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Selection for weight gain in mice at two ages and under ad libitum and restricted feeding

1. Direct and correlated responses in weight gain and body weight

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Summary. Direct and correlated responses in weight gain and body weights were assessed for nine generations of within-family selection. Four selection criteria were used: gain between 28 and 38 or 48 and 58 days of age, and under two feeding regimes, i.e. ad libitum consumption or 80% of the control line. Direct responses to selection and realized heritabilities in the ad libitum lines were greater in the first period. Weight gain under ad libitum feeding at later ages appeared to have a lower genetic variability. In the restricted lines the responses and realized heritabilities were higher in the second period. Selection under restricted feeding in both periods led to animals that had lower weight gains than the control line when compared under ad libitum feeding.

Key words: Mice – Selection – Gain – Feed restriction

Introduction

From a quantitative standpoint, growth is a complex character resulting from many interacting processes. Animals allocate their energy intake to either maintenance or growth, and the relative proportions vary with age and weight. Furthermore, the energy allocated to depositing differnt kinds of tissue varies with age and weight.

Hayes and McCarthy (1976) proposes a model that implies that selection for increased growth at different ages is based on exploiting different types of genetic variances. Selection at an early age would mainly exploit the genetic variance in appetite while selection at later ages would also exploit genetic variances in the kind of tissue being deposited. Selection under ad libitum feeding allows the exploitation of genetic variances in appetite and in the kind of tissue being deposited, while selection under restricted feeding exploits only variances other than in appetite. Hetzel and Nicholas (1982 a, b) selected for weight gain under ad libitum and restricted feeding during an early post-weaning period and reported that mice selected under restricted feeding improved their growth only one fourth as much as full-fed mice. Reports on selection at later ages are not available, except as part of a longer period that includes the early post-weaning period. Sharp et al. (1984) reported indirect estimates of total body fat percent and lean weight at 10 weeks of age, suggesting the presence of genetic variation in these components at later ages.

A selection experiment which encompasses selection for weight gain at two ages and under restriction and ad libitum feedings has not been carried out to date. Such an experiment would give an insight into the type of genetic variances being utilized by selection, and provide lines for studying, through correlated responses, the genetic nature of physiological differences which are not open to study by direct selection because of the costs involved in their measurement.

Materials and methods

Laboratory procedures

Selection lines. The foundation population for this study was obtained from a random mating population kept at the Animal Research Institute in Ottawa. This random mating population was initially synthesized from four inbred strains (C3J/He, CBA/J, C57BL/6J and SWR/J) in the Animal Resarch Institute in Ottawa (Nagai and Kristjansson 1970; Nagai et al. 1975). After arrival, three generations of random mating were allowed for adaptation to the new conditions. Individuals were then randomly allocated to five lines. After one generation of selection each line was divided randomly into two replicates. The ten line replicates established were: EPR1 and EPR2, Early Period Restricted replicates 1 and 2, selected for increased gain between 28 and 38 days of age under a restricted feeding regime; EPA1 and EPA2, Early Period ad libitum replicates 1 and 2, selected for increased gain between 28 and 38 days of age under an ad libitum feeding regime; LPR1 and LPR2, Late Period Restricted replicates 1 and 2, selected for increased gain between 48 and 58 days of age under a restricted feeding regime; LPA1 and LPA2, Late Period ad libitum replicates 1 and 2, selected for increased gain between 48 and 58 days of age under ad libitum feeding regime; and C1 and C2, control line replicates 1 and 2, fed ad libitum and maintained by random selection. A control line under restricted feeding was not maintained due to limitations of space and labour, and because the objective of the experiment was to investigate the nature of responses under ad libitum feeding in feed intake, efficiency and body composition that could result from this kind of selection. The restricted regime in both periods of selection consisted of feeding 80%, every two days, of what the control line at ad libitum in the same period in the previous two generations.

Each replicate of a line consisted of twenty pair matings, and within family selection was practiced. Matings within line were at random with the exception that no full sib matings were allowed. All litters were standardized to six young, three males and three females where possible. Litters of less than six were augmented with foster mice belonging to the same line replicate. Fostered mice were identified and discarded at weaning. At 12 days of age the young were permanently identified by toe clipping. Weaning was at 21 days of age and the weaning weight of each individual was recorded. They were then relocated by sex in groups of four, allowing only two litter mates at most in the same cage. At 28 days of age, lines EPR1, EPR2, EPA1 and EPA2 were weighed. All individuals in lines EPR1 and EPR2 were individually caged and fed the restricted diet. At 38 days of age, lines EPR1, EPR2, EPA1 and EPA2 were weighed and their gain for that period calculated. The male and female with the greatest gain in each litter were selected to be parents.

