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Growth, efficiency and body composition of mice selected for post-weaning weight gain on *ad libitum* or restricted feeding

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Summary

After seven generations of selection, a line of mice selected for post-weaning (21–42 days) weight gain on full feeding (SF) showed significant increases of 49% in weight gain, 31% in efficiency and 14% in food intake, when compared with its control on full feeding between 21 and 42 days. After day 42, SF mice continued to eat more food and were 28% heavier than control mice at 91 days. Because SF mice were heavier than control mice at almost all ages, they were fatter on an age basis. There was, however, no change in the rate of deposition of fat, protein and ash relative to body weight. On restricted feeding between 21 and 42 days, SF mice showed a non-significant increase in weight gain, and hence in efficiency, of 12%. They deposited more fat than control mice during the feeding period but there was no significant difference when comparisons were made on a weight basis.

A contemporary line of mice selected for post-weaning (21–42 days) weight gain on restricted feeding (SR) had significant increases of 12% in weight gain, 17% in efficiency but no significant change in food intake, when compared with its control on full feeding between 21 and 42 days. SR mice were the same weight as control mice at all ages except day 21, when they were significantly lighter due to direct genetic effects rather than maternal effects. SR mice had a lower ($P<0{\cdot}10$) rate of fat deposition per unit body weight and became less fat relative to their control as body weight increased. The rate of deposition of other components was not altered by selection. On restricted feeding, SR had a significant increase in weight gain, and hence in efficiency, of 37%. Changes in body composition were similar to those on full feeding.

It was concluded that the use of a restricted feeding regime had enabled the exploitation of heritable variation in the partitioning of energy for growth. This variation was independent of genetic variation for appetite and body weight.

Overall performance at each level of feeding was best improved by selection on that feeding level. The realized genetic correlation between post-weaning weight gain on full and restricted feeding was estimated to be $0{\cdot}28 \pm 0{\cdot}08$, indicating a very different genetic basis for the same character in the two feeding environments.

Introduction

The genetics of growth and feeding in mammals has been the subject of considerable research, as reviewed by Roberts (1979) and McCarthy (1980). However, much remains to be understood about the genetic interrelationships between growth rate, food intake, efficiency and body composition.

An increased understanding of these interrelationships may be obtained by selecting on a feeding regime which eliminates variation between animals in their food intake, and by subsequently comparing the performance of selected animals on restricted feeding and on *ad libitum* feeding. This has been done in mice by Falconer & Latyszewski (1952), McPhee *et al.* (1980) and Yüksel, Hill & Roberts (1981), in pigs by Fowler & Ensminger (1960) and in rats by Park *et al.* (1966). As pointed out by Yüksel *et al.* (1981), it is particularly important in such studies that the progress of selection be monitored adequately, and that the performance of selected animals be measured outside the age period of selection. Despite the considerable effort

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expended in conducting each of the above studies, none of them fulfils these two criteria. In the present paper, the results of selection for weight gain from 21–42 days on full and restricted feeding are evaluated on full feeding, in terms of body weight and skeletal growth from birth to 91 days and individual food intake from 21 days to 56 days. In addition, the body composition of the lines is compared on days 21, 42, 70 and 91 on full feeding, and on days 21 and 42 on restricted feeding. A detailed description of the progress of selection is given by Hetzel & Nicholas (1982).

The experiment of Falconer & Latyszewski (1952) was designed specifically to investigate the more general question of genotype–environment interaction, and all the above experiments can be interpreted in a similar context. When viewed in this light the results of the different experiments are not always in agreement. Thus the first study in mice and the studies in pigs and rats found considerable interaction, but the two most recent studies did not. In order to provide more evidence in this regard, the results of the present experiment will also be interpreted in relation to genotype–environment interaction.

