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Changes in Growth, Appetite, Food Conversion Efficiency and Body Composition in Mice Selected for High Post-weaning Weight Gain on Restricted Feeding

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Summary. This study aimed to test the hypothesis that if animals were fed the same amount over the same time period, selection of the fastest growers would result in a change in the partitioning of metabolisable energy toward more protein and less fat deposition. Two mouse lines (S1 and S2) were selected for high 5 to 9 week weight gain corrected to mean 5 week weight. Appetite variation between mice was eliminated by feeding a fixed amount to each mouse daily. After 6 generations of selection, the lines were compared with an unselected control (C) on restricted and ad libitum levels of feeding for growth rate, appetite, food conversion efficiency and chemical body composition.

Realised heritabilities of 5 to 9 week gain were 0.36 ± 0.05 and 0.19 ± 0.04 for S1 and S2 respectively. Nine week weights were increased by an average of 13% on both feeding levels. Most of this increase, particularly in S2, occurred before 5 weeks and was therefore outside the period of measurement used in selection. On ad libitum feeding, selection increased food intake per unit time by 6% but there was no increase per unit body weight. Food conversion efficiency (gain/food) increased by 12%. Compared with controls at 9 weeks, 3% more of the body weights of selected mice was fat and 1% less was protein. These differences were reduced but were still in the same direction when comparisons were made at the same body weight. Thus the expected change in energy partitioning toward greater protein and less fat deposition in the S lines did not occur.

It was concluded that the increased growth and energy retention in the S lines was brought about by a reduction in maintenance requirement. To achieve the desired change in energy partitioning using a similar selection scheme, higher levels of dietary protein should be fed, and some measure of protein deposition rather than growth rate used as the selection criterion.

Key words: Protein deposition – Fat deposition – Appetite – Food conversion – ad libitum feeding – Post-weaning period – Mouse

Introduction

To improve the efficiency of lean tissue growth in pigs, Kielanowski (1968) proposed a testing regimen in which all animals were fed the same amount over a given time period. Selection for high weight gain would then favour those which were efficient because they directed more metabolisable energy toward protein and less toward fat synthesis.

This study examined this proposition using mice, a species extensively used to model selection for growth rate in livestock (Roberts 1965). Two lines of mice were selected for increased growth rate in a post-weaning period in which all mice were fed the same amount. After 6 generations of selection, the lines were compared with an unselected control line on both restricted and ad libitum feeding regimens for growth rate, appetite and carcase composition.

Method

Selection Procedure

Two selection lines S1 and S2 were established by sampling within full sib families of the control line C described by McPhee and Neill (1976). In the base generation each selection line consisted of 15 pairs housed in separate cages. In subsequent generations, lines comprised 7 sires each mated to 3 dams at 10 weeks of age. Two weeks after mating, males were removed and females placed in individual cages. Within 24 hr after birth, litters were standardised to 8 and dams with litters of similar birth date were grouped in pairs. These operations aimed at minimising maternal effect differences between litters. Weaning occurred at 4 wks of age when 25 males and 25 females were sampled across litters of each line, omitting extremes of both high and low body weight. Each mouse was placed in a separate cage compartment and fed daily for 5 wks on a standard laboratory ration comprising on a dry matter basis, 17.4 MJ/kg gross energy, 22.1% crude protein, 2.0% Ca, 1.4% P and 3.8% ether extract. The daily allowance over the test period was fixed at 5.7 g from preliminary trial work and represented 83% of the average daily ad libitum intake of the C lines. Mice were weighed at 5 and 9 weeks of age. A 5 to 9 week test period was chosen as a period of rapid deposition of protein from an earlier study of body composition changes in the C line by McPhee and Neill (1976) in which there was a linear increase in body protein of 84% over this period. The selection criterion was weight gain adjusted by linear regression to the average 5 week weight of each line x sex class. Using this criterion, the fastest growing 7 males and 21 females per line were selected as parents of the following generation giving selection intensities of 7/25 for males and 21/25 for females. These were mated assortatively. Selection was continued in this way for 6 generations.