Exactly the same procedure was follwed between 48 and 58 days for lines LPR1, LPR2, LPA1 and LPA2. The control line was weighed at all ages, and one male and one female were randomly chosen as parents from each litter.

In generation nine selection was relaxed, all animals were fed ad libitum and their body weights and weight gain recorded in their respective periods.

All mice were fed standard Laboratory Chow from Purina in all generations. Water was available ad libitum at all times. Lights were kept in a standard regime of 12 h and 12 h dark. The temperature in the mouse laboratory varied between 18° and 23° C.

Stastical analysis

Responses in weight gain. Responses to selection were examined separately for each selection period. In a preliminary analysis the differences between the sexes were found to be significant; therefore the direct and correlated responses were analyzed separately for each sex. Response in weight gain was estimated as the linear regression of the line-sex generation mean, measured as a devitation from the control line-sex generation mean in ad libitum fed lines. In the case of the lines selected under restricted feeding, environmental trends were estimated using the method of Richardson et al. (1968), since a control line was not maintained under restricted feeding. The environmental trend in the early period was estimated using the generation means of EPR1 and EPR2 as the dependent variable in the following model:

$$Y_{jk} = \alpha + \phi_{\cdot\varkappa} + \beta_j Z_{jk} + E_{jk}$$

where Y_{jk} is the mean of the j^{th} replicate ($j = 1,2$) in generation $\varkappa$, α is the expected performance of the base population (under restricted feeding), $\phi_{\cdot\varkappa}$ is the environmental effect common to both replicates (EPR1 and EPR2) in generation $\varkappa$, Z_{jk} is the cumulative selection differential in replicate j up to generation $\varkappa$, B_j is a regression coefficient and E_{jk} is random error. The environmental trend in LPR1 and LPR2 was estimated similarly. Responses in weight gain in the restricted lines were measured as the linear regression of the line sex mean corrected for environmental trend ($Y_{jk} - [\alpha + \phi_{\cdot\varkappa}]$) on generation number. Since in generation nine the restriction in feed was not practiced, estimates of response in the restricted lines do not include generation nine.

Data on weight gain in generation nine were analyzed for each selection period using the General Linear Models procedures of the Statistical Analysis System (1985). Since the interactions between sex and line were not significant sexes were analyzed jointly. The model was:

$$Y_{ijklm} = \mu + L_i + R_{ij} + F_{ijk} + S_l + SL_{il} + SRL_{ijl} + b\ WT_{ijklm} + e_{ijklm}$$

where:

Y_{ijklm} = observation for the m^{th} mouse of the $ijklm^{th}$ subclass,
μ = mean of the population,
L_i = fixed effect of the i^{th} line,
R_{ij} = random effect of the j^{th} replicate nested within the i^{th} line,
F_{ijk} = random effect of the k^{th} litter nested within the j^{th} replicated nested within the i^{th} line,
S_l = fixed effect of the l^{th} sex,
SL_{il} = interaction of the l^{th} sex with the i^{th} line,
SRL_{ijl} = interaction of the l^{th} sex with the j^{th} replicate of the i^{th} line,
b = regression coefficient of Y on body weight at the start of the selection period,
WT_{ijklm} = weight of the ijklm mouse at the start of the selection period, and
e_{ijklm} = random error, assumed $N \sim (0, \sigma)$.

Differences between the lines in generation nine were tested using linear contrasts. The error term used to test the level of signifcance of contrasts was constructed using the mean square for replicate within line. The standard errors of the contrasts, therefore, take into account genetic drift.

Realized heritabilities. Selection differentials were the mean difference in weight gain between the selected individuals and the mean of their sex in their litter. Selected individuals that did not produce offspring were excluded.

Realized heritabilities were calculated as the regression of response, measured as a deviation from the control in ad libitum lines and corrected for environmental trend as previously outlined in the case of restricted lines, on cumulative selection differential. Standard errors of realized heritabilities estimates were calculated as in Hill (1972, 1980).

Correlated responses in body weights. Correlated responses in body weights at weaning and start and end of each respective selection period were examined. Responses were estimated as the linear regression of the line-sex generation mean, measured as a deviation from the control line-sex generation in ad libitum lines and corrected for environmental trend as previously described except using correlated selection differentials in restricted lines, on generation number.

