

## Growth and body composition changes in mice selected for high post-weaning weight gain on two levels of feeding

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**Summary.** Two lines of mice were selected for high post-weaning weight gain (3 to 6 weeks) adjusted for 3 week weight. One line (F) was grown on freely available food and the other (S) on a feeding scale set at the same level for all mice. Food intake of the S line averaged 80% of the F line. The realised heritabilities after 6 generations of selection were  $0.38 \pm 0.06$  and  $0.33 \pm 0.07$  for the F and S lines, respectively. In generation 7, mice from the F and S lines and from an unselected control line (C) were compared on both free and set levels of feeding from 3 weeks to 9 weeks of age. Measurements taken were growth rate, appetite, food conversion efficiency (weight gain/food intake) and body composition (fat, protein, ash, water). The F and S lines grew more rapidly and efficiently than the C line on both levels of feeding, each line performing best on the level of feeding on which it was selected. The average genetic correlation between growth rates of the same line on the two feeding levels was  $0.54 \pm 0.10$ . The F line grew 19% faster and was 9% more efficient than the S line on free feeding but the S line grew 15% faster and was 15% more efficient than the F line on set feeding. Relative to the C line, food intake per day on free feeding was 4% higher in the F line and 6% lower in the S line. There was no difference between the lines in food intake/g body weight. The rate of deposition of all body components increased in both selection lines. In the F, S and C lines respectively, efficiencies of gains in body components ( $10^2 \times \text{gain/food}$ ) were 1.79, 1.31 and 1.06 for fat, 1.53, 1.63 and 1.22 for protein and 5.88, 6.45 and 4.98 for protein + water. Apparently energy lost as heat was reduced in both the F and S lines. The partitioning of energy retained was altered in favour of more fat in the F line and more protein in the S line.

**Key words:** Selection – Feeding levels – Growth – Body composition – Mice

### Introduction

To improve the efficiency of lean tissue growth in pigs, Fowler et al. (1976) proposed a testing regimen in which all animals were given a set amount of food 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.

Two mouse studies which tend to confirm this hypothesis were carried out by Falconer and Latyszewski (1952) and Hetzel and Nicholas (1986). The latter selected two lines for high 3 to 6 week growth, one on restricted and the other on ad libitum feeding. By testing the lines on both feeding levels, they found that growth rate on each feeding level was best improved by selection on that level. However, the line selected on restricted feeding had a greater ratio of lean to fat gain overall than the one selected on ad libitum feeding. The interpretation of this study was clouded by a reduction in 3 week weight in the line selected on restricted feeding.

McPhee et al. (1980) selected mice for 5 to 9 week gain on a set feeding ration, the same for all mice. When tested on both the set scale and ad libitum feeding it was found that gains had been made in the rate and efficiency of growth but the mice had also become fatter. This study did not include a line selected on a feeding level which allowed appetite to be expressed.

This paper reports a selection experiment in mice which examines again the hypothesis of Fowler et al. (1976) and attempts to overcome some of the deficiencies of earlier studies. Two lines were selected for high 3 to 6 week weight gain, at the same time restricting the change in 3 week weight. Food was made freely available at all times to one line and the other was fed according to a set scale. Response was evaluated in

terms of rate and efficiency of growth and changes in body composition on both feeding levels.

## Methods

### *Selection procedure*

In the base generation, 20 pairs of mice were selected at 8 weeks of age from a wide cross-section of litters from the control line (C) described by McPhee and Neill (1976). From their progeny, two selection lines were established by sampling within full sib families. These were designated F, to be selected on freely available food, and S, to be selected on a set amount of food. In subsequent generations, lines F and S comprised 10 sires each mated assortatively to 2 dams at 7 weeks of age. Two weeks after mating, males were removed and females placed in individual cages. Within 24 h after birth, litter sizes were adjusted to a maximum of 8 pups. Weaning occurred at 3 weeks of age when 32 males and 32 females from each of the selected lines were chosen from litters from the highest performing parents.

All lines were fed on a standard laboratory diet comprising, on a dry matter basis, 18.3 MJ/kg gross energy, 26.8% crude protein, 3.0% Ca, 1.8% P and 3.4% ether extract.

Each S line mouse was housed separately and fed at 2 day intervals. In setting the ration for the S line, the aim was to satisfy the appetites of most mice during their 3 week to 6 week growth period. It was expected that, at this level of feeding, there would be a few mice unable to eat all of their rations. It was also expected that appetite would change as selection proceeded. To accommodate for this, adjustments were made to the feeding scale based subjectively on the size and frequency of food residues in the preceding generation. In the base and first selected generations (G0 and G1), the period of feeding of S line mice extended for 22 days after 3 week weighing. Food was given in four 8 g meals followed by seven 10 g meals. In the second and third generations, the level was increased to four 9 g, three 10 g and four 11 g meals successively.

