

# Selection for growth on normal and reduced protein diets in mice

## I. Direct and correlated responses for growth

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### Summary

Mice were selected for growth from 3 to 9 weeks of age on a normal protein diet (N) containing 19.3% protein and a reduced protein diet (R) containing 5.1% protein. On each diet there were 3 high (H), 3 low (L) and 3 unselected control (C) lines. After 6 generations of selection, half of the mice in each line were tested on each diet. Responses were obtained when selecting for both increased and decreased growth on both diets. The realized heritabilities from within-family selection were 33 and 26% for the divergences on the normal and reduced protein diets, respectively. Consistent genotype-environment interactions were found when all lines were tested on both diets in generation 7. Performance on each protein level was best improved by selection on that protein level. Further, the correlated response was significantly less than the direct response when selecting on both diets. The estimates of the genetic correlation between growth on the two protein levels were low,  $r_N = 0.16$  from selection on the normal protein diet and  $r_R = 0.51$  from selection on the reduced protein diet. Selection resulted in a change in environmental sensitivity in the lines, dependent on the diet and direction of selection. The average of the divergences on the two diets was not dependent on the selection environment.

### 1. Introduction

In animal breeding it is important to perform selection in the environment which results in maximum progress under the circumstances of production. Hammond (1947) recommended a breeding environment with optimal conditions for expression of the character considered. He argued that a character is best selected for under such circumstances, and that once developed it can also be used in another environment. This reasoning seems to assume that the genetic background for the character is essentially the same in all environments. Falconer (1952) on the other hand argued that performance in one environment may have a different genetic basis from performance in another environment. He therefore recommended that selection should be carried out under the environmental conditions in which the improved stock is destined to perform. The extent to which selection in one environment leads to a response in another environment depends on the presence of genotype-environment interaction. By considering a character measured in two different environments as two characters, the

problem may be treated as one of genetic correlation between them, as first suggested by Falconer (1952).

Several experiments have investigated the importance of genotype-environment interactions. However, few studies include replicates (Bailey *et al.* 1970; Kownacki & Gebler, 1974; Yüksel *et al.* 1981), even though these are essential for the evaluation of estimated correlated responses (Hill, 1980). In the present study replicate lines of mice were selected on a normal and a reduced protein diet. This report examines the selection responses and the genotype-environment interactions found.

### 2. Materials and Methods

#### (i) Establishment of lines

A base population with large genetic variation was made by crossing mice from eight different populations (Fig. 1). To reduce linkage disequilibrium this population was kept for three generations before establishing the base population (generation 0) of the experiment. The selection experiment started in generation 1.

In generation 0 the offspring groups were divided into three genetically similar blocks ( $R_1, R_2, R_3$ ) (Fig. 2) with the intention to include in all blocks most of

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Gen.

