Effects of selection for independent changes in two highly correlated body weight traits of mice*

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SUMMARY

Mice were selected for high and low body weight at 5 and at 10 weeks of age. Selection was performed (1) separately for each trait, and (2) for various combinations of the two traits, using (*a*) independent culling levels and (*b*) restricted indices. Two-way selection for each trait separately gave large responses and correlated responses. Selection by independent culling levels intended to increase 5-week weight while restricting change in 10-week weight gave no demonstrable response; selection by culling levels intended to decrease 5-week weight while restricting change in 10-week weight resulted in decreases in body weights at both ages. Index selection, intended to change weight at one age while holding that at the other age constant, was generally successful. Observed responses did not conform very well with predicted responses for either index or culling levels selection. The significance of these observations in regard to the problem of selection involving restriction of traits is discussed.

1. INTRODUCTION

The possibility of producing changes in the mean of one quantitative trait while simultaneously selecting for lack of change in the mean of another correlated one has been explored using 'restricted' indexes in a few experiments. Okada & Hardin (1967, 1970) selected during 13 generations for change in larval weight, while holding adult weight constant in *Tribolium*. In general, the method worked, but there were several features of the results including asymmetry between responses in High and Low lines and wide discrepancy between estimates of genetic parameters obtained in the base population and ones estimated from realized responses which could not be satisfactorily explained. In particular, the observed response in larval weight was much less than expected. Scheinberg, Bell & Anderson (1967) selected during ten generations for changes in larval weight *or* developmental time *or* pupal weight while restricting the other two traits. They observed responses in the unrestricted traits, which were much lower than expected from estimates of genetic parameters in the base population. They also failed to suppress changes in

the restricted traits in most cases. Abplanalp, Ogasawara & Asmundson (1963) selected during seven generations in turkeys, using an index designed to increase 8-week weight while holding 24-week weight constant. They obtained a linear response in the unrestricted trait which was considerably less than that expected from estimates of genetic parameters in the base populations; they successfully restricted changes in 24-week weight, however.

One possible reason for the lack of agreement between observed and expected results in these experiments was the inappropriateness of the estimates of baseline parameters used for predicting responses and for computing indexes. For example, Okada & Hardin (1967) quoted widely different estimates for the genetic correlation (0·2 in the base population and 0·4 from response in selection lines). Abplanalp *et al.* (1963) used an estimate of 0·8 for the genetic correlation between the traits in computing their index but quoted realized estimates of 0·5 and 1·0 in selected lines. (One of us, J. McC., has recomputed the realized estimates and found consistent values of 0·6.) In theory, the realized value of the genetic correlation between a pair of traits is of critical importance in determining the rate of response to selection by a restricted index; only a portion $(1 - r_G^2)$ of the additive variance in the unrestricted trait is exploitable. Changes in the value of the genetic correlation, if they occur during selection, would be reflected in a rapidly changing rate of response to selection in the unrestricted trait.

The experimental results reported below pertain to two traits in mice (weights at 5 and 10 weeks of age) which are more highly correlated than any of those referred to above. The objectives of the experiment were (1) to determine the realized estimates of genetic parameters of the two traits and (2) to select for changes in one weight while holding the other constant using realized estimates of genetic parameters to guide selection and to predict its outcome. Selection was exercised in two directions: (1) in the case of each single trait and (2) in the case of pairs of traits, using independent culling levels and restricted indexes. The number of generations of selection was greater than in any of the previous experiments discussed above. The results are relevant to the question of the predictability of selection for independent changes in correlated characters. They also have a particular significance for the field of animal breeding in regard to the question of modifying the shape of growth curves. That aspect will be published elsewhere (McCarthy and Bakker, in preparation).

2. MATERIALS AND METHODS

(i) *Control lines*

All the selected lines described below were derived from the same population, but as will be explained, at different generations. This base population was constituted in 1964 by mating 16 pairs of mice from six replicates of a control stock (Q/Fa) from the Institute of Animal Genetics, Edinburgh (McCarthy, 1967). It was subsequently maintained by mating 16 males and 16 females in a rotational scheme designed to minimize inbreeding. This population, which acted as a source

of selected lines as well as a control for one group of selected lines, was designated QA. A replicate control (QB) was bred contemporaneously with the other group of selected lines.