In response to the observation that most food residues were left at the end of the first two day feeding period, in the last three generations the first body weighing was advanced to 3 week + 2 days of age, shortening the duration of the test period to 20 days. During this period, the feeding pattern was, in order, three 9 g, four 10 g and three 11 g meals.

In the F line, mice were fed from a feeder designed to permit free access to food and the collection of spillage. Food intakes were measured weekly. The C line mice were fed *ad libitum* but intakes were not measured during the course of selection.

Mice were weighed weekly between 3 and 6 weeks of age. The selection criterion was weight gain adjusted by linear regression to the average 3 week weight of each line  $\times$  sex class. Using this criterion, the fastest growing 10 males and 20 females were selected as parents of the following generation, giving theoretical selection intensities of 10/32 for males and 20/32 for females. Selection was continued for 6 generations. The C line was maintained with 30 pairs of parents, randomly selected within litters and mated in cyclic fashion.

### *Measurement of response*

At generation 7, 40 mice of each sex were randomly chosen at 3 weeks of age across families of each of the three lines F, S and C. From these, 8 of each sex per line were slaughtered immediately for carcass analysis. The remaining mice were equally allocated to either a free or a set feeding regimen. At 5 and 9

weeks of age, 8 mice of each sex on each feeding regimen were sampled for slaughter and carcass analysis. A 5 week rather than a 6 week sampling age was chosen as giving a more intermediate body weight between 3 and 9 weeks of age. This permitted a more satisfactory fitting of the allometric relationship between body components and total body weight. Measurements of growth rate and food intake were taken on all mice from 3 weeks of age to slaughter.

Observations made in generation 7 when the F, S and C lines were grown on both free and set feeding, enabled the estimation of the genetic correlation between weight gains on the two levels of feeding using direct (R) and correlated (CR) responses. The general formula taken from Falconer (1960) was  $r^2 = CR_1/R_1 \cdot CR_2/R_2$ . The standard error was calculated according to Hill (1972).

### *Carcass analysis*

Food was removed from the mice 24 h before slaughter. Mice were killed by spinal dislocation, opened along the ventral surface and dried to a constant weight at 80°C for 2 days in individual Petri dishes. The entire dried contents of each Petri dish were crushed, transferred to a Soxhlet thimble, and extracted for 16 h with petroleum ether. After this fat extraction, the residue in the thimble was heated at 600°C for 4 h and the ash determined. Protein was estimated as dry matter minus the fat and ash components.

### *Statistical analysis*

Data were subjected to an analysis of variance using the mixed model least-squares computer programme of Harvey (1977). The model chosen was Model VII, viz:

$$y_{ijklm} = u + a_i + b_{ij} + c_k + (ac)_{jk} + (bc)_{ijk} + F_1 + e_{ijklm}$$

$a_i$  and  $c_k$  are the fixed effects of line and feed and  $b_{ij}$  is the random effect of litter of birth within line.  $F_1$  represents the effect of sex and its interactions with other fixed effects and  $e_{ijklm}$  is the residual error term. The main significance tests of interest were  $a_i$  against  $b_{ij}$  and  $(ac)_{jk}$  against  $(bc)_{ijk}$ .

## Results

### *Selection process*

Over the 6 generations of selection, average daily weight gains from 3 to 6 weeks for the F and S lines, respectively, were  $0.87 \pm 0.03$  g and  $0.57 \pm 0.04$  g and their pooled within generation standard deviations were 0.14 g and 0.20 g. The average regression of daily gain on 3 week weight was higher in the S than the F line ( $P < 0.01$ ). Respective values were  $0.033 \pm 0.002$  and  $0.022 \pm 0.002$ . Correction of daily gain for 3 week weight gave a selection criterion with standard deviations averaging 0.08 g and 0.09 g in the F and S lines, respectively.

Daily food intake over the whole of the selection period averaged  $5.99 \pm 0.08$  g in the F line and  $4.74 \pm 0.02$  g in the S line and pooled within generation standard deviations were 0.59 g and 0.14 g.

Selection differentials accumulated over 6 generations were 0.63 g/day in the F line and 0.42 g/day in the S line.