2. Materials and Methods

A detailed description of the two selection lines, their controls, the management of the mice and the progress of selection has been given by Hetzel & Nicholas (1982). Briefly, one line was selected for increased post-weaning weight gain from 21 to 42 days of age on *ad libitum* or full feeding (SF) and the other was selected for the same character on a restricted level (SR). The restriction was in absolute amount of food, being increased with age, and totalling 83% of the *ad libitum* intake of unselected mice over the same age period. Controls were maintained for each feeding level (CF and CR respectively).

(i) *Comparison of the lines*

After seven generations of selection, mice from second litters of each line were compared under both feeding regimes, in the following manner. Litters were standardized to 12 mice at birth and to eight (four of each sex) at two days of age. At weaning (21 days), 20 litters were chosen at random from each selection line. From each control line, 10 litters were chosen so that as far as was possible, each family from the previous generation was represented by one male and one female parent. In the selection lines, two males and two females from each litter were allocated to the full feeding group, and one male and one female to the restricted fed group. For the control lines, the numbers were six (three of each sex) and two (one of each sex) respectively. Since 20 mice from each line were killed for carcass analysis at weaning, 60 animals from each selection line and 40 from the controls were measured on full feeding. On restricted feeding, the numbers were 40 and 20 respectively

(a) *Growth, food intake and efficiency*

Full feeding. At weaning, mice were weighed and placed in individual cages. They were fed a finely ground laboratory chow (Allied Feeds) in glass jars designed to eliminate spillage and wastage of the food. Weekly food intake was recorded, and animals were weighed twice weekly up to 56 days of age. They were then transferred to larger cages, fed a cubed diet *ad libitum* and weighed weekly until 91 days of age. Tail length (as a measure of skeletal size) was recorded at 21, 42, 70 and 91 days of age.

Restricted feeding. Mice were weighed at weaning and twice weekly thereafter. They were placed in individual cages and fed every two days according to the same schedule as was used throughout the selection experiment (Hetzel & Nicholas, 1982). Tail length was measured at 21 and 42 days of age.

(b) *Body composition*

Sampling of the lines. Since the body composition of the strain of mice used in this study had not previously been examined, a preliminary study was conducted at generation four to establish ages at which changes in body composition were greatest. Based on this experience, at generation seven, mice were killed at four ages: 20 mice (10 of each sex) were sampled at each age. Mice sampled from each line at 21 days served as common observations for both full-fed and restricted groups. On full feeding, a random sample with equal family representation was taken at 42 and 91 days from all lines with an additional sample at 70 days from SF and SR. On restricted feeding, a sample of mice from each line was taken at 42 days, being the end of the feeding period.

Carcass analysis. Mice were generally weighed and fed in the morning. On the days when mice were to be slaughtered, those chosen for carcass analysis were deprived of food in the morning and starved for 5–8 h. They were then killed by neck dislocation, weighed (the weight being referred to as carcass weight) and stored in individual plastic bags at −18 °C until the time of analysis. At this time the carcass was thawed, chopped roughly into little pieces and the whole mouse homogenized with the addition of water, in a Sorvall Omni-mixer for about two minutes. The homogenate was then freeze-dried for approximately 24 h. This procedure provided a homogeneous mixture from which subsamples could be taken for chemical analysis. Protein was determined on two, approximately 0·25 g subsamples, using the macro-Kjeldahl method. Fat was estimated from 1·5 g of dried material using a chloroform–methanol–water extraction as outlined by Atkinson *et al.* (1972). A 1 g subsample was heated for 2 h at 600 °C to measure ash content.

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(ii) *Genotype–environment interaction*

Since the performance of each line was measured on both feeding levels, direct and correlated responses were observed on both levels of feeding. Separate estimates of the extent of interaction were obtained by estimating the genetic correlation between weight gain on the two feeding levels, following Falconer (1952). For example, on full feeding,

$$r_G = \frac{CR \cdot h_1}{R \cdot h_2},$$

were R and CR are the direct and correlated response in post-weaning weight gain on full feeding when selection is on full feeding and the restricted level respectively, and h_1 and h_2 are the square roots of the heritabilities of weight gain on full feeding and restricted feeding respectively. The separate estimates were combined according to Falconer (1960), and an approximate standard error calculated after Hill (1971).