(ii) *Single trait selection for weight*

Selection was carried out for high and low body weight at 5 weeks of age (lines H_5 and L_5, respectively) and for high and low body weights at 10 weeks of age (lines H_{10} and L_{10}, respectively). Selection began simultaneously in all four lines from first and second litters of the same 14 pairs of Q mice. All selection was based on within litter deviations of body weight at the appropriate ages. Fourteen matings were made per generation; two mates were chosen from each full-sib family and paired using a rotational mating system. Selection was continued for 15 generations.

(iii) *Selection by independent culling levels for combinations of high and low weights*

Two lines were selected for contrasting combinations of 5- and 10- week weights. Line $H_5L_{10}(1)$ was selected for high 5-week weight combined with low 10-week weight; line $L_5H_{10}(1)$ for low 5-week weight combined with high 10-week weight. Selection was carried out entirely within litters. In $H_5L_{10}(1)$, for example, if there were 2–6 mice of one sex in a litter, the two with the *highest* 5-week weights would be chosen; if there were more than six, the three with the highest 5-week body weights were chosen. From among these two or three mice from each sex-litter group, the one with the *lowest* 10-week weight was then selected to be used in matings. The proportion selected at each weight was, on the average, about 0·45. While this approach was empirical at the outset, it became clear that in theory the outcome should involve changes mainly in 5-week weight. The litters in the Q base stock used as the origin of the H_5L_{10} and L_5H_{10} lines were those used to produce the H_5, L_5, H_{10} and L_{10} lines. Again there were 14 matings per generation, and a rotational scheme for pairing mates was used. Selection was continued for 22 generations.

A second pair of lines, $H_5L_{10}(2)$ and $L_5H_{10}(2)$, was selected from the base population three generations after the origin of $H_5L_{10}(1)$ and $L_5H_{10}(1)$. The $H_5L_{10}(2)$ and $L_5H_{10}(2)$ lines were selected for 20 generations, using the same selection criteria and mating scheme as for $H_5L_{10}(1)$ and $L_5H_{10}(1)$.

(iv) *Selection by restricted indexes for change in weight at a particular age but not at another*

After seven generations of selection for weight at a single age in the H_5, L_5, H_{10} and L_{10} lines, estimates of realized genetic parameters were obtained as explained below. The pooled estimates were then used to compute indexes to (1) increase 5-week weight and hold 10-week weight constant (H_5R_{10}), (2) decrease 5-week weight and hold 10-week weight constant (L_5R_{10}), (3) increase 10-week weight and hold 5-week weight constant (R_5H_{10}) and (4) decrease 10-week weight and hold 5-week weight constant (R_5L_{10}). The index in the case of the H_5R_{10} and L_5R_{10}

lines was $1 \cdot 6(W_5) - 1(W_{10})$. For the R_5H_{10} and R_5L_{10} lines the index value was computed as $1 \cdot 1(W_{10}) - 1(W_5)$; this was rounded to $W_{10} - W_5$, i.e. the weight gain between 5 and 10 weeks of age. The computational methods were given by Abplanalp, *et al.* (1963). Selection was based on within litter deviations in index value in each sex. In lines H_5R_{10} and R_5H_{10}, the largest positive index values were chosen; in L_5R_{10} and R_5L_{10}, the largest negative values. Lines comprised 14 families, and mates were paired using the same rotational scheme employed in the other selected lines. Selection was continued for 14 generations.

Table 1. *Summary of selection objectives*

Type of selection and line	Selection objective	Duration (generations)
(a) Single trait (s.t.)		
H_5	Increase W_5*	15
L_5	Decrease W_5	15
H_{10}	Increase W_{10}	15
L_{10}	Decrease W_{10}	15
(b) Independent culling levels (i.c.l.)		
$H_5L_{10}(1)$	Increase W_5, Decrease W_{10}	22
$L_5H_{10}(1)$	Decrease W_5, Increase W_{10}	22
$H_5L_{10}(2)$	Increase W_5, Decrease W_{10}	19
$L_5H_{10}(2)$	Decrease W_5, Increase W_{10}	19
(c) Restricted index (r.i.)		
H_5R_{10}	Increase W_5, Restrict W_{10}	14
L_5R_{10}	Decrease W_5, Restrict W_{10}	14
R_5H_{10}	Restrict W_5, Increase W_{10}	14
R_5L_{10}	Restrict W_5, Decrease W_{10}	14

* W_5 and W_{10} indicate 5-week and 10-week weights, respectively.