### Selection response

In Table 1 are given average body weights, growth rates, food intakes and food conversion ratios of F, S and C line mice grown from 3 to 9 weeks on free and set feeding in generation 7. Using the ratios of deviations from the C line over cumulative selection differential gave heritabilities of  $0.38 \pm 0.06$  and  $0.33 \pm 0.07$  for the F and S lines respectively. Heritability estimates from full sib correlations of 3 to 6 week daily gain were  $0.98 \pm 0.13$  and  $0.97 \pm 0.12$  for the F and S lines. These compare with heritability values of  $0.38 \pm 0.11$  and  $0.36 \pm 0.11$  for daily gain corrected for 3 week weight, obtained using the same method.

On free feeding, the direct response in daily gain of the F line was  $0.24 \pm 0.06$  g and the correlated response of the S line was  $0.12 \pm 0.06$  g. On set feeding, the direct response of the S line was  $0.14 \pm 0.06$  g and the correlated response of the F line was  $0.08 \pm 0.06$  g. Using these values, the genetic correlation between the F and S line responses on the two levels of feeding was  $0.54 \pm 0.10$ .

Table 2 gives the average weights of fat, protein, water and ash in the bodies of mice sampled at 3, 5 and 9 weeks in generation 7. Table 3 expresses these components as a percentage of body weight. Values are set out as for the performance traits in Table 1. The following observations of significance for the present study are made from the analysis of variance of traits in Tables 1, 2 and 3.

### Body weights and gains (Table 1)

From 3 week weights which were the same for all lines, F and S line mice grew faster than C mice from 3 to 6 weeks and from 6 to 9 weeks. A feed  $\times$  line interaction ( $P < 0.01$ ) resulted from the F line growing faster than the S line on free feeding and the S line growing faster than the F line on set feeding. This was most marked in the 3 to 6 week growth period. From 3 to 9 weeks on the free and set levels respectively, the F line averaged  $0.68$  and  $0.40 \pm 0.02$  g/day and the S line  $0.57$  and  $0.46 \pm 0.02$  g/day.

### Food intakes (Table 1)

On set feeding, as expected, daily food intakes were essentially the same for all three lines. However line differences did occur on free feeding. This gave rise to feed  $\times$  line interactions for 6 to 9 week ( $P < 0.01$ ) and 3 to 9 week ( $P < 0.05$ ) intakes. Line differences on free feeding were due to the unusually low intakes in the S line. Average 3 to 9 week intakes for the F, S and C lines were  $6.98$  g,  $6.34$  g and  $6.74 \pm 0.12$  g, respectively.

Linear regressions of daily food intake on body weight were calculated. No significant difference was found between the lines, the average for all lines being  $0.1 \pm 0.02$ .

**Table 1.** Least squared means of body weights, growth rates, food intakes and conversion efficiencies (weight gain/food intake) of 3 to 9-week old mice grown on free and set feeding after 6 generations of selection

| Body weight (g)            |        | F line    | S line  | C line  | SE <sup>a</sup> |
|----------------------------|--------|-----------|---------|---------|-----------------|
| Free feed                  | 3 wk   | 14.78 a + | 14.49 a | 14.93 a | 0.63            |
|                            | 6 wk   | 35.55     | 32.30 a | 30.49 a | 0.73            |
|                            | 9 wk   | 43.25     | 37.60   | 34.41   | 0.69            |
| Set feed                   | 6 wk   | 24.72 ab  | 26.15 a | 23.55 b | 0.73            |
|                            | 9 wk   | 30.64 a   | 33.26   | 29.46 a | 0.69            |
| Daily weight gain (g)      |        |           |         |         |                 |
| Free feed                  | 3-6 wk | 1.00      | 0.88    | 0.76    | 0.04            |
|                            | 6-9 wk | 0.37      | 0.25    | 0.19    | 0.02            |
|                            | 3-9 wk | 0.68      | 0.57    | 0.47    | 0.02            |
| Set feed                   | 3-6 wk | 0.51 ab   | 0.57 a  | 0.43 b  | 0.04            |
|                            | 6-9 wk | 0.30 a    | 0.36    | 0.30 a  | 0.02            |
|                            | 3-9 wk | 0.40 a    | 0.46    | 0.36 a  | 0.02            |
| Daily food intake (g)      |        |           |         |         |                 |
| Free feed                  | 3-6 wk | 6.39 a    | 6.07 a  | 6.41 a  | 0.13            |
|                            | 6-9 wk | 7.57      | 6.62    | 7.07    | 0.13            |
|                            | 3-9 wk | 6.98 a    | 6.34    | 6.74 a  | 0.12            |
| Set feed                   | 3-6 wk | 4.97 a    | 5.00 a  | 5.11 a  | 0.13            |
|                            | 6-9 wk | 5.74 a    | 5.80 a  | 5.76 a  | 0.13            |
|                            | 3-9 wk | 5.37 a    | 5.41 a  | 5.44 a  | 0.12            |
| Food conversion efficiency |        |           |         |         |                 |
| Free feed                  | 3-6 wk | 0.157     | 0.147   | 0.120   | 0.007           |
|                            | 6-9 wk | 0.049 a   | 0.038 a | 0.027   | 0.004           |
|                            | 3-9 wk | 0.098     | 0.090   | 0.071   | 0.004           |
| Set feed                   | 3-6 wk | 0.104     | 0.115   | 0.084   | 0.007           |
|                            | 6-9 wk | 0.052 a   | 0.061 a | 0.051 a | 0.004           |
|                            | 3-9 wk | 0.075 ab  | 0.086 a | 0.066 b | 0.004           |

