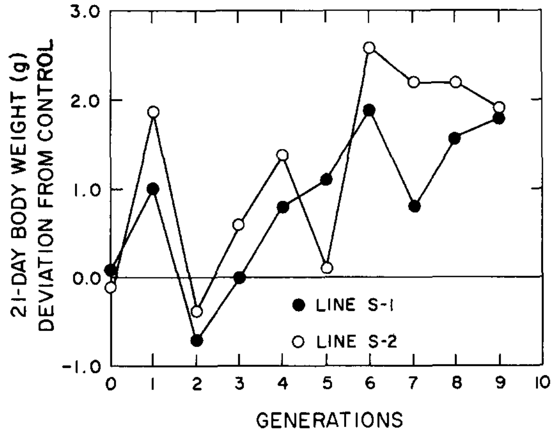

Fig. 5. Correlated response in 21-day body weight as deviations from controls

There were significant negative trends in the control lines for 12-day weight and 21-day weight which paralleled those previously shown for 12-day litter weight. The slightly negative trends in the controls for 42- and 56-day weight were similar to those reported by Eisen *et al.* (1970).

Significant positive linear correlated responses in female body weight at 12-, 21-, 42- and 56 days of age were found in both selection lines (Table 6 and Fig. 4, 5, 6). There was no significant heterogeneity between the two selection lines for these traits, and there was no significant deviation from linearity. As would be expected from the genetic correlations reported by Jara-Almonte and White (1973), the responses in the preweaning traits (1.28% of the original mean increase per generation for 12-day weight and 1.45% for 21-day weight) were relatively larger than for the postweaning traits (0.77% for 42-day weight and 1.02% for 56-day weight). The regressions for 42- and 56-day weight were approximately double those reported by Eisen *et al.* (1970).

In contrast to the results of Eisen *et al.* (1970), who reported a very small but significant positive correlated response, no significant correlated responses were detected for postweaning gain from 21 to 42 days or 42 to 56 days. These results are in basic agreement with those of Jara-Almonte and White (1973) who reported the genetic correlation between 12-day litter weight and gain from 21 to 42 days to be -0.31 ± 0.40. However, LaSalle, White and Vinson (1974) selected for increased gain from 21 to 42 days for 12 generations and reported a small but significant positive correlated response in 12-day litter weight. Therefore, the real genetic relationship between 12-day litter weight and gain from 21 to 42 days is likely very small if they are genetically related at all. An experiment involving reciprocal

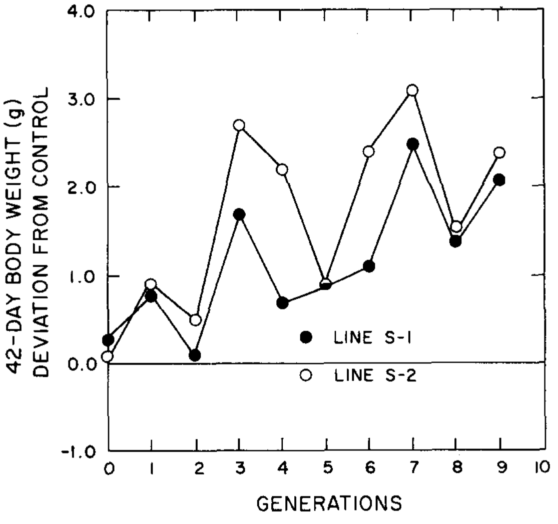

Fig. 6. Correlated response in 42-day body weight as deviations from controls

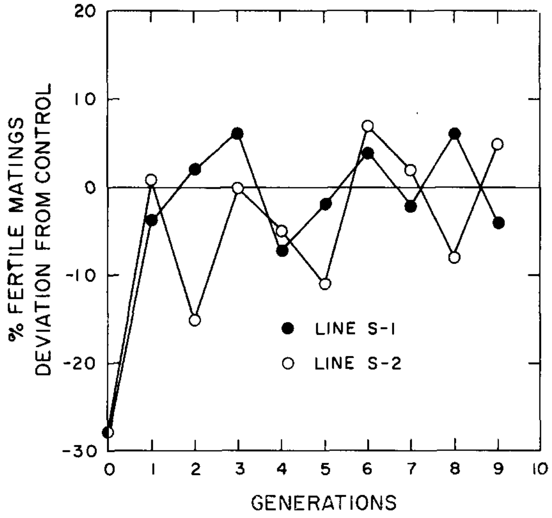

Fig. 7. Correlated response in % fertile matings as deviations from controls

cross-fostering as described by White *et al.* (1968) would have to be completed before the relationship could be determined.

Correlated responses in reproductive traits are shown in Table 7. There was no significant correlated response detected for number born. Young *et al.* (1965) found no relationship between number born and 12-day litter weight while Legates and Farthing (1962) reported a decline in number born per litter as selection for 12-day litter weight progressed. Eisen *et al.* (1970) found a slight positive correlated response. Therefore, it is likely that very little genetic relationship exists between litter size and 12-day litter weight.

There appeared to be a positive correlated response in percent fertile matings (Table 7). However, examination of Fig. 7 shows that the positive regression was a result of the selection lines having a 72% littering rate in generation zero while the littering rate in the controls was 100%. After generation zero, there were no differences in percent fertile matings between the selection and the control. Similar results were reported by Eisen *et al.* (1970).

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