A summary of the selected lines, their nomenclature, the intended effect on weights at 5 and 10 weeks, and the duration of selection, is given in Table 1. In this and subsequent tables, W_5 is used to designate 5-week and W_{10} 10-week weights.

In all lines at each generation, litters were weighed at birth, then reduced to 12 animals if larger than this. All mice were weaned at 3 weeks old, and individually weighed at 3, 5 and 10 weeks of age. Generation means were computed as the unweighted averages of sex-litter group mean values. No adjustments were made for differences in litter size.

Selection responses were measured as deviations of selected line generation means from the mean of the contemporary control generation. Regressions of the response values on generation number were used to evaluate the effects of selection.

As selection was based on individual deviations from the mean of the sex-litter group, estimates of selection differentials were obtained by averaging such deviations for males and females who had offspring.

3. RESULTS

(i) *Control lines*

Two unselected control lines were maintained in this study. Body weight means were similar, and results were pooled. The means for 5- and 10-week body weights in control lines showed no significant time trend. Regressions of either weight value on generation number were not significantly different from zero. Average body weights in the control lines over all generations were 20·3 g at 5 weeks and 27·2 g at 10 weeks of age.
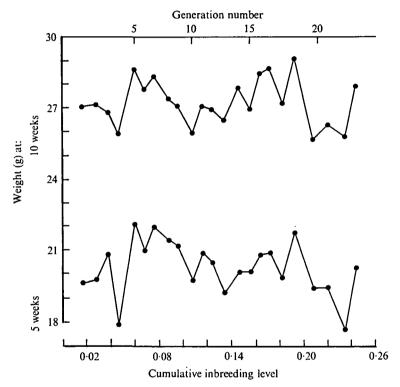

Fig. 1. Mean weights of unselected control mice at 5 and 10 weeks of age during the course of the experiment.

Inbreeding coefficients, calculated from the effective breeding size of the line, increased at a rate of about 1·1 % per generation in the control lines, reaching approximately 25 % in generation 23. Inbreeding at this rate and to this extent did not seem to affect body weight at either age. Correlations of body weight values with inbreeding levels were not significant. In Fig. 1, 5- and 10-week weights are plotted against inbreeding coefficients.

Within sex-litter group estimates of body weight variances were calculated. Pooled estimates of the standard deviation over four successive periods, generations 1–5, 6–10, 11–15 and 16–23, and over all generations, are presented in Table 2. Neither 5- nor 10-week weights showed any significant change in variance

Table 2. *Pooled within sex-litter group standard deviations*

| Line | Trait | Generation | | | | |
		1–5	6–10	11–15	16–	All
Q	W_5	2·04	1·87	1·92	1·96	1·95
	W_{10}	2·05	2·10	2·48	2·30	2·23
H_5	W_5	2·04	2·13	2·11	—	2·08
	W_{10}	2·13	2·28	2·70	—	2·35
L_5	W_5	1·78	1·77	1·67	—	1·75
	W_{10}	2·41	1·90	1·86	—	2·09
H_{10}	W_5	1·93	2·09	2·18	—	2·07
	W_{10}	2·07	2·63	2·55	—	2·42
L_{10}	W_5	1·82	2·30	1·78	—	1·98
	W_{10}	2·07	2·63	2·55	—	2·42
$H_5L_{10}(1)$	W_5	1·84	1·80	1·61	1·98	1·82
	W_{10}	2·14	2·10	2·00	2·57	2·14
$L_5H_{10}(1)$	W_5	2·13	2·01	2·32	2·06	2·07
	W_{10}	2·26	2·29	2·39	2·36	2·30
$H_5L_{10}(2)$	W_5	1·86	1·79	1·89	1·88	1·85
	W_{10}	2·09	2·12	1·93	2·22	2·08
$L_5H_{10}(2)$	W_5	1·89	1·83	1·72	1·98	1·84
	W_{10}	2·14	2·27	2·02	2·21	2·15
H_5R_{10}	W_5	2·42	1·83	2·82	—	2·34
	W_{10}	2·21	2·10	2·38	—	2·21
L_5R_{10}	W_5	1·83	2·19	1·78	—	1·95
	W_{10}	2·02	2·59	2·26	—	2·30
R_5H_{10}	W_5	2·08	2·07	2·51	—	2·18
	W_{10}	2·35	2·41	2·96	—	2·52
R_5L_{10}	W_5	1·91	1·76	1·71	—	1·81
	W_{10}	2·26	2·14	1·81	—	2·11

between periods in the control lines. Estimates of the standard deviation pooled over all generations were 1·95 g for 5-week and 2·22 g for 10-week weight.