Estimates in the restricted lines are up to generation eight, since in generation nine all were fed ad libitum.

Results

Response in weight gain

Direct responses in weight gain between 28 and 38 days in each generation for both sexes are presented in Fig. 1. Responses were similar in both sexes up to generation five. After generation five, the responses in the ad libitum line were larger in the males than in the females. In the restricted line the responses were larger in the males also, but the sexes were closer than in the ad libitum line.

Regression coefficients estimates of weight gain in the Early Period of Selection on generation number are presented in Table 1. Regression coefficients were significant for both replicates of the ad libitum line. Regression coefficients for the restricted lines, while larger in magnitude than in the ad libitum line, were not significant.

Direct responses in weight gain between 48 and 58 days for both sexes are shown in Fig 2. Responses in the ad libitum line for both sexes were very small. Responses in the restricted line for both sexes increased constantly up to generation five. This pattern of response is very

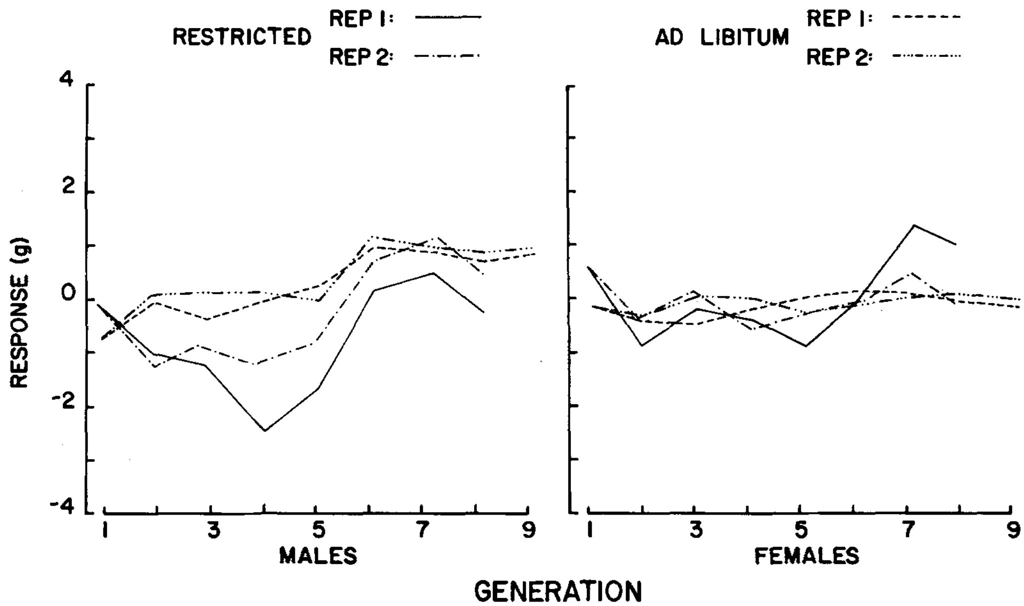

Fig 1. Direct response in weight in the early period of selection

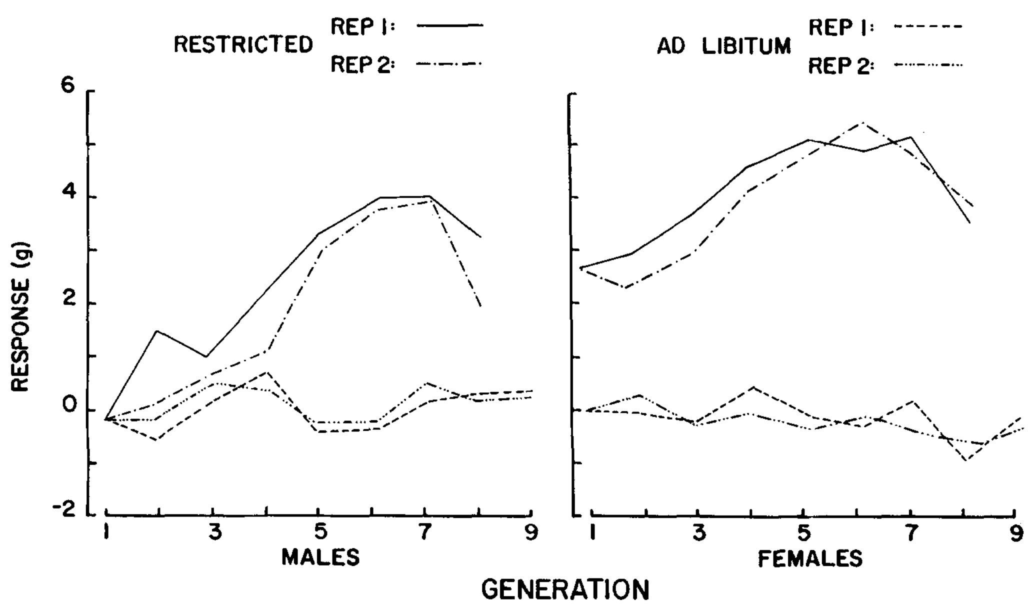

Fig 2. Direct response in weight in the late period of selection

Table 1. Regression coefficient estimates of direct response in weight gain on generation number $\pm$ SE in grams. Early Period of selection

	Regression coefficient estimates	
	Males	Females
EPR1	0.14 ± 0.20	0.07 ± 0.16
EPR2	0.29 ± 0.17	0.19 ± 0.19
EPA1	0.20 ± 0.04**	0.09 ± 0.03*
EPA2	0.19 ± 0.05**	0.06 ± 0.03
C1	0.00 ± 0.01	0.00 ± 0.01
C2	0.00 ± 0.01	0.00 ± 0.01

* $P < 0.05$; ** $P < 0.01$

Table 2. Regression coefficient estimates of direct response in weight gain on generation number $\pm$ SE in grams. Late Period of selection

	Regression coefficient estimates	
	Males	Females
LPR1	0.57 ± 0.19*	0.19 ± 0.12
LPR2	0.57 ± 0.19*	0.28 ± 0.12 ($P = 0.06$)
LPA1	0.04 ± 0.04	-0.06 ± 0.02*
LPA2	0.07 ± 0.05	-0.04 ± 0.05
C1	-0.02 ± 0.02	-0.03 ± 0.02
C2	0.02 ± 0.03	0.03 ± 0.02

* $P < 0.05$

different from the pattern in the restricted line in the Early Period. The restricted line in the Early Period started responding at approximately generation five, while response in the line in the Late Period began to decrease after generation five.