(iii) *Statistical methods*

Results are generally expressed with each selection line being compared with its own control. This was done for two reasons. First, the object of the comparison was to establish what changes had been brought about by selection on each of two different feeding levels. Secondly, even though the controls rarely differed significantly from each other, it was not known whether there were any permanent effects of the restricted diet which may have affected selection responses. Significance tests were carried out using Student's t test.

Comparisons of body composition were first made on an age basis. There being no consistent sex by line interactions, the data were pooled over both sexes. Comparisons between lines were also made on a weight basis by use of the allometric equation $Y = aX^b$. The allometric approach has been used widely in developmental studies of body composition (see Seebeck, 1968). The data were therefore transformed to logarithms; linear regressions were then fitted, where Y and X were the component weight and carcass weight respectively. The components analysed were protein, fat and ash. Regressions were first fitted to some of the data at various ages for each sex separately. However, while the elevation of the lines differed significantly in some cases, the slopes did not. Subsequently, all analyses were performed with both sexes pooled at each age. Data from each line were then analysed on a within-age basis. There being no significant difference between the individual within-age regression coefficients and the combined within-age regression coefficient, the data were best described by the overall regression, ignoring age structure. This was the case for each of the lines on both feeding levels. A one-way analysis of covariance to compare regression equations was then performed (Snedecor & Cochran, 1967). Each selection line was compared with its control. Tests of significance were made first for the difference in slope and secondly for the difference in elevation of the regression equations. If the slopes were significantly different, the test of elevation had no meaning and was not carried out.

3. Results

(i) *Comparison of lines*

(a) *Growth, food intake and efficiency*

Full feeding. Mean body weight and tail length of the lines at various ages are given in Table 1. There was no significant difference in birth weight between either selection line and its respective control. However, SF was heavier than its control at all subsequent ages. There was no significant difference in body weight between SR and CR except at 21 days. When measurements stopped at 91 days, all lines were still growing, although differences between the lines were well established.

SF has significantly longer tails than CF from 42

Table 1. *Mean body weight and tail length of the lines on full feeding, and average standard error* (S.E.) *of the difference between a selection line and its control*

	Age (days)	Line				Av. S.E. S()-C()
		SF	CF	SR	CR	
Body weight (g)	Birth	1·70	1·65	1·66	1·73	0·05
	12	8·8*	8·4	8·1	8·5	0·2
	21	16·0**	14·8	14·2**	15·4	0·3
	42	35·5**	27·9	28·0	27·5	0·7
	70	40·2**	31·6	31·8	31·8	1·0
	91	42·8**	33·5	33·9	33·8	1·2
Tail length (cm)	21	5·7	5·6	5·5*	5·8	0·1
	42	8·4**	7·8	7·6	7·7	0·1
	70	9·2**	8·5	8·5	8·5	0·1
	91	9·5**	8·8	8·8	8·8	0·1

* $P<0·05$, ** $P<0·01$ for the comparison of a selection line with its control.

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days onwards. Tail length is positively correlated with skeletal size (Baker & Cockrem, 1970). Therefore, in general SF mice had a larger skeletal size as well as a higher body weight. Except at 21 days (at which body-weight differences were at their greatest), there was no significant difference in tail length between SR and its control.

In all lines, mice reached their maximum food intake at between 28 and 35 days of age. Thereafter intakes remained constant until 56 days. The differences between the lines were fairly consistent over all ages, with SF mice eating considerably more than all other lines.

Weight gain, food intake and efficiency over the periods 21–42 and 42–56 days are given in Table 2. SF had a higher weight gain, a larger appetite and a greater efficiency of growth than its control for both periods. Between 21 and 42 days of age, SR had a significantly higher weight gain, a slightly lower food intake and was considerably more efficient than its control, i.e. selection for weight gain on a restricted diet was effective at improving both weight gain and efficiency of growth on full feeding. When intake was expressed relative to the mean estimated metabolic body weight (mean body weight$^{0.75}$) from 21–42 or 42–56 days, neither SR nor SF was different from its control.