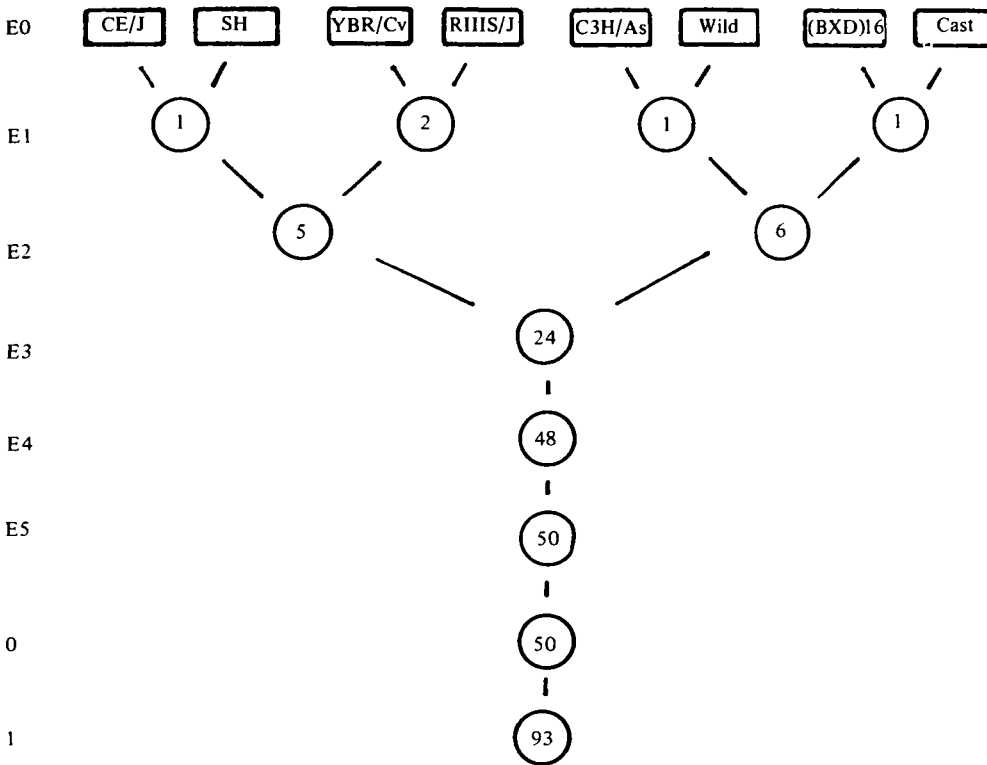


Fig. 1. Establishment of the base population (generation 0). Mice were obtained from: four inbred strains (CE/J, C3H/As, RIIIS/J, YBR/Cv); a recombinant inbred strain ((BXD)16); a colony-bred strain of *Mus musculus castaneus* (Cast); a wild Danish population (Wild); a selected strain (SH) previously founded on three inbred

strains (A/J/A/BOM, AKR/A/BOM, BALB/c/A/BOM). The number inside a circle is the number of litters from which parents were obtained for the next generation. The selection experiment started in generation 1.

the genetic variation originally introduced from the eight founder lines. Thus variation between blocks is expected to be less than the random sampling variance. From the offspring groups in each block, parents were obtained for the establishment of a selection line (S) and a control line (C) on each protein level (N, R) by randomly taking two male and two female offspring from each offspring group and placing sibs of opposite sex on different protein levels. Of the sibs on the same protein level, one was used in the selection line and the other in the control line. Details concerning the establishment of lines are described by Nielsen (1986).

(ii) Diets

The protein content in the diets used in the test period from 3 to 9 weeks of age was determined after a

preliminary growth and reproduction experiment (Nielsen & Andersen, 1982). The normal protein diet (N) contained 19.3% crude protein, and the reduced protein diet (R) was limited to 5.1% crude protein. The reduced protein diet caused a reduction in growth but not in reproductive performance, and the effect on growth was not carried over to the young. After the test period and during reproduction all the mice received a commercial standard diet (Rostock) containing 20% digestible protein.

(iii) Procedure in the selection experiment

In the selection experiment litters were standardized at birth by reduction or augmentation, if possible to eight young, four of each sex. Litters were weaned at 3 weeks, the males and females being separated, and a

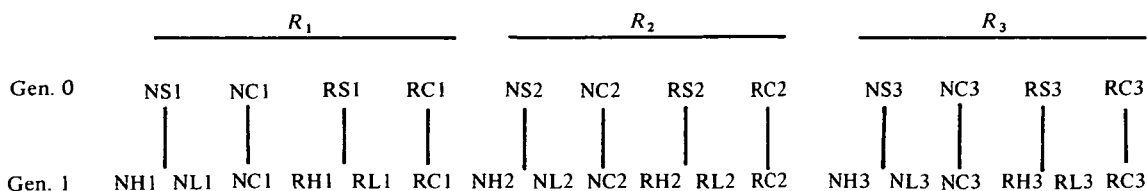


Fig. 2. Establishment of lines. For details see the text.

maximum of four mice kept in a cage. Selection was performed within litters for growth from 3 to 9 weeks of age. The selection lines were established by selecting in generation 1, within each litter, the one male and one female with the largest weight gain for the high lines (H) and the one male and one female with the smallest weight gain for the low lines (L) (Fig. 2). In the control lines (C) a male and female were chosen at random within each litter.

Matings of least relationship were made using a mating scheme similar to that of Falconer (1973). Each line consisted of 8 pair-matings per generation. In the cases (4–15% over generations) where a mating failed to produce offspring, replacement for the missing mice was made from the most similar available mating. In the cases (0–3% over generations) where the first litter was lost (mostly due to parental cannibalism) the parents reared a second or third litter. Selection was then performed within these litters, but the weight results from these mice have been omitted in the analysis of the data. Matings in a generation were made simultaneously and matings in the different generations were made (with one exception) at regular intervals of 14 weeks. Due to this fixed generation interval, some litters (1–7% over generations) did not reach the age of 9 weeks before selection was performed. These mice were then selected on the basis of their performance up to the date of mating. Data from these mice also have been omitted from the analysis.

(iv) Exchange of diets in generation 7

In generation 7, half of the mice in each line were tested on each of the two diets as follows. The four female offspring groups from the matings 1–4 were assigned randomly to one of the diets. For each of these female offspring groups the female offspring group from the reciprocal mating received the opposite diet. In all cases the male offspring received the opposite diet to that of their sisters. In this way an equal distribution of genotypes on the two diets was obtained for each line.