Regression coefficient estimates of weight gain in the Late Period of Selection on generation number are presented in Table 2. Regression coefficients in the ad libitum line were close to zero, positive for the males and negative for the females. In the restricted lines, regression coefficients were significant for males in both replications and very close to significance for females in replicate LPR2.

Least-squares estimates of weight gain in generation nine, corrected for body weight at the start of the selection period, are presented in Table 3 for the Early and Late Period of selection, respectively. Linear contrasts are provided in part 'b' of the table.

For both periods of selection, the lines selected under ad libitum feeding had the highest and the restricted lines the lowest weight gain when compared under ad libitum feeding. The difference between restricted and ad libitum lines was significant in the Late Period. The lines selected under ad libitum feeding had significantly higher weight gains than the control line in the Early Period, but not in the Late Period of Selection.

Realized heritabilities

Total cumulative selection differntials, standarized selection differentials (average per sex per generation divided by the within litter standard deviation) and realized heritabilities are presented in Table 4 for the Early Period and Table 5 for the Late Period of selection.

Cumulative selection differentials for both periods were higher in the restricted lines. Standardized selection differentials in the Early Period on average were the same in the restricted line as in the ad libitum line; however, there was considerable variation between replicates of the restricted line. In the Late Period, standardized selection

Table 3. Weight gain in generation 9 corrected for weight at the start of the selection period

a) Least-squares means $\pm$ SE

Line	Weight gain (28–38 days)		Line	Weight gain (48–58 days)	
EPR1	3.51	0.11	LPR1	1.70	0.13
EPR2	3.78	0.12	LPR2	1.70	0.14
EPA1	4.45	0.11	LPA1	1.94	0.17
EPA2	4.64	0.11	LPA2	2.13	0.14
C1	4.11	0.11	C1	1.82	0.19
C2	4.12	0.12	C2	1.92	0.18

b) Linear contrasts

C-EPR	0.47 ($P = 0.06$)	C-LPR	0.17 NS
C-EPA	-0.43*	C-LPA	-0.17 NS
EPA-EPR	0.90*	LPA-LPR	0.34**

* $P < 0.05$; ** $P < 0.01$
NS = Not significant

differentials were higher in the restricted line. Becker (1984, Table of Order Statistics) gives an expected selection differential of 0.85 for the same conditions (i.e., selecting one out of three within sex-litter). Therefore, the restricted lines were closer to expectation than the ad libitum lines.