Phenotypic correlations between 5- and 10-week weights were also estimated within sex-litter groups. Pooled estimates for the same periods as used in Table 2 are presented in Table 3. There was no significant change in phenotypic correlation in the control lines, the pooled estimate over all generations being 0·66.

(ii) *Single-trait selection lines*

Responses in the four single-trait selection lines are shown in Fig. 2, as differences between the generation mean of a selected line and the mean of the contemporary unselected control line. For each line, both the direct response in weight at the age at which that line was selected and the correlated response in weight at the other age are shown.

Calculating responses as deviations from control-line means corrected the responses for time fluctuations in environment, and also for inbreeding effects up
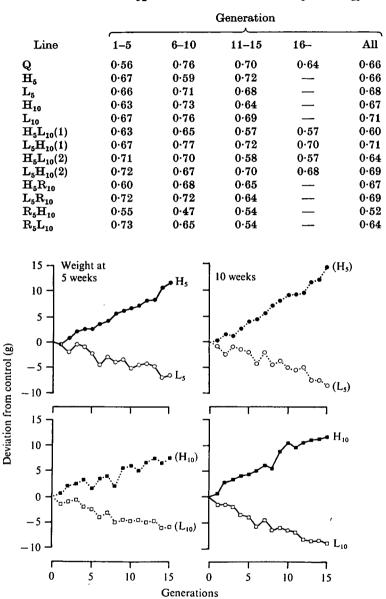
Table 3. *Phenotypic correlations between* W_5 *and* W_{10}

Line	Generation				
	1–5	6–10	11–15	16–	All
Q	0·56	0·76	0·70	0·64	0·66
H_5	0·67	0·59	0·72	—	0·66
L_5	0·66	0·71	0·68	—	0·68
H_{10}	0·63	0·73	0·64	—	0·67
L_{10}	0·67	0·76	0·69	—	0·71
$H_5L_{10}(1)$	0·63	0·65	0·57	0·57	0·60
$L_5H_{10}(1)$	0·67	0·77	0·72	0·70	0·71
$H_5L_{10}(2)$	0·71	0·70	0·58	0·57	0·64
$L_5H_{10}(2)$	0·72	0·67	0·70	0·68	0·69
H_5R_{10}	0·60	0·68	0·65	—	0·67
L_5R_{10}	0·72	0·72	0·64	—	0·69
R_5H_{10}	0·55	0·47	0·54	—	0·52
R_5L_{10}	0·73	0·65	0·54	—	0·64

Fig. 2. Mean weights at 5 and 10 weeks of lines selected for weight at 5 weeks (H_5 and L_5) or for weight at 10 weeks (H_{10} and L_{10}).

to the contemporary level of inbreeding in the control line. Selected lines were slightly more inbred than controls, but the difference was small. Since inbreeding up to about 25 % did not seem to have affected body weights in the controls, it has been assumed that body weight responses have not been affected by inbreeding in any of the selected lines.

All lines progressed under selection. Five-week weight increased in H_5 and decreased in L_5; 10-week weight increased in H_{10} and decreased in L_{10}. The regressions of weight responses on generation number were significant in all four lines (Table 4). The divergences between lines selected in opposite directions at the same age also increased significantly under selection.

Table 4. *Regressions on generation number of deviations of selected line means from control (grams per generation)*

Line	5-week weights	10-week weights
H_5	0·77**	0·93**
L_5	− 0·42**	− 0·53**
H_{10}	.0·48**	0·80**
L_{10}	− 0·40**	− 0·58**
$H_5L_{10}(1)$	0·03	− 0·03
$L_5H_{10}(1)$	− 0·22**	− 0·16**
$H_5L_{10}(2)$	0·05	− 0·03
$L_5H_{10}(2)$	− 0·11*	− 0·08
H_5R_{10}	0·13**	0·04
L_5R_{10}	− 0·36**	− 0·25**
R_5H_{10}	− 0·07	0·26**
R_5L_{10}	− 0·22**	− 0·41**

    * Significantly different from zero ($P < 0.05$).
   ** Significantly different from zero ($P < 0.01$).