Restricted feeding. Results when samples of the four lines were compared on the restricted level of feeding are presented in Table 3. SF was significantly heavier at 21 days than CF, and gained more weight than its control on the same amount of food, such that it was still heavier at 42 days. However, the higher weight gain and efficiency were not statistically significant. SR had the highest weight gain of all lines on restricted feeding. However, it had the lowest weight at commencement of the feeding period, which would have reduced maintenance requirements at this age. Nevertheless it was heavier than its control for most of the 21 days. Over this period SR was considerably more efficient than CR.

The measurements of tail length show that all lines

Table 2. *Mean weight gain, food intake and efficiency of the lines on full feeding, and average standard error* (S.E.) *of the difference between a selection line and its control*

	Age (days)	Line SF	CF	SR	CR	Av. S.E. S()-C()
Weight gain (g)	21–42	19·5**	13·1	13·7**	12·2	0·6
	42–56	2·7*	1·9	1·9	1·7	0·4
Food intake (g)	21–42	143·0**	125·3	119·7	123·2	2·0
	42–56	101·5**	86·5	83·3	84·6	2·0
Efficiency†	21–42	0·136**	0·104	0·115**	0·098	0·004
	42–56	0·026	0·022	0·023	0·019	0·004
Food intake bodyweight$^{0.75}$	21–42	12·6	12·6	12·1	12·4	0·3
	42–56	6·8	7·0	6·7	6·9	0·2

* $P < 0·05$, *** $P <> 0·01$ for the comparison of a selection line with its control.
† Weight gain/food intake.

Table 3. *Mean weight gain, food intake, efficiency between* 21 *and* 42 *days, and tail length at* 21 *and* 42 *days of the lines on restricted feeding, and average standard error* (S.E.) *of the difference between a selection line and control*

	Age (days)	Line SF	CF	SR	CR	Av. S.E. S()-C()
Body weight (g)	21	15·9**	14·5	13·8**	15·0	0·4
	42	24·6**	22·3	24·2**	22·6	0·4
Weight gain (g)	21–42	8·7	7·8	10·4**	7·6	0·5
Food intake (g)	21–42	100·5	100·5	100·4	100·5	–
Efficiency†	21–42	0·087	0·078	0·104**	0·076	0·005
Tail length (cm)	21	5·7	5·6	5·4*	5·8	0·1
	42	7·2	7·0	7·0	7·0	0·1

* $P < 0·05$, ** $P < 0·01$ for the comparison of a selection line with its control.
† Weight gain/food intake.

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increased in body length or skeletal size by about the same amount, although at 42 days SR was significantly heavier than CR, yet has the same skeletal size. Therefore a higher proportion of the extra weight gain for SR came from the production of body tissue rather than skeletal growth.

(b) *Body composition*

It is common knowledge that the proportion of fat in the carcass of a mouse increases with both age and weight, while the protein percentage increases to a certain level and remains fairly constant thereafter (see, for example, Cheek & Holt, 1963). Because fatty tissue contains a lower proportion of water compared with muscle tissue, overall water content declines with age. An important consequence of these changes is that the age and weight at which comparisons between animals or lines are made can make a large difference to the conclusion reached. Therefore, in this study, comparisons were made at a number of different ages as well as on a weight basis. Since water content is a reflexion of the proportions of protein and fat, for the sake of brevity results are not presented here but can be found in Hetzel (1978). Body weights of the samples were in all cases representative of the lines at that age.

(i) *Comparison on an age basis*

Full feeding. Overall there were very few significant differences when selection lines were compared with their respective controls (Table 4). SF had a lower protein percentage at 21 days and tended to have a lower protein content at subsequent ages. SF was significantly fatter at 91 days. The fat percentage of CF at 42 days was unusually high, both in relation to its subsequent fatness at 91 days and to the other control, CR, at 42 days; it must therefore be viewed with some scepticism. Bearing this in mind, the general trend was for SF to have a lower proportion of lean tissue and a higher fat content than its control after 21 days of age.