(v) Statistical analysis of results in generation 6

For each line the generation mean of growth from 3 to 9 weeks of age was calculated as the average of the two sexes. The average in each sex was calculated as the unweighted mean of litter-means. For each diet the means in generation 6 were analysed using the model:

$$X_{jb} = \mu + \alpha_j + \epsilon_{jb},$$

where

- $X_{jb}$  is the observation in block  $b$  of the  $j$ th direction of selection;
- $\mu$  is the overall mean;
- $\alpha_j$  is the effect of selection direction ( $j = H, C, L$ ); and
- $\epsilon_{jb}$  describes the variation within a block ( $b = 1, 2,$

3) and the residual variation,  $E(\epsilon_{jb}) = 0,$   
 $\text{var}(\epsilon_{jb}) = \sigma^2$

and

$$\text{cov}(\epsilon_{jb}, \epsilon_{j'b}) = v \quad (j \neq j').$$

Contrasts, of asymmetry of response,  $(\alpha_H + \alpha_L)/2 - \alpha_C,$  and of divergence of response,  $\alpha_H - \alpha_L,$  were tested for each diet.

Selection differentials were calculated as the average difference in weight gain between each selected mouse and its litter-sex mean, averaged over sexes. Responses were calculated as the deviation of the line mean from the mean of the three control lines on the same protein level. Realized heritabilities were calculated for generation 1–6 from the regression of response on cumulated selection differential assuming selection differentials in the control lines to be zero. Only data where records of 3- to 9-week weight gain were available for both parents and offspring of both sexes were used for estimation of selection differentials and realized heritabilities in the selection lines.

(vi) Statistical analysis of results in generation 7

Let  $Y_{pjbt}$  denote the growth from 3 to 9 weeks of age on selection diet  $p$  ( $p = N, R$ ), selection direction  $j$  ( $j = H, C, L$ ), block  $b$  ( $b = 1, 2, 3$ ) and test diet  $t$  ( $t = N, R$ ) in generation 7, averaged over the two sexes. The observations  $Y_{pjbt}$  were analysed using the model:

$$Y_{pjbt} = c_{pt} + \frac{1}{2}d_{pt} \text{sel}_j + a_{pt} \text{sel}_j^2 + G_b + L_{pjb} + \epsilon_{pjbt}, \quad (1)$$

For each combination of selection diet  $p$  and test diet  $t$ :

- $c_{pt}$  is the mean of the control lines;
- $d_{pt}$  is a divergence parameter ( $H - L$ );
- $a_{pt}$  is an asymmetry parameter  $\frac{1}{2}(H + L) - C$ ; further
- $\text{sel}_j$  is a dummy regression variable,  $\text{sel}_H = 1,$   
 $\text{sel}_C = 0, \text{sel}_L = -1$ ;
- $G_b$  is a random block effect;
- $L_{pjb}$  is a random line effect; and
- $\epsilon_{pjbt}$  is a random error term.

It is assumed that  $G_b, L_{pjb}$  and  $\epsilon_{pjbt}$  are independent. The statistical analysis of model (1) was performed as two separate analyses on the variables

$$\text{DIF}_{pjb} = Y_{pjbN} - Y_{pjbR}$$

and

$$\text{SUM}_{pjb} = Y_{pjbN} + Y_{pjbR},$$

which are, respectively, the difference and the sum of the performances of a line on test diet N and R. The difference is the environmental sensitivity of a line. From the sum the average performance of a line on the two diets can be calculated. From (1):

$$\text{DIF}_{pjb} = c_{pN} - c_{pR} + \frac{1}{2}(d_{pN} - d_{pR}) \text{sel}_j + (a_{pN} - a_{pR}) \text{sel}_j^2 + \epsilon_{pjbN} - \epsilon_{pjbR}, \quad (2)$$

and

$$\text{SUM}_{pjb} = c_{pN} + c_{pR} + \frac{1}{2}(d_{pN} + d_{pR}) \text{sel}_j + (a_{pN} + a_{pR}) \text{sel}_j^2 + 2G_b + 2L_{pjb} + \varepsilon_{pjbN} + \varepsilon_{pjbR}. \quad (3)$$

Under the assumptions of the model the set of differences is independent of the set of sums. Interaction and environmental sensitivity are studied using model (2), and average performance is studied using model (3). For each selection diet the hypotheses

$$a_{pN} - a_{pR} = 0 \quad \text{and} \quad d_{pN} - d_{pR} = 0 \quad \text{were tested.}$$

From the theory of selection for correlated characters the relationship between the direct response in the selection environment and the correlated response in the alternative environment can be obtained. Let  $R_{ij}$  denote the expected response in environment  $j$  ( $j = 1, 2$ ) when selecting in environment  $i$  ( $i = 1, 2$ ). Then  $R_{11}$  and  $R_{22}$  are the direct responses and  $R_{12}$  and  $R_{21}$  the correlated responses. The following relationship is expected when selection is performed in environment 1:

$$R_{12} = rR_{11} \frac{h_2 \sigma_{P2}}{h_1 \sigma_{P1}}. \quad (4)$$

For selection in environment 2 it is:

$$R_{21} = rR_{22} \frac{h_1 \sigma_{P1}}{h_2 \sigma_{P2}}. \quad (5)$$

In the formula  $r$  is the genetic correlation between the characters in the two environments,  $h_1^2$  and  $h_2^2$  are the heritabilities in environments 1 and 2, respectively, and  $\sigma_{P1}$  and  $\sigma_{P2}$  are the phenotypic standard deviations in the two environments. Further,

$$P_{ij} = R_{ij} + C_j, \quad (6)$$

where  $P_{ij}$  is the expected performance in environment  $j$  of a line selected in environment  $i$  and  $C_j$  is the expected performance of a control line in environment  $j$ . From (4) and (6) the environmental sensitivity of a line selected in environment 1 and be expressed as:

$$P_{11} - P_{12} = R_{11} \left( 1 - r \frac{h_2 \sigma_{P2}}{h_1 \sigma_{P1}} \right) + C_1 - C_2.$$

For a line selected in environment 2 it is from (5) and (6):

$$P_{21} - P_{22} = R_{22} \left( r \frac{h_1 \sigma_{P1}}{h_2 \sigma_{P2}} - 1 \right) + C_1 - C_2.$$

These relationships were tested by plotting for each selection diet DIF<sub>pjb</sub> for each line against the response obtained in the line in generation 6.

For each selection diet  $p = (N, R)$  and for each block  $b = (1, 2, 3)$  an estimate  $r_{pb}$  of the genetic correlation was obtained from:

$$r_{Nb} = [(Y_{NHbR} - Y_{NLbR}) / (Y_{NHbN} - Y_{NLbN})] \frac{h_N \sigma_{PN}}{h_R \sigma_{PR}},$$

and

$$r_{Rb} = [(Y_{RHbN} - Y_{RLbN}) / (Y_{RHbR} - Y_{RLbR})] \frac{h_R \sigma_{PR}}{h_N \sigma_{PN}}.$$

In these formulae  $h_N^2$  and  $h_R^2$  are the realized heritabilities from mass selection obtained from 6 generations of selection on the normal and reduced protein diet respectively, whereas  $\sigma_{PN}$  and  $\sigma_{PR}$  are the phenotypic standard deviations on the two diets estimated from the control lines.

For each selection diet a combined estimate of the genetic correlation,  $r_p$ , was obtained as a simple average,  $r_p = (r_{p1} + r_{p2} + r_{p3})/3$ . The standard error of  $r_p$  was estimated from the pooled empirical variation of  $r_{pb}$ .

### 3. Results

#### (i) Control lines

In the control lines the growth from 3 to 9 weeks averaged over generations 1–6 was 12.5 g on diet N and 10.5 g on diet R, a decrease of 16%. Nine-week weight averaged 22.7 and 20.6 g on the normal and reduced protein diets, respectively. The phenotypic standard deviation on the reduced protein diet was increased by 25% (Table 2).

The generation means in the control lines were clearly influenced by environmental factors on both protein levels (Fig. 3). Variations from generation to

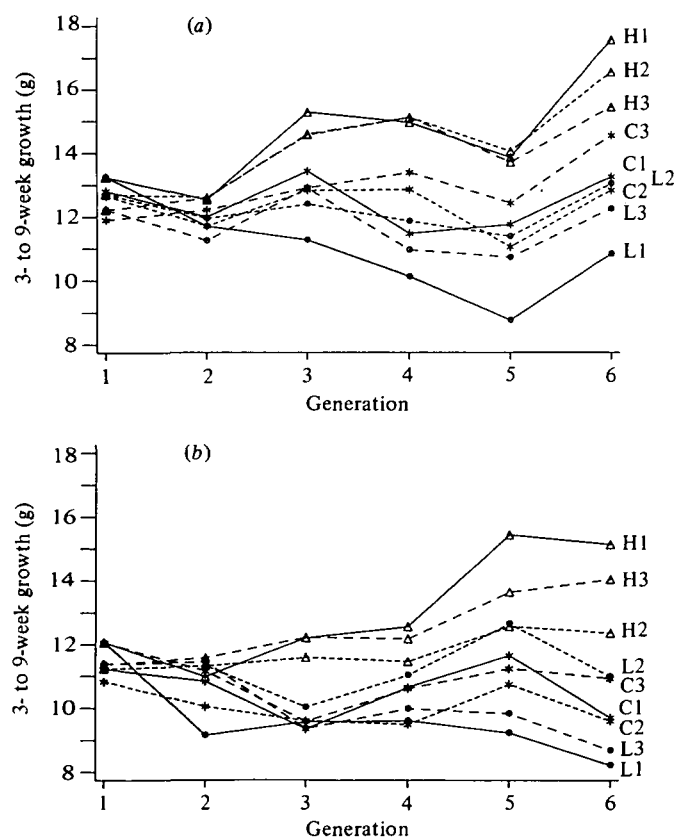


Fig. 3. Results of selection on (a) the normal protein diet and (b) the reduced protein diet. The selection experiment started in generation 1.

generation often differed on the two protein levels, indicating that variations in food quality were the main cause of environmental fluctuations.