Measurement of Response

At generation 6, 32 mice of each sex were selected across litters from each of the three lines and divided into 8 groups of 4. Each group was housed in a single cage with an ad libitum feeder designed to allow free access to food and the collection of spillage. Measurements of growth and food intake were made from 5 to 9 weeks of age. At 9 weeks of age all 64 mice per line were slaughtered for carcase analysis.

Progeny of mice retained without selection for continuation of the C lines were used to evaluate response in the selected lines on restricted feeding. The growths of 20 of each sex of the three lines were measured from 5 to 9 weeks under the food restriction programme used during selection. At 9 weeks of age, all 40 mice per line were subject to carcase analysis.

Carcase Analysis

Mice were killed by spinal dislocation, opened along the ventral surface and dried to constant weight at 80°C in individual petri dishes. The entire dried contents of each petri dish was crushed, transferred to a Soxhlet thimble, and extracted for 16 hrs with petroleum ether. After this fat extraction, the residue in the thimble was heated at 600°C for 4 hrs and the ash determined. Protein was estimated as the difference between dry matter and the sum of the fat and ash components.

Results

Selection Differentials

Table 1 shows the selection differentials accumulated over 6 generations in S1 and S2, for the selection criterion; corrected 5 to 9 week gain, and for the characters not selected for directly; actual 5 to 9 week gain, 5 week weight and 9 week weight.

The use of corrected 5 to 9 week gain as the selection criterion achieved 88% of the possible selection differential in actual 5 to 9 week gain. The consequent indirect selection differential accumulated in 5 week weight was an almost negligible -0.30 standard deviations. Had actual 5 to 9 week gain been used instead for selection, an estimated -1.95 s.d. of selection differential would have accumulated in 5 week weight. As expected considerable selection differential accumulated in 9 week weight as a consequence of applying selection for 5 to 9 week gain but not for 5 week weight.

Table 1. Selection differentials accumulated over 6 generations in the selection criterion (corrected 5 to 9 week gain) and in traits not directly under selection. Measurements are in standard deviations

	Cumulative selection differential			
Line	5 to 9 wk gain		5 wk	9 wk
	Corrected[a]	Uncorrected	Weight	Weight
S1	4.42	3.99	–0.31	3.84
S2	5.15	3.66	–0.29	2.70

[a] corrected by linear regression to average 5 wk weight of line x sex class

Selection Response

Mean 5 and 9 week weights of the foundation population and of the S lines through 6 generations of selection are given in Figure 1. Mean weights of C line mice were available for generations 0 and 6 only.

Increase in both 5 and 9 week weights with time is evident. That some of the increase was due to changing environment is suggested by rises in 5 and 9 week weight of the C line between generations 0 and 6. The difference between these weights appears to be little affected however. Linear regressions of body weight on generation number for S1 and S2 respectively were 1.0 ± 0.2 g and 1.1 ± 0.3 g for 5 week weight and 1.6 ± 0.3 g and 1.3 ± 0.4 g for 9 week weight. Differences between these slopes indicated an increasing difference between 5 and 9 week weights which was greater for S1 than S2, as selection proceeded.

Realised heritability estimates were obtained from the regression of gain on cumulative selection differential each generation (Falconer 1960). These were 0.36 ± 0.05 for S1 and 0.19 ± 0.04 for S2, the standard errors being calculated by the method of Hill (1972).