Responses were asymmetrical, however. The absolute value of the regression of 5-week weight responses on generation number in H_5 was significantly greater than the absolute value of the corresponding regression in L_5. Similarly, the regression of 10-week weight response on generation number was significantly greater in absolute value in H_{10} than in L_{10}.

Variances of both 5- and 10-week body weights increased significantly in both H_5 and H_{10}; there was no significant change in body-weight variance in L_5 and L_{10} (Table 2). The increased variance in H_5 and H_{10} may reflect a tendency for variation, in body-weight measurements, to increase as the mean value increases. The coefficient of variation did not increase in these lines.

Realized selection differential estimates over the 15 generations of selection averaged 2·0 g/generation in H_5, − 1·7 g/generation in L_5, 2·4 g/generation in H_{10} and − 1·7 g/generation in L_{10}. Realized heritabilities were estimated as the ratio of cumulative responses to cumulative selection differentials, and are given in Table 5. Variances for these estimates were calculated from the formulae given by Hill (1972). (Since responses were calculated as divergences from the control lines, Hill's formulae for variance of ratio estimates in the case of two-way selection were used.) The heritability of 5-week weight was significantly greater in H_5 than in L_5; that of 10-week weight was the same in both H_{10} and L_{10}.

The asymmetry of response previously noted, greater response being obtained for increased weight, can be explained principally by asymmetrical selection

differentials; greater differentials were obtained in H_5 and H_{10} than in L_5 and L_{10}. This may have been due in part to the greater variance of body weight in H_5 and H_{10}. In the case of 5-week weight, however, heritability was also greater for upward selection; perhaps for this reason, the asymmetry of response was greater between H_5 and L_5 than between H_{10} and L_{10}.

Heritability estimates in Table 5 are given for generations 1–5, 6–10, and 11–15, as well as over all 15 generations. Estimates do not vary significantly from period to period except in H_{10}, where the last period estimate was significantly lower than previous estimates.

Table 5. *Estimates of genetic parameters – single-trait selection lines*

	Generation			
	1–5	6–10	11–15	1–15
Heritability, W_5				
H_5	0·24 ± 0·06	0·41 ± 0·05	0·52 ± 0·07	0·39 ± 0·02
L_5	0·23 ± 0·11	0·33 ± 0·22	0·16 ± 0·17	0·24 ± 0·05
H_5-L_5	0·24 ± 0·05	0·37 ± 0·12	0·37 ± 0·10	0·32 ± 0·03
Heritability, W_{10}				
H_{10}	0·41 ± 0·07	0·52 ± 0·12	0·08 ± 0·06	0·32 ± 0·03
L_{10}	0·40 ± 0·07	0·31 ± 0·13	0·33 ± 0·12	0·35 ± 0·04
H_{10}-L_{10}	0·40 ± 0·04	0·43 ± 0·06	0·17 ± 0·06	0·33 ± 0·02
Genetic Correlation, W_5, W_{10}				
H_5, H_{10}	0·80	0·96	1·19	0·89
L_5, L_{10}	0·72	0·96	1·07	0·91
H_5-L_5, H_{10}-L_{10}	0·78	0·95	0·97	0·91

Phenotypic correlations between 5- and 10-week weights (Table 3) differed very little from the estimate over all generations obtained in control lines. There was no significant regression of estimates on generation number in any of the lines.

A positive genetic correlation between 5- and 10-week weight was indicated by significant regressions of the unselected weight response on generation number in each line. Unselected weights also diverged significantly between lines selected in opposite directions (Table 4).

The ratio of the product of correlated to the product of direct responses (Falconer, 1960) was used to estimate genetic correlations from the pairs of lines H_5, H_{10} and L_5, L_{10}, and also by pairing divergences, H_5–L_5, H_{10}–L_{10}. These estimates are given in Table 5. The overall estimate was approximately 0·9, and the correlations appeared to increase as selection progressed.

(iii) *Independent culling levels selection lines*

Responses in 5- and 10-week body weights, as deviations from contemporary control values, are shown in Fig. 3 (*a*) and (*b*) for the independent culling levels selection lines. Mean weights did not change in the H_5L_{10} lines; regressions of either body weight on generation number were not significant. In $L_5H_{10}(1)$, however, significant negative regressions were obtained for both 5- and 10-week weights, and in $L_5H_{10}(2)$, for 5-week weight (Table 4).