(ii) Direct responses to selection

The responses to selection for 3- to 9-week weight gain on the normal and reduced protein diets are presented in Fig. 3. The generation means are the average of the two sexes. Responses (mean of lines in generation 6) were obtained when selecting for increased and decreased growth on both protein levels. Divergences were similar and significantly different from zero on the two diets, being 4.5 g or 2.1 phenotypic standard deviations on diet N and 4.5 g or 1.7 phenotypic standard deviations on diet R (Table 1). On the normal protein diet the divergences in generation 6 were 6.7, 3.5 and 3.2 g between the lines in blocks 1, 2 and 3, respectively. On the reduced protein diet they were 6.9, 1.4 and 5.3 g. A positive but not significant asymmetry of response was obtained on each diet (Table 1).

(iii) Cumulated selection differentials and realized heritabilities

Total cumulated selection differentials are given in Table 2. Clearly no overall selection occurred in the control lines. In the selection lines, the selection differentials tended to be larger on the reduced protein diet, due to the larger phenotypic standard deviation (Table 2). Responses (mean of lines) are plotted

Table 1. Estimates of asymmetry and divergence of response ( $\pm$  s.e.) calculated from line means in generation 6

	Normal protein diet	Reduced protein diet
Asymmetry	0.73 $\pm$ 0.88	1.48 $\pm$ 1.08
Divergence	4.46 $\pm$ 1.02	4.53 $\pm$ 1.24

Table 2. Cumulated selection differentials (g) to generation 6 and phenotypic standard deviations

Direction of selection	Block			Mean	Phenotypic standard deviation
	1	2	3		
Normal protein diet					
High	9.0	7.2	7.2	7.8	2.18
Low	-6.0	-6.9	-7.5	-6.8	
Control	0.4	-0.5	0.5	0.1	
Reduced protein diet					
High	10.0	9.9	8.5	9.5	2.72
Low	-7.9	-6.7	-7.8	-7.5	
Control	2.6	-1.0	1.5	1.0	

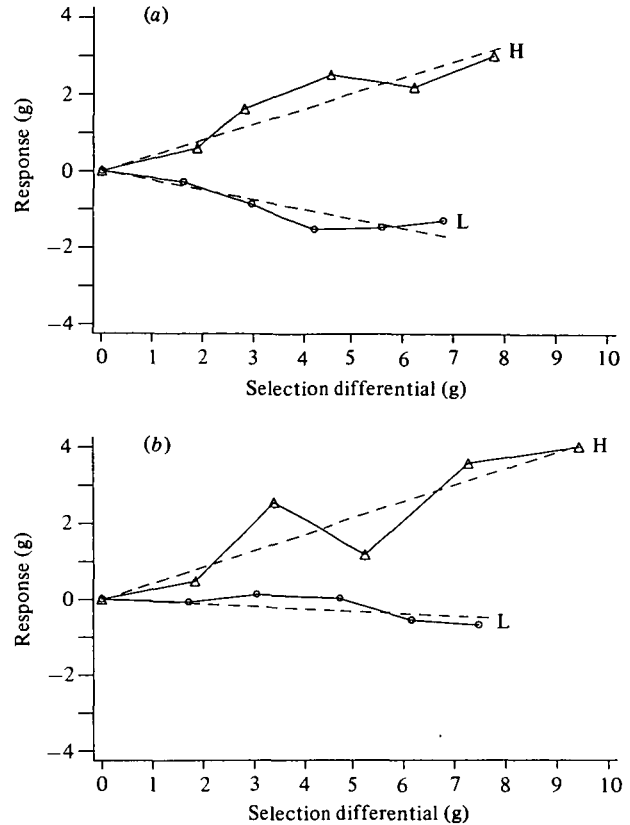


Fig. 4. Mean responses plotted against mean cumulated selection differentials for lines selected for high (H) and low (L) growth on (a) the normal protein diet and (b) the reduced protein diet.

against the mean cumulated selection differentials in Fig. 4.

The realized heritability was calculated separately for each line from the regression of response on cumulated selection differential up to generation 6. Table 3 shows the regression coefficients and their standard errors. Due to genetic drift the standard errors calculated assuming the standard regression model are biased downwards (Hill, 1972). The 'mean' estimates in Table 3 are the unweighted means of the regression coefficients in the three lines and the standard errors are the empirical standard errors of these means, which are unbiased.