Regression coefficient of response on cumulative selection differentials or realized heritabilities were higher for the ad libitum line in the Early Period, while in the Late Period the heritabilities estimates were higher in the restricted line. The realized heritabilities obtained in this study were large but could not be declared significant because of their large standard errors.

Correlated response in body weights

Figures 3 and 4 show correlated responses in body weights at weaning, start and end of the selection period for the Early and Late Periods of Selection, respectively.

Table 4. Cumulative selection differentials, standardized selection differentials, and realized heritabilities ± SE. Early Period of selection

	Total		Standardized		Heritability estimates	
Line	Males	Females	Males	Females	Males	Females
EPR1	5.01	5.33	0.43	0.39	0.19 ± 0.46	0.07 ± 0.27
EPR2	6.23	6.52	0.84	0.83	0.34 ± 0.49	0.25 ± 0.38
EPA1	4.23	4.16	0.66	0.65	0.40 ± 0.39	0.18 ± 0.22
EPA2	3.47	3.48	0.55	0.56	0.45 ± 0.45	0.14 ± 0.20

Table 5. Cumulative selection differentials, standardized selection differentials, and realized heritabilities ± SE. Late Period of selection

	Total		Standardized		Heritability estimates	
Line	Males	Females	Males	Females	Males	Females
LPR1	6.69	6.68	0.94	0.97	0.62 ± 0.48	0.22 ± 0.31
LPR2	6.63	6.66	0.93	0.93	0.62 ± 0.50	0.31 ± 0.36
LPA1	3.79	3.81	0.53	0.54	0.09 ± 0.25	−0.13 ± 0.26
LPA2	4.12	4.20	0.65	0.65	0.11 ± 0.27	−0.09 ± 0.21