SR had a higher protein percentage at 21 days as compared with CR, but the difference was not apparent at subsequent ages. Although never significant, SR was less fat than CR at every age. In addition, SR had a higher proportion of ash in the carcass at 91 days. A final generalization which can be made is that at any age SR was less fat than SF, the difference being greatest at 91 days.

Coefficients of variation for fat percentage were highest (33–42%) at 42 days in all lines (see Hetzel, 1978), indicating that fat synthesis may have been near its maximum rate at around this age (Reid *et al.* 1968). In addition, at around five weeks of age, mice in this study reached sexual maturity, which is often associated with increased fat production. Therefore for this strain of mice, fat synthesis appears to be well advanced by 42 days of age.

Restricted feeding. When compared with its control, SF had a significantly lower protein percentage at both 21 and 42 days (Table 4). SF was also fatter at 42 days ($P<0{\cdot}10$). There was no significant difference

Table 4. *Body composition* (%) *of the lines on* (*a*) *full feeding and* (*b*) *restricted feeding and the average standard error* (S.E.) *of the difference between a selection line and its control*

	Age (days)	Line SF	CF	SR	CR	Av. S.E. S()-C()
		(a) Full feeding				
Protein	21	16·7*	17·2	17·1*	16·7	0·2
	42	17·7	18·1	18·2	18·2	0·3
	70	18·2	—	18·4	—	—
	91	18·0	18·2	18·1	18·2	0·3
Fat	21	8·0	7·7	7·5	7·7	0·5
	42	10·7	11·3	9·4	10·5	1·2
	70	10·5	—	8·2	—	—
	91	12·4*	9·3	9·2	10·2	0·8
Ash	21	2·9	3·9	2·9	3·0	0·1
	42	3·0	3·0	3·0	3·1	0·1
	70	3·0	—	3·1	—	—
	91	3·2	3·2	3·3*	3·1	0·1
		(b) Restricted feeding				
Protein	21	16·7*	17·2	17·2*	16·7	0·2
	42	17·4*	18·0	17·9	18·4	0·3
Fat	21	8·0	7·7	7·5	7·7	0·5
	42	9·8	8·4	9·1	8·3	0·8
Ash	21	2·9	3·0	2·9	3·0	0·1
	42	3·3	3·2	2·1	3·1	0·1

* $P<0{\cdot}05$, ** $P<0{\cdot}01$ for the comparison of a selection line with its control.

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between SR and CR in any component at either 21 or 42 days. The proportions (%) of body-weight gain due to fat or protein deposition during the restricted feeding period were 26 and 19, 10 and 20, 12 and 20, 10 and 22 for SF, CF, SR and CR respectively. Thus the composition of weight gain was remarkably similar for all lines except SF which lay down more fat on restricted feeding than CF.

(ii) *Comparison on a weight basis*

Regression coefficients and tests of significance are given in Table 5, and the regression lines for fat content on full feeding are presented in Fig. 1.

Full feeding. There was no significant difference between SF and its control in either slope or elevation of the regression for any component of body composition except for a small but significant reduction in protein content at a given weight. Therefore selection for weight gain on full feeding has not substantially changed body composition on a weight basis. However, it can be seen from Table 4 that while the rate of fat deposition was not altered in the SF line, SF mice reached higher body weights than CF and therefore were fatter at 91 days.

On full feeding, SR had a lower rate of fat deposition ($P<0{\cdot}10$) than CR. SR was also significantly less fat at a given carcass weight and became less fat relative to its control as body weight increased. Protein deposition relative to body weight was not altered by selection on the restricted diet.