Table 3. Realized heritabilities (%) ( $\pm$ S.E.) to generation 6

Direction of selection	Block			Mean <sup>a</sup>
	1	2	3	
Normal protein diet				
High	41 $\pm$ 11	33 $\pm$ 12	23 $\pm$ 17	33 $\pm$ 5
Low	34 $\pm$ 25	18 $\pm$ 6	16 $\pm$ 11	23 $\pm$ 6
Divergence	42 $\pm$ 4	29 $\pm$ 3	29 $\pm$ 4	33 $\pm$ 5
Reduced protein diet				
High	54 $\pm$ 12	36 $\pm$ 26	34 $\pm$ 15	41 $\pm$ 6
Low	12 $\pm$ 21	-12 $\pm$ 8	34 $\pm$ 5	12 $\pm$ 13
Divergence	37 $\pm$ 4	11 $\pm$ 6	30 $\pm$ 3	26 $\pm$ 8

<sup>a</sup> Mean: arithmetic mean of regression coefficients with empirical S.E. from variance of regression between lines.

The realized heritabilities are within-family heritabilities. The heritability was larger selecting for increased than for decreased growth on both diets (Table 3), but neither difference was significantly different from zero. The realized heritabilities from mass selection ( $h^2$ ) were estimated using  $h^2 = 2(1-t)h_w^2$  where  $t$  is the full sib intra-class correlation and  $h_w^2$  the within-family realized heritability. The intra-class correlations estimated from the

control lines were 0.60 and 0.55 on diet N and R, respectively. Using the divergences the realized heritability from mass selection was 0.27 on the normal protein diet and 0.24 on the reduced protein diet. The smaller estimates of these heritabilities as compared with the within-family heritabilities are probably caused by a large component of environmental variance common to full sibs, most likely due to maternal effects.

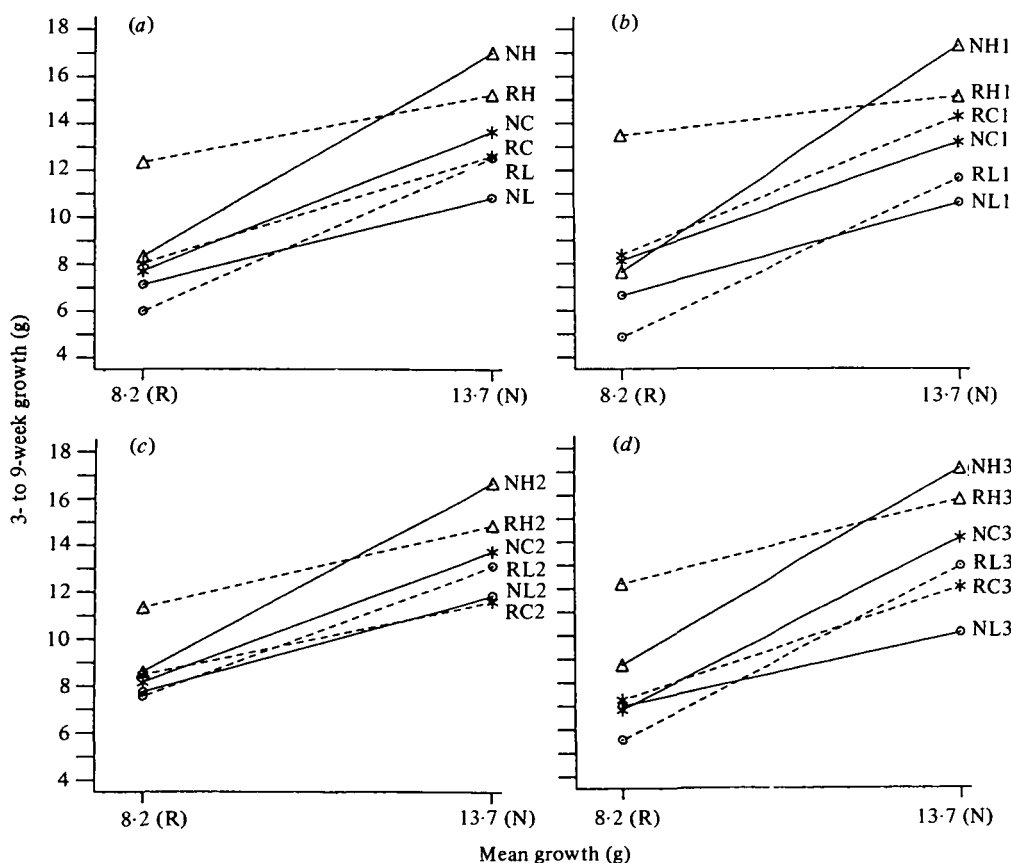


Fig. 5. Performance on the two diets in generation 7 for (a) mean of lines and (b), (c) and (d) lines from block 1, 2 and 3, respectively plotted against the mean growth of all

lines on the normal protein diet (N) and the reduced protein diet (R).