Within sex-litter group variance was unchanged (Table 2) in any of these lines for either 5- or 10-week weight. This was to be expected, since none of the lines increased significantly in weight, and in single trait selection lines, variance changed only when weight was increased.

Phenotypic correlations between body weights at 5 and 10 weeks (Table 3) were similar to those observed in the control lines over all generations. The correlation decreased by about 0·01 units/generation in $H_5L_{10}(2)$; changes with generation number in the other lines were not significant. Since the average correlation in this line (0·64) was very close to the control value, it seems likely that the significance of the change over time in $H_5L_{10}(2)$ was spurious.
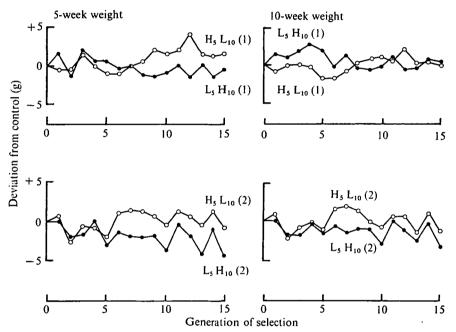

Fig. 3. Mean weights at 5 and 10 weeks of lines selected by independent culling for combinations of High (H) and Low (L) values of weights at 5 and 10 weeks (Replicate number indicated in parenthesis).

Average realized selection differentials per generation for 5-week weights were 0·8 g in $H_5L_{10}(1)$, −0·8 g in $L_5H_{10}(1)$, 0·7 g in $H_5L_{10}(2)$ and −0·7 g in $L_5H_{10}(2)$. Each was thus approximately 0·4 of a within sex-litter group standard deviation, considerably smaller than the differentials (about 1 standard deviation per generation in each line) obtained under single-trait selection. Response of 5-week weight in the two H_5L_{10} lines was, however, nowhere near 0·4 of that obtained under single trait selection (Table 4). Response in the L_5H_{10} lines was significant.

Average realized selection differentials per generation for 10-week weight were 0·2 g in $H_5L_{10}(1)$, 0·1 g in $L_5H_{10}(1)$, −0·1 g in $H_5L_{10}(2)$ and 0·04 g in $L_5H_{10}(2)$. In the H_5L_{10} lines there was no response in 10-week weight, but neither was there any in 5-week weight. In the L_5H_{10} lines, despite the lack of selection for 10-week

weight, this measurement declined nearly as rapidly as 5-week weight (Table 4). The decline was highly significant for both weights in $L_5H_{10}(1)$; in $L_5H_{10}(2)$ the decline was significant at 5 weeks and barely missed significance ($P < 0.10$) at 10 weeks.

It therefore appears that independent culling levels selection was not successful in stabilizing weight at 10 weeks of age while affecting a change in 5-week weight. Upward selection for 5-week weight caused no change in either weight; downward selection caused both weights to change.
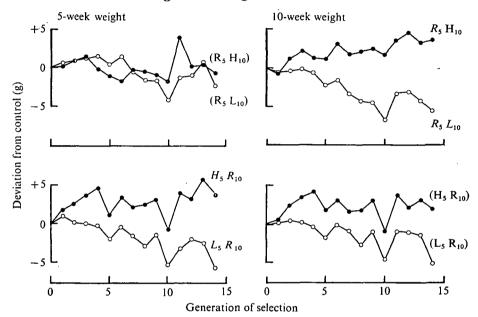

Fig. 4. Mean weights at 5 and 10 weeks of lines selected by index for High (H) and Low (L) values of weights at 5 or 10 weeks *and* restriction (R) of the other weight.

(iv) *Restricted index selection lines*

Four lines were selected by using restricted indices. Figs. 4 (*a*) and (*b*) show the responses of 5- and 10-week weights to selection. Responses in the weights are calculated, as in all selected lines, as deviations from contemporary control values. The objective of selection was clearly accomplished in the H_5R_{10} and R_5H_{10} lines, in each of which a significant response in the unrestricted trait occurred with no correlated change in the restricted trait (Table 4). In L_5R_{10} and R_5L_{10}, both weights changed in the same direction, but the change in the unrestricted weight was greater than that in the restricted weight in each case (Table 4). Thus, the objective of restriction was partially accomplished in these lines as well.