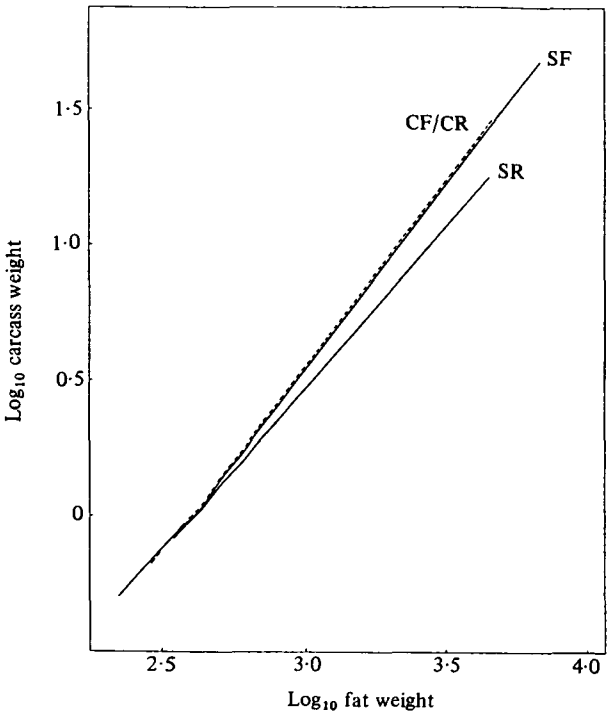

Fig. 1. Regression of log fat weight on log carcass weight for the lines on full feeding.

Table 5. *Allometric coefficients for protein, fat and ash for the lines on (a) full feeding and (b) restricted feeding with standard error* (S.E.) *and tests of significance of the differences between the slopes and between the elevations of the regression lines.*

	Line				Av.
	SF	CF	SR	CR	S.E.
	(a) Full Feeding				
Protein	1·07	1·06	1·07	1·10	·02
Slope	ns		ns		
Elevation†	**(—)		ns		
Fat	1·37	1·39	1·20	1·35	·08
Slope	ns		ns ($P<0{\cdot}10$)		
Elevation	ns		*(–)		
Ash	1·03	1·00	1·06	1·02	·03
Slope	ns		ns		
Elevation	ns		ns		
	(b) Restricted feeding				
Protein	1·23	0·91	1·41	0·82	0·2
Slope	ns		ns		
Elevation	ns		ns ($P<0{\cdot}10$)		
Fat	3·82	2·75	1·80	3·32	1·34
Slope	ns		ns		
Elevation	ns		ns		
Ash	0·57	0·67	0·33	0·22	0·29
Slope	ns		ns		
Elevation	*(+)		**(+)		

* $P<0{\cdot}05$, ** $P<0{\cdot}01$, ns $P>0{\cdot}05$ for the comparison of a selection line with its control. † (+)/(–) indicates that the selection line had a higher/lower elevation than the control.

Restricted feeding. The restricted feeding treatment began only after 21 days of age, so that mice killed at this age had been raised on full feeding. Therefore it was thought advisable to exclude body composition data of mice killed at 21 days from the regression analyses.

Due to the small number of animals involved and the narrow range of body weight, the large standard errors severely limited interpretation of the results. There were few significant differences, although both selection lines had significantly higher ash contents at a given carcass weight, relative to their controls (Table 5). As noted for the lines on full feeding, SR had the lowest rate of fat deposition and SF had a lower protein content at a given weight. In general, the results on restricted feeding did not conflict with those on full feeding.

(ii) *Genotype–environment interaction*

The estimates of genetic correlation between performance on the two feeding regimes were 0·30 from data on full feeding, and 0·25 from restricted feeding, giving a pooled estimate of $0{\cdot}28 \pm 0{\cdot}08$. This is quite low, and indicates a rather different genetic basis for the same character on the two feeding levels.

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4. Discussion

(i) *Comparison of the lines*

The results of selection on full feeding (SF) are in general agreement with most other similar studies; animals eat more, grow faster and are more efficient. Selection on restricted feeding (SR) has increased weight gain and efficiency, without changing food intake. This result is in agreement with the comparable results of Park *et al.* (1966) in rats. However, McPhee *et al.* (1980), when selecting mice at a somewhat later stage (days 35–63), observed a significant increase in food intake over the test period. But when expressed on a body-weight basis, they observed no change.