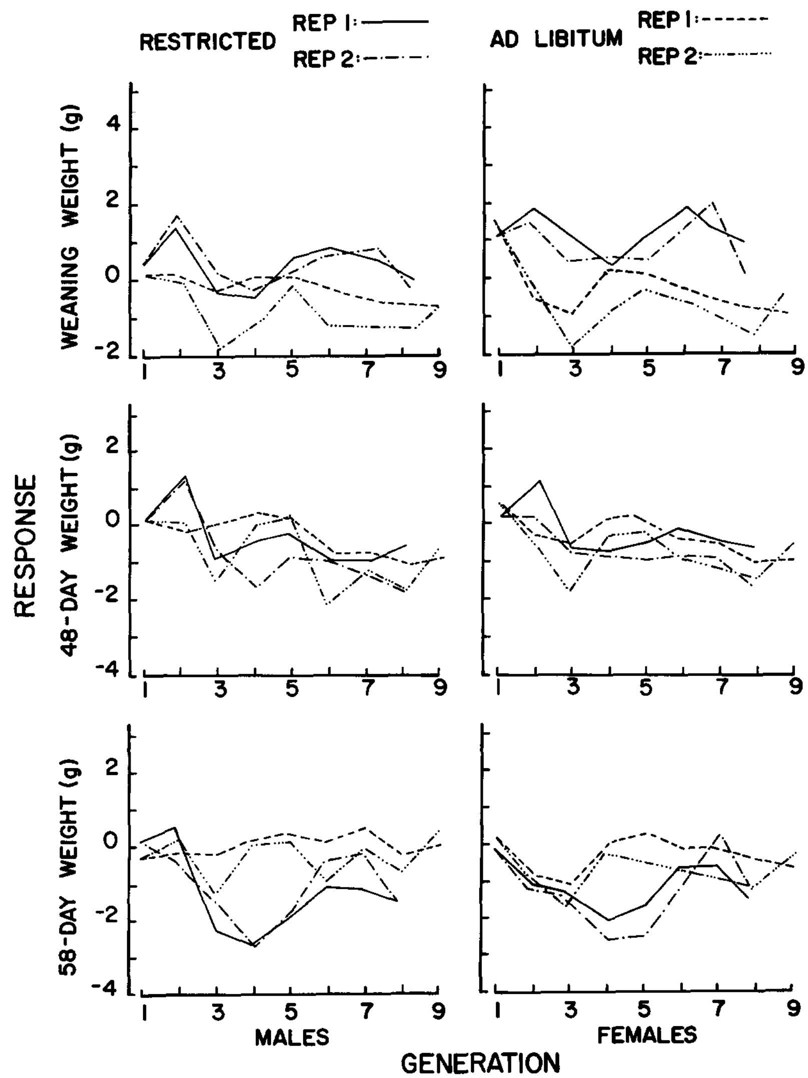

Fig. 3. Correlated responses in body weights in the early period of selection

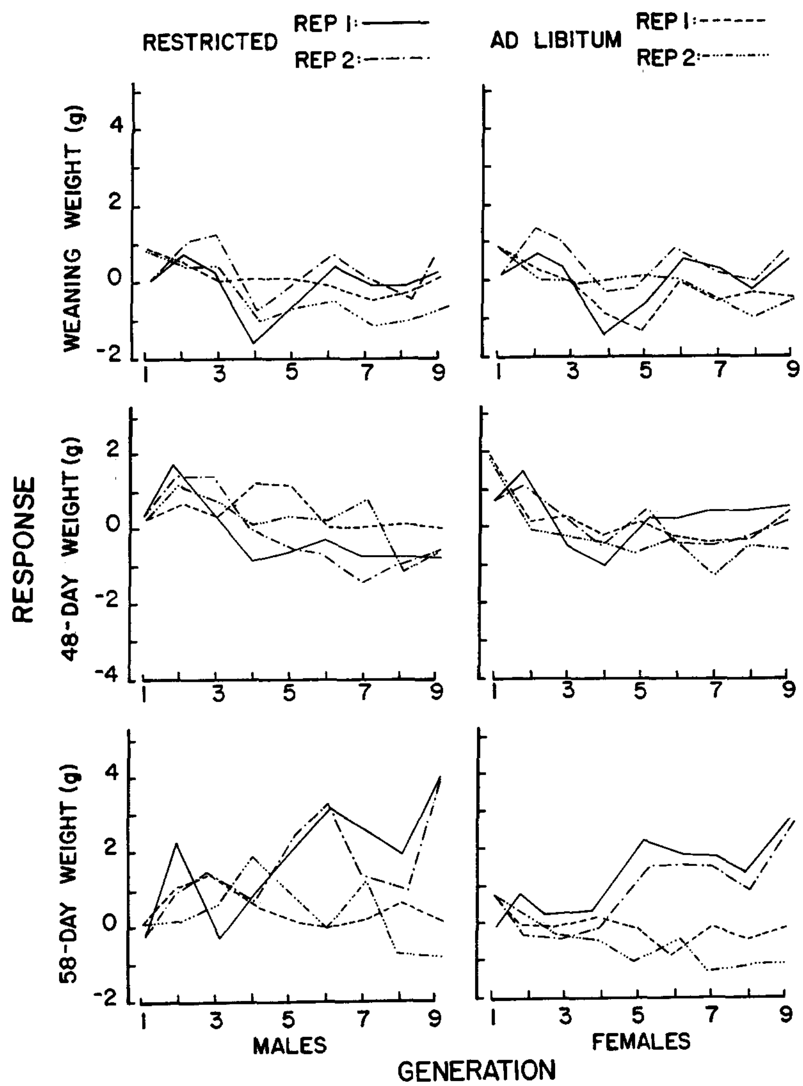

Fig. 4. Correlated responses in body weights in the late period of selection

Table 6. Regression coefficient estimates of correlated response in body weight at weaning, start and end of the selection period on generation number ± SE in grams. Early Period of selection

	Weaning wt.		28-day wt.		38-day wt.	
	Males	Females	Males	Females	Males	Females
EPR1	−0.10 ± 0.10	−0.10 ± 0.08	−0.21 ± 0.12	−0.20 ± 0.07*	−0.13 ± 0.20	−0.10 ± 0.16
EPR2	−0.25 ± 0.09*	−0.20 ± 0.09*	−0.35 ± 0.09**	−0.28 ± 0.08**	−0.04 ± 0.20	−0.06 ± 0.21
EPA1	−0.09 ± 0.03*	−0.09 ± 0.07	−0.15 ± 0.05*	−0.13 ± 0.05*	0.06 ± 0.05	−0.03 ± 0.07
EPA2	−0.10 ± 0.09	−0.11 ± 0.09	−0.16 ± 0.12	−0.10 ± 0.09	0.05 ± 0.09	−0.03 ± 0.08
C1	−0.03 ± 0.03	−0.01 ± 0.05	−0.05 ± 0.04	−0.03 ± 0.04	−0.05 ± 0.03	−0.03 ± 0.04
C2	0.03 ± 0.04	0.02 ± 0.05	0.05 ± 0.05	0.04 ± 0.05	0.06 ± 0.04	0.04 ± 0.05