The total responses in terms of the selection indices were computed and realized heritability estimates for the indices were obtained from the ratio of index response to index selection differentials over the whole experiment. Values were 0.15 ± 0.06 for H_5R_{10}, 0.13 ± 0.06 for L_5R_{10}, 0.15 ± 0.06 for R_5H_{10} and 0.15 ± 0.04 for R_5L_{10}.

Within-family variation in 5- and 10-week weights showed no time trends in these lines (Table 2). Phenotypic correlation between 5- and 10-week weights changed under selection only in line R_5L_{10} (Table 3).

4. DISCUSSION

It is apparent that, at least with restricted index selection, two highly correlated traits such as 5- and 10-week body weight can be selected for independent changes. Restricted index selection in two lines changed weight at one age without affecting weight at the other age over 15 generations. In two other lines, restricted index selection partially suppressed correlated responses in the restricted trait. This contrasts markedly with the typical pattern of correlated responses in lines selected for either 5- or 10-week weight alone (see Table 4).

Bell & Burris (1973) give formulae whereby expected genetic changes under simultaneous selection by independent culling levels could be calculated. Rutledge, Eisen & Legates (1974) gave formulae permitting similar calculations under restricted index selection. Using these formulae, expected responses in the culling levels and restricted index selection lines were calculated, and are presented in Table 6. Observed responses, based on the regressions of responses on generations, were also calculated and are presented in Table 6. Since there was reason to suppose that selection might have changed genetic parameters for these traits, two sets of observed and expected responses are presented in Table 6, one set over all generations of selection and one set over the first five generations only. The former set of predictions might have been rendered invalid by a change in parameters, since the parameter estimates in the prediction equations were those taken from the single trait selection results. But the single trait selection parameters should be more nearly valid for the first five generations of culling levels and restricted index selection.

In fact, observed and expected results in Table 6 did not appear to be in particularly good agreement in any of the lines, for either the first five generations or for all generations. Although it is difficult to compare observed and expected values without confidence limits, in only scattered instances are observed and expected values of similar magnitude.

Expected values were based upon estimates of genetic and phenotypic parameters which were subject to error from different sources. In particular, the possible effects of genetic drift on the realized estimates of genetic parameters in the single trait selection line could not be assessed, nor its possible impact on predictions adjudged, since lines were not replicated. Falconer (1973) has shown very clearly that long-term selection for body weight in replicated populations can yield very different estimates of realized heritability. The asymmetry of responses in the single-trait selection lines in this experiment was probably a reflexion of drift. The use of the realized estimates from these lines was dubious for other reasons as well. The genetic parameters determining responses in the index lines are also subject to variation due to drift. Further, there is a possibility that the

Table 6. *Estimates of short-term and long-term predicted and observed responses in body weight, independent culling level and index lines (g)*

Line		Generations 1–5		All generations	
		W_5	W_{10}	W_5	W_{10}
$H_5L_{10}(1)$	Pred.	0·57	−0·27	3·21	1·61
	Obs.	−0·28	−0·90	0·59	−0·72
$L_5H_{10}(1)$	Pred.	−0·57	0·62	−3·61	−2·05
	Obs.	1·06	2·13	−4·90	−3·59
$H_5L_{10}(2)$	Pred.	0·62	−0·41	2·95	1·75
	Obs.	−1·84	−0·99	0·87	−0·55
$L_5H_{10}(2)$	Pred.	−0·85	−0·09	−3·37	−2·08
	Obs.	−2·44	−1·14	−2·14	−1·43
H_5R_{10}	Pred.	2·42	0·06	7·95	−0·51
	Obs.	2·09	2·84	1·86	0·59
L_5R_{10}	Pred.	−1·42	0·19	−5·04	−0·09
	Obs.	−2·04	−1·54	−5·00	−3·50
R_5H_{10}	Pred.	−0·53	2·74	−0·43	3·56
	Obs.	−0·91	1·60	−0·98	3·69
R_5L_{10}	Pred.	0·37	−2·81	0·34	−2·96
	Obs.	0·65	−1·64	−3·08	−5·76

process of selection itself affects parameters directionally, particularly genetic covariance (Bohren, Hill & Robertson, 1966).

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