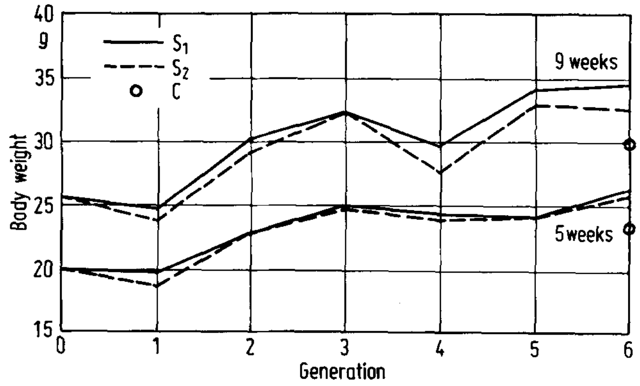

Fig. 1. Generation means of 5 and 9 week weights of the selected (S1 and S2) and control (C) lines

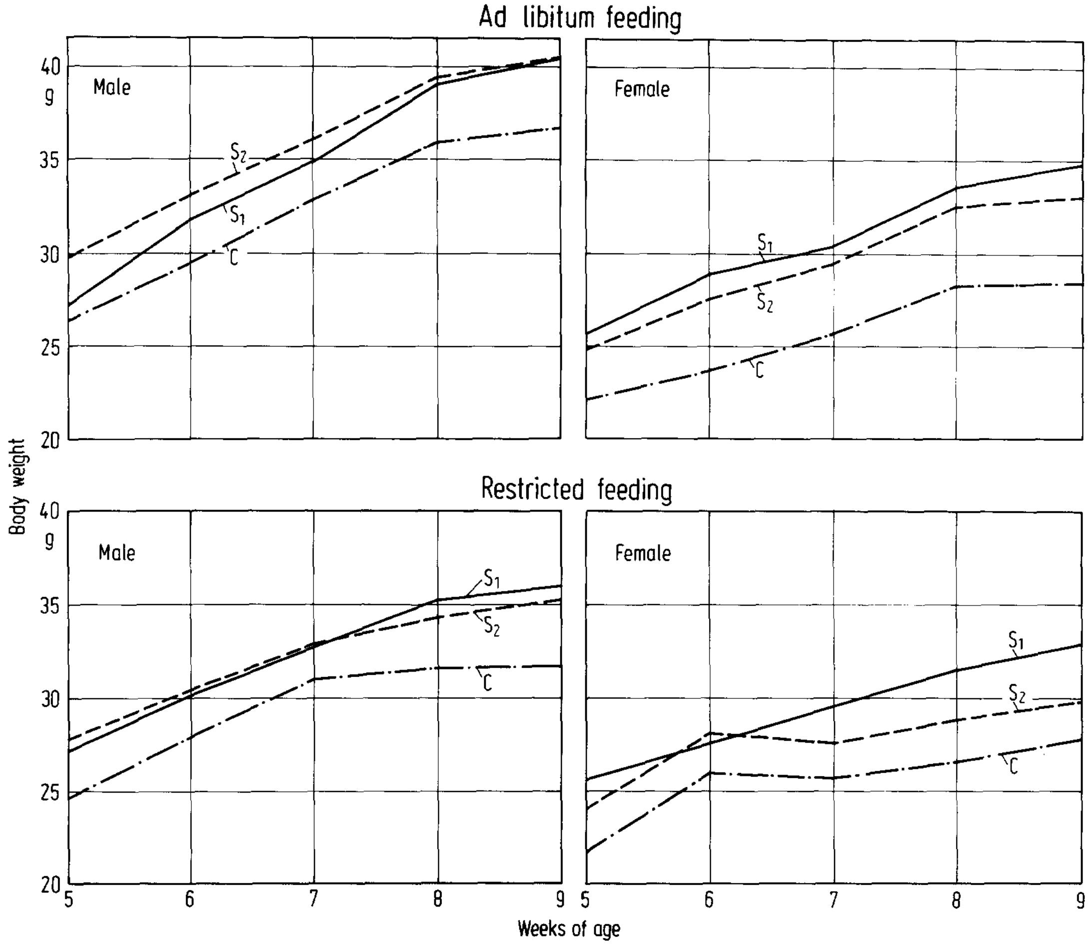

Fig. 2. 5 to 9 week curves of mice growth on ad libitum and restricted feeding

In Figure 2 mean weekly body weights between 5 and 9 weeks of age at generation 6 are plotted for the S and C lines on ad libitum and restricted feeding.