* $P < 0.05$; ** $P < 0.01$

In both periods of selection, body weights at weaning and at the start of the selection period decreased in both selected lines in both sexes. Body weights at the end of the selection period fluctuated more in the restricted lines than in the ad libitum lines. In the ad libitum lines, body weights were not affected in the Early Period and decreased slightly in the Late Period.

Regression coefficient estimates of body weights at weaning, start and end of the selection period on generation number are presented in Tables 6 and 7 for the Early and Late Period of selection, respectively.

For both periods of selection, regression coefficient estimates of body weights at weanning and at the start of the selection period were negative for lines selected under

Table 7. Regression coefficient estimates of correlated response in body weight at weaning, start and end of the selection period on generation number ± SE in grams. Late Period of selection

	Weaning wt.		48-day wt.		58-day wt.	
	Males	Females	Males	Females	Males	Females
LPR1	−0.12 ± 0.10	−0.10 ± 0.09	−0.30 ± 0.09**	−0.08 ± 0.07	0.34 ± 0.25	0.07 ± 0.13
LPR2	−0.17 ± 0.06*	−0.16 ± 0.07*	−0.33 ± 0.07**	−0.16 ± 0.06*	0.53 ± 0.57	0.09 ± 0.15
LPA1	−0.22 ± 0.07*	−0.16 ± 0.07	−0.18 ± 0.08*	−0.15 ± 0.05*	−0.13 ± 0.09	0.21 ± 0.05**
LPA2	−0.03 ± 0.07	−0.12 ± 0.04*	−0.07 ± 0.06	−0.09 ± 0.05	0.00 ± 0.09	−0.09 ± 0.05
C1	−0.03 ± 0.03	−0.01 ± 0.05	−0.07 ± 0.04	−0.01 ± 0.05	−0.09 ± 0.05	0.04 ± 0.05
C2	0.07 ± 0.04	0.02 ± 0.05	0.07 ± 0.05	−0.01 ± 0.05	0.09 ± 0.05	0.04 ± 0.06

* $P < 0.05$; ** $P < 0.01$

restricted and ad libitum feeding in both sexes. Body weights at the end of the Early Period of Selection were not significantly altered by selection. Body weights at the end of the Late Period of Selection were also not significant except for a negative regression coefficient in females in one replicate of the ad libitum line.

Control line regression coefficients were close to zero for all traits in both sexes and in both periods of selection. Standard errors were similar in both replicates for all traits. Since selection was practised within families and single pair matings were used, the influence of genetic drift was expected to be small.

Discussion

The presence of sexual dimorphism for post-weaning gain has been previously reported by other workers (Eisen and Legates 1966; Rahnefeld et al. 1963; Hanrahan et al. 1973), but it has not been a consistent finding in all selection experiments (Baker et al. 1984; Falconer 1960; LaSalle et al. 1974; Frahm and Brown 1975; Bradford 1971). The most frequent reason for sexual dimorphism has been decreased variability in females, and thus reduced selection differentials. In the present study selection differentials for the sexes within line were virtually identical, and the difference in response between the sexes was larger than previously reported. The difference between the sexes under both feeding regimes were of similar magnitude.

Regression coefficient estimates for response to within-family selection for early post-weaning gain range from 0.25 to 0.36 in the literature (Baker et al. 1984; Dalton 1967; Frahm and Brown 1975). Estimates of heritabilities for weight gain during early post-weaning in the literature range, range from 0.18 (Rahnefeld et al. 1963) to 0.36 (Baker et al.1984) with intermediate estimates by Hetzel and Nicholas (1982 a, b), LaSalle et al. (1974), Frahm and Brown (1975), Bradford (1971), Wilson (1973), Hanrahan et al. (1973), and Falconer (1960). Estimates from males in the Early Period in this study are at the upper end of this range. Estimates from females are at the lower end of the range reported in the literature. Hanrahan et al. (1973) and Rahnefeld et al. (1963) also reported lower heritabilities for weight gain in female.