When evaluated on full feeding over a longer period, from birth to near maturity, it is clear that selection on full feeding has increased body weights at all ages from birth, with SF individuals ending up 28% heavier at 91 days. In contrast, SR individuals had the same body weight as their controls at all times except at 21 days, when they were significantly lighter. It is evident that the increased weight gain of SR mice between days 21 and 42 serves only to bring SR mice up to the same 42-day body weight as the controls. Thereafter, SR mice show the same performance on full feeding as do the controls. Thus neither weight gain, food intake nor efficiency has been altered in SR after the period of selection. In an attempt to investigate the cause of the reduction in 21-day weight in the present experiment, a cross-fostering experiment was undertaken, with body weights being recorded every 3 days between birth and 21 days. The results are described in detail by Hetzel (1978). Briefly, they indicated a complete absence of maternal effect on the difference in body weight of SF and SR mice from birth to weaning. Thus it can be concluded that the reduced 21-day weight of SR individuals in the present experiment was due to a direct genetic change.

The explanation for the reduction in 21-day weight in the SR line probably lies in a consideration of maintenance requirements. Animals, lighter at the start of the restricted feeding period, will have a lower energy requirement for maintenance and thus a greater proportion of their intake can be used for growth. Yüksel *et al.* (1981) observed a similar reduction in initial weight in their comparable (E) lines. However, McPhee *et al.* (1980) were able to prevent the change by adjusting weight gain for the initial weight. In an effort to determine whether maintenance requirement per unit of body weight had been altered by selection, mice from each of the lines were placed on a constant feed intake from the age of four weeks (Hetzel, 1978). The body weights of SR mice were the same as for the control mice, suggesting that maintenance requirement per unit body weight had not been changed by selection.

After seven generations of selection, SF had a substantially higher bodyweight on full feeding at all ages from birth, so therefore it might be expected to be fatter when comparisons with its control are made on an age basis. The differences in fatness between SF and CF at 91 days and probably therefore at maturity were very marked. This agrees with the majority of other studies, in which selection for postweaning growth rate or body weight has resulted in a correlated increase in fatness at a given age after weaning, (Hull, 1960; Biondini, Sutherland & Haverland, 1968; Timon, Eisen & Leatherwood, 1970; Hayes & McCarthy, 1976; McPhee & Neill, 1976). The C-strain studied by Fowler (1958), and the high line of Lang & Legates (1968) showed no such increase, although the practice of looking at body composition at only one age is dangerous (Hayes & McCarthy, 1976), and does not allow examination of developmental changes brought about by selection.

The model proposed by Robertson (1973) predicts that selection at an early age, before fat synthesis has reached an appreciable level, will largely exploit genetic variation in appetite. However, selection at a later age will exploit variation between animals in the partitioning of energy for growth between fat or protein synthesis. In the study reported here, it appeared that fat synthesis was well under way by 42 days of age, so that the measurement period in this selection programme may fall between these two categories. The SF line displayed no correlated increase in the rate of fat deposition, in contrast to most of the previous reports. However, the increase in feed intake in the SF line was only 14% compared with nearly 27% in the M16 line of Eisen, Bakker & Nagai (1977). In addition, the genetic correlation between gain and feed intake estimated in the base population was considerably lower than the estimate for 6-week weight and feed intake (Hetzel, 1978).

In the model of Robertson (1973), if variation in food intake is eliminated, most of the genetic variation in growth rate is in the form of partitioning of energy for growth. Selection for body weight or weight gain under these conditions should favour those animals which direct a greater proportion of energy above that required for maintenance into synthesis and deposition of lean tissue, since fat is energetically more expensive to lay down per unit of body weight by a factor of almost five (Webster, 1977). This has been verified by the performance of the SR line on full feeding. Selection on a restricted diet improved growth rate on full feeding by a small but significant amount without altering mature weight. At the same time, there was a correlated decrease in the proportion of fat in the carcass at any given weight such that the SR line became leaner relative to its control as growth progressed. This result supports the findings of Falconer & Latyszewski (1952), who reported that mice from a line selected for high 6-week body weight on a restricted diet similar to the one used here were leaner at this age.