Differences between the lines in their growth curves are evident. Growth has clearly slowed by 9 weeks of age, particularly in S2 and C and on restricted feeding. Line, feeding level and sex differences in body weight and gains at generation 6 are studied in greater detail in Table 2.

Mice fed ad libitum gained an average of 9.6 g from 5 to 9 weeks versus 6.9 g for mice fed restricted. Standard deviations of these gains were 2.6 g and 2.1 g respectively. There were no significant line x feeding level interactions for either weights or gains. 5 week weights of S1 and S2 were similar and both higher than that of C. 5 to 9 week gains of S2 and C were similar and both lower than that of S1. S1 had a higher 9 week weight than S2 and both were higher than C. The positive association between 5 week weight and 5 to 9 week gain between lines contrasted with a negative association within lines. At generation 6 the within line regressions of gain on 5 week weight were -0.55 ± 0.10 on restricted feeding and -0.28 ± 0.05 on ad libitum feeding. Using these regressions to correct 5 to 9 week gains to the mean 5 week weight of all lines, considerably increased the differences between the S and C lines.

Compared with females, males were heavier at 5 and 9 weeks and grew more between these ages. A sex x feed level interaction in 9 week weight ($P<0.01$) resulted from an increase between restricted and ad libitum feeding in male weight which was 2.5 times that in females.

Feed Intakes and Conversion Efficiencies

In Table 3 are given average food intakes and conversion efficiencies (gain/food) of 6th generation mice grown from 5 to 9 weeks of age on ad libitum feeding.

Average food intakes of S1 and S2 mice were 6% higher than those of C line mice. Despite this there was no difference in food conversion efficiency between S2 and C, while that of S1 was higher than that of C. When the data were corrected by covariance to mean mid-week

Table 2. Mean 5 and 9 week body weights and 5 to 9 week weight gains of selected (S1 and S2) and control (C) lines on ad libitum and restricted feeding at generation 6

	Ad libitum feeding								
	5 week body wt (g)			9 week body wt (g)			5 to 9 week weight gain (g)		
Line	Male	Female	Mean	Male	Female	Mean	Male	Female	Mean
S1	27.2 ± 0.5	24.5	25.8*	40.1 ± 0.5	34.7	37.4	12.6 ± 0.5	9.6	11.1a (11.2a)**
S2	29.6	25.1	27.3b	40.2	33.1	36.6a	10.5	8.0	9.2b (9.6b)
C	26.2	22.0	24.1c	36.7	28.4	32.5b	10.5	6.3	8.4b (7.9c)
Mean	27.6x	23.8y		39.0x	32.1y		11.2x	8.0y	
	Restricted feeding								
S1	27.0 ± 0.6	25.8	26.4a	36.0 ± 0.5	32.9	34.4a	9.3 ± 0.6	7.2	8.3a (8.8a)
S2	27.6	24.1	25.8a	35.3	29.9	32.6b	7.8	4.9	6.4b (6.8b)
C	24.6	21.9	23.3b	31.7	27.9	29.8c	7.2	5.1	6.2b (5.2c)
Mean	26.4x	23.9y		34.3x	30.2y		8.1x	5.8y	

* When comparing between lines and sexes within feeding levels, means followed by different letters are significantly different ($P < 0.05$)

** Values in parenthesis are corrected by linear regression to the mean 5 week weight of all mice on the same feeding level

Table 3. Average food intakes and conversion efficiencies of 6th generation mice growing between 5 and 9 weeks of age on ad libitum feeding

	Intakes (g)			Conversion efficiencies (gain/food x 10^2)		
Line	Male	Female	Mean	Male	Female	Mean
S1	208.4 ± 4.4	202.5	205.5a* (201.9a)**	6.0 ± 0.5	4.5	5.1a (5.6a)
S2	213.1	197.5	205.3a (201.8a)	4.9	3.8	4.3b (4.7b)
C	196.0	190.5	193.1b (200.1a)	5.3	3.4	4.2b (4.0c)
Mean	205.7x	196.8y		5.4x	3.9y	

* Means of lines and sexes followed by different letters are significantly different ($P < 0.05$)

** Values in parenthesis are corrected by regression to the mean mid-week body weight of all lines

weight (the average of 2 successive weighings), differences between the S and C lines in intake disappeared and both S1 and S2 became significantly more efficient food converters than C.