In the Late Period of selection the lack of response in the ad libitum line can hardly be attributed to such factors as linkage disequilibrium (considering the orgin of the lines), fitness, health problems, or inbreeding. These factors would have been reflected in the cumulative selection differential which was not affected, and inbreeding was below 5% in all lines at geneation nine. A period of selection similar to the Late Period of the present study has not been reported in the literature, but it has been included as part of a much larger period. Wilson (1973) reported that when selecting for post-weaning gain between 21 and 63 days, most of the increase in growth occurs between 21 and 33 days and almost no change in growth was obtained between 42 and 63 days of age. Biondini et al. (1968), selecting for increased growth between 4 and 11 weeks, also reported that most of the increased growth occurred in the early post-weaning period. These results, in addition to the ones from the present study indicates that the additive genetic variance for weight gain at later ages may be limited. Thus, this limited genetic variance could also have been the cause of the apparent lack of response in the ad libitum line of the present study.

The heritabilities of weight gain in the restricted line was higher in the Late Period than in the Early Period of selection. In the Early Period, selection for weight gain is expected to favor animals that have essentially a larger consumption (McCarthy 1979, 1982); thus, animals in the restricted lines, where variability in consumption was not allowed to be expressed, were expected to have a lower response to selection and thus a lower heritability. In the Late Period, selection for weight is supposed to have a broader genetic base and rely on variability present in consumption and in maintenance. Therefore, results from this study, where selection for post-weaning gain was more successful under ad libitum condition at an early age, and selection under restriction was more successful at a later age, are in accordance with the genetic basis of weight gain at different ages proposed by McCarthy (1979, 1982).

In most reported studies of the effect of selection for weight gain on body weights the age at the start of the selection period was also the age at weaning. Body weight at this age has been reported to increase with selection for post-weaning gain (Hetzel and Nicholas 1982 a, b; Rahnefeld et al. 1963; Sutherland et al. 1970; Bradford 1971; Frahm and Brown 1975; Wilson 1973). Alternatively, Hanrahan et al. (1973) and Timon and Eisen (1970) suggested that the observed increase in weaning weights was due to postnatal maternal effects. In their study, no differences in weaning weights were observed when cross-fostering was used and pups from selected lines were nursed by controls. It is suggested that the fact that the selection period in this study did not start at weaning may have played a role. Since weaning weights are very dependent on maternal performance, which improves with increased size (Timon and Eisen 1970; Bradford 1971; Roberts 1979), it must be more difficult to increase weight gain by decreasing weaning weights than by increasing weight at the end of the selection period. Only Hetzel and Nicholas (1978), who selected lines under restriction at an early post-weaning period, reported a decrease in weaning weights and weights at the start of the selection period. Mice with low 3-week weight were found to be favored because they used less energy for maintenance and therefore had more energy available for growth. This explanation would also be relevant to the findings of the present study.

The results of this experiment, when all lines were compared under ad libitum feeding, do not agree with previous reports. McPhee et al. (1980) and Falconer (1960) reported higher gain in the restricted lines than in the controls when fed ad libitum. McPhee et al. (1980) did not keep lines selected under ad libitum, but Falconer (1960) did have lines selected under ad libitum feeding and these performed better than both controls and restricted lines when all fed ad libitum. This is in agreement with the performance of the ad libitum lines in the present study.

The most likely explanation for the difference in weight gains in the restricted lines lies in the source of variability being exploited by selection. It may be assumed that McPhee et al. (1980) were feeding mice at a level above maintenance and allowing the expression of variability in growth. The increase in growth observed McPhee et al. (1980) probably came from a reduction in energy discrepancy, as defined in Stephenson and Malik (1984), since they reported finding no increase in efficiency of growth, which would have been the other alternative. Falconer (1960) reported on selection under a lower plane of nutrition, which probably affects a different mechanism than the one previously discussed. Results from the present experiment indicate that selection under ad libitum and restricted feeding are based on different genetic mechanisms. In the present study, selection under feed restriction favored the animals that lost the least weight during their respective periods. Selection was successful; positive responses to selection and sizeable heritability estimates were obtained. The fact that the restricted lines had reduced body weights and in generation nine, when all animals were feed ad libitum, had lower weight gain at all ages indicates that selection was based on reducing maintenance requirements, and confirms the positive correlation between maintenance and growth potential postulated by Pym (1982). Thus, selection under feed restriction penalizes animals with high maintenance requirements that also have a higher growth potential, in favor of animals with reduced maintenance requirements and also a reduced growth potential.

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