Table 4. Differences  $\pm$  S.E. (environmental sensitivities) and means  $\pm$  S.E. (averages) of performances on the two test diets in generation 7 for the mean of lines. The standard errors are calculated from the analyses of models (2) and (3)

Diet of selection	Direction of selection		
	High	Control	Low
	Differences		
Normal protein diet	8.70 $\pm$ 0.59	5.98 $\pm$ 0.59	3.72 $\pm$ 0.59
Reduced protein diet	2.92 $\pm$ 0.59	4.60 $\pm$ 0.59	6.57 $\pm$ 0.59
	Means		
Normal protein diet	12.67 $\pm$ 0.42	10.68 $\pm$ 0.42	8.97 $\pm$ 0.42
Reduced protein diet	13.79 $\pm$ 0.42	10.33 $\pm$ 0.42	9.26 $\pm$ 0.42

(iv) Direct and correlated responses to selection in generation 7

All lines were tested on both protein levels in generation 7. Three- to 9-week weight gains averaged over sexes on the two protein levels are shown in Fig. 5. On each protein level the line with the best performance according to the direction of selection is the line selected on the protein level in question. The average weight gain of the three NC lines is larger than that of the three RC lines on diet N whereas the opposite is the case on diet R (Fig. 5). Comparing the

lines from the different blocks, there was, as expected, no consistent relation between the control line kept on the normal protein diet and the control line kept on the reduced protein diet.

The nature of the genotype-environment interactions thus obtained is supported by the results of the analysis of model 2, where the difference,  $DIF_{pjb}$ , between performances on the two diets is analysed for each line. This provides a rather precise evaluation of the interactions as genetic drift essentially is eliminated (Hill, 1978). The difference between the asymmetry parameters of model 2 on the two test diets is estimated to be 0.23 (S.E. 0.73) and -0.14 (S.E. 0.73) for selection on diet N and R, respectively. The difference between the divergence parameters evaluates the difference between the direct and correlated response. It is 4.98 (S.E. 0.84) for selection on the normal protein diet and 3.64 (S.E. 0.84) for selection on the reduced protein diet. Both differences are significantly different from zero. Ignoring the asymmetry parameters the dependence of the difference,  $DIF_{pjb}$ , on the selection diet and the direction of selection is seen from the reduced model. As the differences are measures of environmental sensitivity, upward selection on diet N and downward selection on diet R results in high sensitivities while downward selection on diet N and upward selection on diet R results in low sensitivities. The sensitivity in the control lines corresponds to the expected average of the sensitivities in the two selection lines on the same diet (Table 4). The results for the different lines on the two diets are shown in Fig. 6, where the difference is shown as a function of the response in generation 6.

The comparison of the results of selection on the two diets indicates that the genetic correlation between growth on the two protein levels is low. The estimates of the genetic correlation ( $r$ ) calculated using the responses obtained in the lines from block 1, 2 and 3 respectively, were 0.13, 0.15 and 0.21 for selection on the normal protein diet, and 0.48, 0.55 and 0.52 for selection on the reduced protein diet. Combined estimates of the genetic correlation were  $r_N = 0.16$

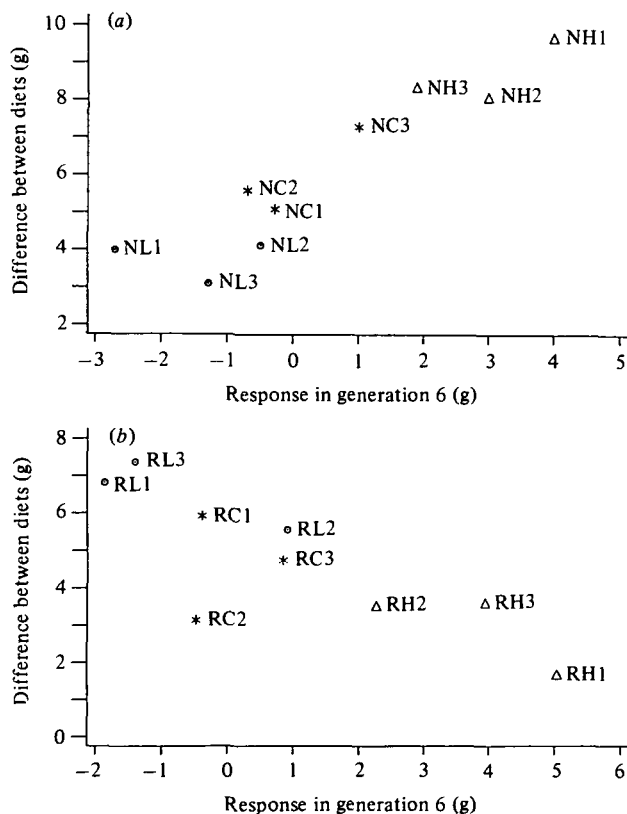


Fig. 6. Difference in growth on the two diets (environmental sensitivity) in generation 7 in lines selected on (a) the normal protein diet and (b) the reduced protein diet plotted against response in generation 6.