With a 5 to 9 week intake of 159.6 g for all mice on restricted feeding, food conversion efficiencies × 10^2 were 5.2, 4.0 and 3.9 for S1, S2 and C respectively, very close to those recorded on ad libitum feeding.

Body Composition

Table 4 gives the weights and percentages of fat and protein in the bodies of mice slaughtered at 9 weeks of age. In Figures 3 and 4 are plotted the linear regressions of fat and protein weights on body weight at slaughter. With the relatively narrow range of body weights, log transformation of the data did not improve the fit of the regressions.

Fat

Selection increased both the amount and percentage of fat in the S lines relative to the C line. This increase was

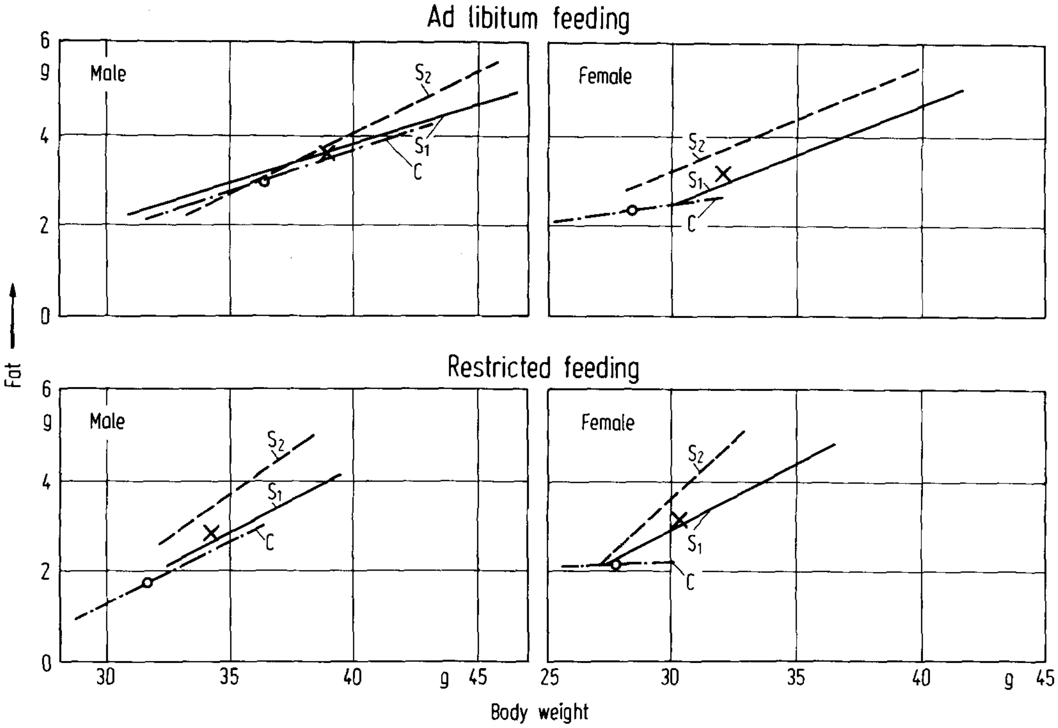

Fig. 3. Linear regressions of 9 week body fat on body weight. + marks the mean of all 3 lines and 0 the mean of the C line