In two subsequent studies, mice selected for growth

rate on restricted feeding were not leaner than unselected mice. Yüksel *et al.* (1981) reported that on full feeding, mice from the comparable E lines were fatter at both the beginning and end of the feeding period, yet were still more efficient than control mice. However, it was not clear whether the selected mice were also heavier at these ages, since growth measurements were not reported for these mice. The amount of fat produced may have been lower than for the control. There was also some variation in intake for the restricted mice, due to a failure to measure feed residues. In this case selection pressure against fat deposition would have been reduced.

In addition, McPhee *et al.* (1980) selected mice for 5- to 9-week weight gain, corrected for 5-week weight, on a restricted intake and found that on full feeding, selected mice were fatter and contained less lean at 9 weeks of age, even when differences in body weight were removed. It is possible that in adjusting for 5-week weight, mice which were relatively fatter were favoured because fatty tissue has a lower turnover rate (Paigen, 1971) and therefore lower energy requirement for maintenance than does protein. Therefore much of the selection pressure may have been for lower maintenance costs rather than for a reduction in fat synthesis and deposition.

It was clear from the present study that selection on a restricted level of feeding was able to exploit heritable variation for the partitioning of energy for growth. The reduction in the rate of fat deposition was apparent both on restricted and full feeding. Therefore genetic variation for fat deposition independent of genetic variation for appetite and for body weight has been demonstrated by the use of a restricted feeding regime.

(ii) Genotype–environment interaction

In the first mouse experiment on genotype–environment interaction, Falconer & Latyszewski (1952) selected for 6-week body weight, which is highly correlated to the selection criterion used in the present study, namely weight gain from 3 to 6 weeks. The two environments used by Falconer & Latyszewski (1952) were very similar to those used here, except that their restriction was about 75% of *ad libitum* intake, compared with about 83% in the present study. When estimating the genetic correlation between performance in the two environments, Falconer (1952) obtained estimates of 0·65 and 0·0 from the two selection lines. In determining the extent of genotype–environment interaction, Falconer ignored the latter estimate. But Hill (1978) has shown that it should not be neglected, because such asymmetry may be due to genetic drift. Thus the pooled estimate of genetic correlation from the experiment of Falconer & Latyszewski (1952) is 0·33, which is in good agreement with the estimate of 0·28 obtained in the present experiment. It is interesting to note that in a preliminary exchange of environments conducted at generation 4 in the present experiment, the two estimates of genetic correlation were 0·65 and −0·12 (Hetzel, 1978), which are as different as the two estimates obtained by Falconer & Latyszewski (1952). The pooled estimate, however, was $0{\cdot}27 \pm 0{\cdot}12$, in good agreement with the estimates above.

In other experiments in pigs (Fowler & Ensminger, 1960) and in rats (Park *et al.* 1966), considerable genotype–environment interaction was also detected. However, in the only other comparable mice experiments, neither McPhee *et al.* (1980) nor Yüksel *et al.* (1980) detected any significant interaction. A possible reason for the apparent lack of agreement in the case of McPhee *et al.* (1980) is that only one of the two possible estimates of genetic correlation could be obtained, because selection was conducted in only one environment. Given the likelihood of asymmetry in realized genetic correlations (Hill, 1978), it is possible that McPhee *et al.* (1980) might have detected interaction if both estimates of genetic correlation could have been obtained. The most likely reason for the lack of interaction in the results of Yüksel *et al.* (1981) is that they were selecting for a different character, namely efficiency. In the population of mice used in the study reported here, the genetic correlation between efficiency on full and restricted feeding was found to be $0{\cdot}95 \pm 0{\cdot}23$, so that an interaction would not be expected. Bearing this in mind, it can be concluded that at least for the characters body weight and weight gain, performance on a particular level of feeding is best improved by selection on that feeding level.

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