(S.E. 0.02) and  $r_R = 0.51$  (S.E. 0.02) when selecting on diet N and R, respectively. These estimates were significantly different.

A comparison of the average performances on the two protein levels of mice selected on the respective diets is made using model (3). Selection on the reduced protein diet resulted in the largest overall divergence between H and L lines, the average over the two test diets being 4.5 g while 3.7 g was obtained when selecting on the normal protein diet. The difference of 0.8 (S.E. 0.8) was, however, not significant. The means of performances on the two diets for the average of lines are shown in Table 4. The average  $\frac{1}{2}(a_{pN} + a_{pR})$  of the asymmetry parameters was estimated to be 0.14 (S.E. 0.51) and 1.20 (S.E. 0.51) when selection was performed on diet N and R, respectively.

#### 4. Discussion

##### (i) Direct responses

The realized heritabilities from within family selection ( $0.33 \pm 0.05$  and  $0.26 \pm 0.08$  on diet N and R, respectively) were larger than those obtained by Park *et al.* (1966) selecting for individual gain in rats ( $0.105 \pm 0.009$  and  $0.119 \pm 0.033$  on the normal and reduced protein diet, respectively). This difference in heritabilities probably resulted from a higher level of genetic variation in the base population in the present experiment. Kownacki & Gebler (1971) found the heritability of 5-week weight in mice estimated from a hierarchical analysis of variance to be larger on the normal protein diet, the average of sexes being 0.25 compared to 0.13 on the reduced protein diet, but the difference was not significant. In chickens previous selection for the same character in the line on the normal protein diet probably resulted in the lower realized heritability of 6-week weight on this diet  $0.18 \pm 0.05$  compared to  $0.30 \pm 0.10$  on the reduced protein diet (Sørensen, 1986).

The phenotypic variance was larger on the diet with the reduced protein content in the study of Park *et al.* (1966) and Kownacki & Gebler (1974) in agreement with the results of the present study. As the heritabilities were of the same order of magnitude on the two diets, the results probably indicate that the additive genetic variance was also larger as found by Sørensen (1977). The increase in additive variance may be the result of the contribution of genetic variance in protein utilization to the genetic variance in weight gain.

##### (ii) Direct and correlated responses

Consistent genotype–environment interactions were found in the present experiment. The genetic correlation between growth on the two protein levels was low, and this indicates that growth on the two diets has a rather different genetic basis. The low genetic

correlation is probably due to the large difference in the protein content in the two diets. Sørensen (1980) found the genetic correlation between growth rate on a normal and a reduced protein diet in chickens to be 0.5. The difference between the protein content in the diets was smaller in this study.

The discrepancy between the estimates of the genetic correlation obtained when selecting on the normal and the reduced protein diet, respectively, is not consistent with genetic theory. The discrepancy may be due to changes in the genetic parameters that took place during the course of selection as suggested by Falconer (1960). The genetic correlation was shown to be particularly sensitive to changes in gene frequencies (Bohren *et al.* 1966). The similarity between the estimates obtained when selecting on each protein level suggests, however, similar changes in the parameters in the lines selected on the same diet, which brings into question the independence of these changes.

Adaptation to the selection environment is found in several previous studies (Falconer & Latyszewski, 1952; Falconer, 1960; Park *et al.* 1966; Hetzel & Nicholas, 1986; Sørensen, 1986). Dalton (1967), McPhee *et al.* (1980) and Yüksel *et al.* (1981) working with mice and Bailey *et al.* (1970) working with rats found no genotype–environment interactions. The reason for the lack of interaction in the study of Yüksel *et al.* (1981) may be that they selected for efficiency instead of gain or weight as in most studies. They found, however, a very high genetic correlation between gain and efficiency. Bailey *et al.* (1970) probably obtained too little differentiation between lines to detect sire line–diet interaction, as they selected for only five generations and as the final test was made with progeny from matings between selected males and control females. There was, however, evidence of a genotype–environment interaction within sire lines.

The practical conditions of breeding are often that selection has to be carried out in a single environment while the improved animals have to perform well under different circumstances of production. The best average performance was obtained by selection for high growth on the inferior diet, while the smallest average growth was obtained by selection for low growth on the normal diet, as also found by Falconer (1960). The average growth in the lines selected on the two diets was not significantly different in either direction of selection. Difference between selection in opposite directions is not expected from genetic theory either.

Selection in the present study resulted in a change in sensitivity in the lines, as expected when the correlated responses are smaller than the direct responses. Similar changes were obtained by Falconer (1981). The agreement between the sensitivity in the control lines and the average of the sensitivities in the two selection lines on the same diet was less pronounced in Falconer's experiment, probably due



to a larger degree of asymmetry of the correlated responses than of the direct responses. On each protein level the sensitivity seems to be linear dependent on the selection response. The apparent larger absolute value of the slope obtained when selecting on the normal protein diet reflects the lower value of the genetic correlation on this protein level.

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