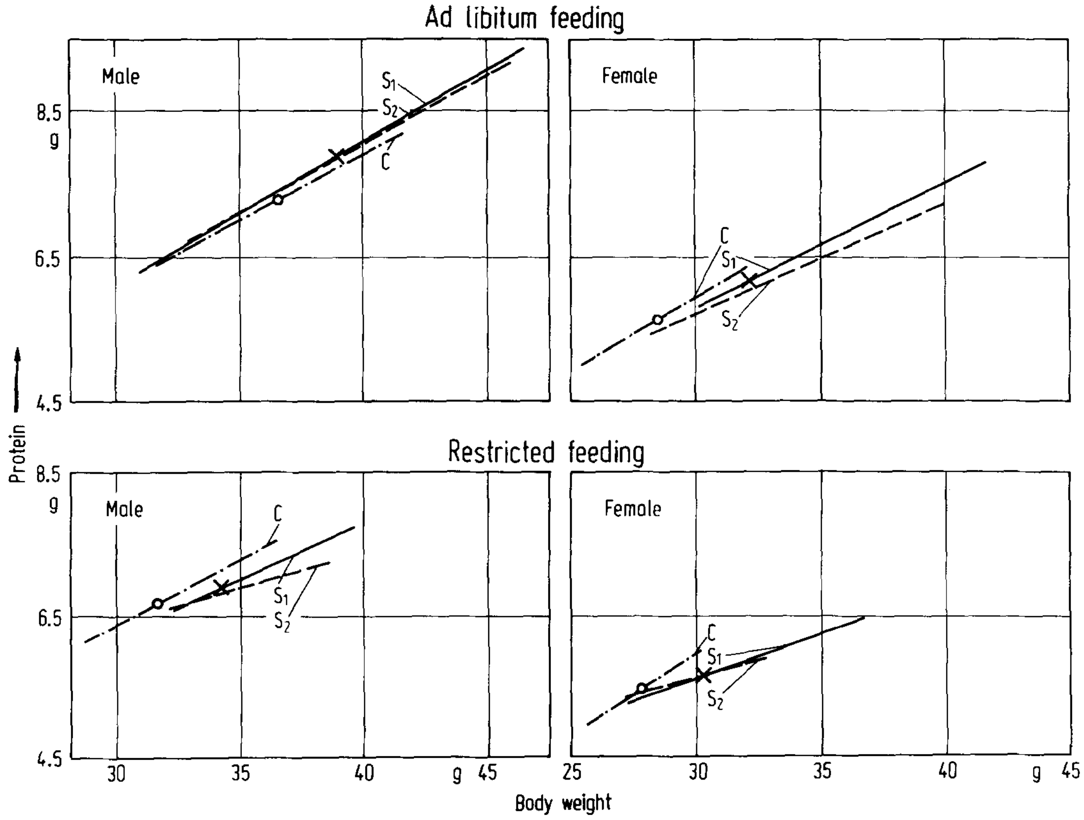

Fig. 4. Linear regressions of 9 week body protein on body weight. + marks the mean of all 3 lines and 0 the mean of the C line

Table 4. Protein and fat weights and percentages of total body weight of 9 week old mice grown on ad libitum and restricted feeding after 6 generations of selection

	Ad libitum feeding											
	Fat						Protein					
	Weight (g)			Percent body wt			Weight (g)			Percent body wt		
Line	Males	Females	Mean	Males	Females	Mean	Males	Females	Mean	Males	Females	Mean
S1	3.76 ± 0.20	3.45	3.60a* (3.24a)**	9.2 ± 0.5	9.9	9.6a	8.09 ± 0.05	6.60	7.34a (7.00ab)	20.2 ± 0.1	19.0	19.6a
S2	4.01	3.84	3.92a (3.73b)	9.9	11.6	10.7b	8.08	6.17	7.12a (6.93b)	20.1	18.8	19.4a
C	3.00	2.33	2.66b (3.24a)	8.1	8.2	8.2c	7.30	5.64	6.47b (7.02a)	20.0	19.9	19.9b
Mean	3.59x	3.21y		9.1x	9.9y		7.82x	6.14y		20.1x	19.2y	
	Restricted feeding											
S1	3.12 ± 0.27	3.80	3.46a (2.77a)	8.6 ± 0.8	11.4	10.0a	7.17 ± 0.08	5.99	6.58a (6.27a)	19.9 ± 0.2	18.3	19.1a
S2	3.75	3.58	3.67a (3.56b)	10.6	11.9	11.2a	6.91	5.65	6.28b (6.23a)	19.6	18.9	19.3a
C	1.75	2.22	2.10b	6.2	8.0	7.1b	6.72	5.52	6.12c	21.2	19.8	20.5b
Mean	2.87x	3.20y		8.3x	10.4y		6.93x	5.72y		20.2x	19.0y	

* Means of lines and sexes followed by different letters are significantly different ($P < 0.05$)

** Values in parenthesis are corrected by linear regression to the mean slaughter weight of all mice on the same feeding level

greater for S2 than for S1. A line × feeding level interaction resulted from an increase in fat between restricted and ad libitum feeding which was much greater for C mice (34%) than for S1 and S2 mice (4%, 7%). Most of this increase in fat between the feeding levels occurred in males. Males had 10% less fat than females on restricted feeding but 12% more on ad libitum feeding.

The apparent difference between lines in their fat/body weight regressions in Figure 3 fell short of significance ($p<0.10$) but the differences between their intercepts were highly significant as was that between the sexes ($p<0.01$). Fat deposition of 0.31 ± 0.05 g/g body weight under ad libitum feeding was significantly higher than 0.19 ± 0.02 g/g on restricted feeding ($p<0.01$). These regressions were used to correct the level of fat in each line to the mean body weight of all three lines at slaughter. These adjusted fat weights are given in Table 4. Due to the convergence of the S and C line regressions from high to low body weight apparent in Figure 3 (but not significant), the difference between the lines in fat was reduced by this adjustment. At mean body weight, S1 and C mice were equally fat but S2 mice were still 25% fatter than C mice. It is evident from Figure 3 that the difference between the lines in fat disappears altogether at the mean body weight of the C line.

Protein

Table 4 shows that selection increased the weight but reduced the percentage of protein in 9 week old mice. A line × feeding level interaction in protein weight ($p<0.01$) arose from an increase in protein between restricted and ad libitum feeding which was greater in the S than the C lines, the converse of the fat observations.

Linear regressions of protein weight on body weight are plotted in Figure 4. As with the fat regressions, apparent differences between the lines fell short of significance ($p<0.10$). Slopes differed between feeding levels ($p<0.01$) being 0.19 ± 0.01 g/g on ad libitum and 0.14 ± 0.01 g/g on restricted feeding. Using these regressions to adjust protein weights to the mean body weight of the 3 lines gave a reversal of the ranking of the C and S lines on protein weight to a ranking akin to that on percentage protein.

Moisture and Ash

The high contribution of moisture to total body weight is reflected in the close agreement between moisture and body weight rankings of the lines at 9 weeks of age i.e. S1: 23.2 ± .2 g, S2: 21.5 g and C: 20.6 g. When corrected to mean slaughter weight, moisture levels were inversely related to similarly corrected fat levels. Thus S2 had 2% less moisture than S1 and C. The correlation between moisture and fat percentages within lines was 0.98.

Ash levels also followed the 9 week slaughter weight rankings of the lines i.e. S1: 1.20 ± 0.01 g; S2: 1.14 g and C: 1.11 g. Correction to mean slaughter weight gave ash levels of C mice which were 3% higher than the average of the S line mice.

Discussion

Changes in the growth curves of the S lines resembled those found by other workers who selected mice for high post-weaning weight gain on ad libitum feeding (Legates and Farthing 1962; Rahnefield et al. 1963; Timon and Eisen 1970; Sutherland et al. 1970; Bradford 1971; Frahm and Brown 1975). Growth increased to 9 weeks of age but only a small part of this increase occurred between 5 and 9 weeks, most having occurred before 5 weeks, the start of the measurement period. The freeing of 5 to 9 week gain from its negative association with 5 week weight, by using deviations from the regression of the former on the latter as the selection criterion, achieved its objective of preventing a decline in initial weight. In selecting for high 3 to 6 week gain on a feeding regimen similar to that used here, Hetzel and Nicholas (1978) observed a decline in 3 week weight. Mice with low 3 week weight were favoured because they used less energy for maintenance and therefore had more available for growth.

In changes of food intake and conversion efficiency, most studies of selection for high post-weaning gain in mice, particularly those on ad libitum feeding, follow the pattern of Timon and Eisen's (1970). In their selected line, food consumed per gram of body weight increased and the associated increased in weight gain produced an improvement in food conversion efficiency. Brown and Frahm (1975) on the other hand, reported an improvement in efficiency without an increase in intake per gram body weight. The same was seen here on restricted feeding where the selected lines had higher 5 to 9 week gains even though their increased appetites were not permitted expression. The evidence is less clear on ad libitum feeding but intakes per gram body weight appear not to have changed with selection whereas the time taken to grow over a given weight range has decreased. Kielanowski (1968) predicted that the elimination of appetite as a source of variation in selecting for body weight gain would lead to a change in the partitioning of metabolisable energy toward less costly lean (and hence protein) deposition and away from fat deposition. Evidence for the existence of genetic variation in such energy partitioning has already appeared in mouse selection studies (Hull 1960; Falconer and Latyszewski 1952; Hayes and McCarthy 1976). Hayes and McCarthy concluded from fat changes in their lines, that selection for high body weight on ad libitum feeding at a young age placed major emphasis on appetite, but at older ages emphasis shifted toward more efficient partitioning of energy in favour of lean. It would appear to follow from their results that if appetite variation were eliminated, even more emphasis would be placed on changing partitioning. This expectation was not realised in the present study. There was no evidence of an increase in protein at the expense of fat in the S lines. On the contrary, S2 became appreciably fatter than C as selection proceeded. Two ways by which the weight and energetic value of gain could have been increased in the S lines are by (I) improved digestive efficiency and (II) reduced maintenance requirement. Digestive efficiency was not measured here but neither Fowler (1962) nor Stanier and Mount (1972) found any difference in digestive efficiency between strains of mice differing in growth habit and food conversion efficiency and Blaxter (1968) concluded that there was very little variation in this trait even between species.

A reduction in maintenance requirement seems a more likely explanation for increased growth in the selected lines. Figure 2 shows all lines approaching different mature sizes even though all had the same intakes on restricted feeding. At 9 weeks of age the average body weight of the S lines was 12% higher than that of the C line. S2 appears to be approaching a lower mature size than S1 but it has a higher fat and therefore energy content than S1. Reduced maintenance requirement in the S lines may be related to a noticeable (but not measured) reduction in activity. Stanier and Mount (1972) attributed a lower energy retention in adult female than male mice to a higher degree of activity in the females due to oestrus. Pullar and Webster (1977), measuring the energy cost of protein and fat gain in fat and lean rats, found that fat rats had appreciably lower heat losses per gram body weight than lean ones. They also found a lower retention of nitrogen in the fat rats. This may explain in part the apparently greater effect of dietary protein restriction on body protein deposition in the S than in the C lines on restricted feeding here. When intakes were increased from restricted to ad libitum levels, the ratio of protein to fat in the resultant increase in body weight was 5.4 in the S lines and only 0.3 in the C line. It is unlikely then that the full expression of variation in protein deposition, including that attributable to energy partitioning, was achieved during selection. Even if it were fully expressed by feeding a diet richer in protein, body weight gain may still be too crude a selection criterion to increase protein deposition through improved energy partitioning. Rate of protein deposition should have been measured and selected for directly. Notter et al. (1976) selected for high post-weaning protein deposition on ad libitum feeding in rats using results of carcase analyses of their full sibs. They succeeded in increasing the rate of protein deposition but this was accompanied by a rise in appetite and fatness. It would be of considerable interest to apply the same selection for rate of protein deposition on a feeding regimen which provided the same intakes for all animals over the same time and whose composition was adjusted to ensure maximum protein deposition.

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