<sup>a</sup> Average standard error of each line  $\times$  age  $\times$  feed sub-class mean

+ Line means followed by different letters are significantly different ( $P < 0.05$ )

### Food conversion efficiencies (weight gain/food intake, Table 1)

The pattern of efficiencies across the lines mirrored those of growth rates. The F and S lines displayed higher efficiencies than the C lines both to 6 and to 9 weeks of age. Line  $\times$  feed interactions for 6 to 9 weeks ( $P < 0.05$ ) and 3 to 9 weeks ( $P < 0.01$ ) resulted from the F line being more efficient than the S line on free feeding and the S being more efficient than the F line on set feeding.

### Fat (Tables 2 and 3)

At 3 weeks the weight and percentage of fat in the bodies of F and C line mice were equal and greater than in S line mice. By 9 weeks of age both these measures of fat were equal in the S and C lines and appreciably less than in the F line. Values for weight and percent of fat averaged over both feed levels in the S and C lines com-

**Table 2.** Weights of body components of 3, 5 and 9 week-old mice from the selection and control lines grown on free and set feeding after 6 generations of selection

|                |      |  | F line<br>g | S line<br>g | C line<br>g | SE <sup>a</sup><br>g |
|----------------|------|--|-------------|-------------|-------------|----------------------|
| <b>Fat</b>     |      |  |             |             |             |                      |
| Free feed      | 3 wk |  | 1.24 a      | 1.01        | 1.26 a      | 0.08                 |
|                | 5 wk |  | 2.63        | 1.80 a      | 1.98 a      | 0.19                 |
|                | 9 wk |  | 6.74        | 3.42 a      | 3.34 a      | 0.39                 |
| Set feed       | 5 wk |  | 2.11 a      | 1.97 a      | 1.75 a      | 0.19                 |
|                | 9 wk |  | 5.06 a      | 4.91 a      | 4.42 a      | 0.39                 |
| <b>Protein</b> |      |  |             |             |             |                      |
| Free feed      | 3 wk |  | 2.44 a      | 2.41 a      | 2.63 a      | 0.09                 |
|                | 5 wk |  | 5.10 a      | 4.92 a      | 4.94 a      | 0.08                 |
|                | 9 wk |  | 6.95 a      | 6.72 a      | 6.11        | 0.14                 |
| Set feed       | 5 wk |  | 4.04 a      | 4.18 a      | 3.80        | 0.08                 |
|                | 9 wk |  | 5.83 a      | 6.14 a      | 5.40        | 0.14                 |
| <b>Water</b>   |      |  |             |             |             |                      |
| Free feed      | 3 wk |  | 9.36 a      | 9.37 a      | 9.92 a      | 0.36                 |
|                | 5 wk |  | 17.45 a     | 16.63 ab    | 16.40 b     | 0.30                 |
|                | 9 wk |  | 22.47       | 21.52       | 19.45       | 0.31                 |
| Set feed       | 5 wk |  | 14.08 ab    | 14.85 b     | 13.28 a     | 0.30                 |
|                | 9 wk |  | 18.90 a     | 20.93       | 18.28 a     | 0.31                 |
| <b>Ash</b>     |      |  |             |             |             |                      |
| Free feed      | 3 wk |  | 0.47        | 0.46 a      | 0.49 a      | 0.02                 |
|                | 5 wk |  | 0.92 a      | 0.91 a      | 0.88 a      | 0.02                 |
|                | 9 wk |  | 1.34 a      | 1.32 a      | 1.18        | 0.04                 |
| Set feed       | 5 wk |  | 0.80 a      | 0.79 a      | 0.71        | 0.02                 |
|                | 9 wk |  | 1.09 a      | 1.23        | 1.11 a      | 0.04                 |

<sup>a</sup> Average standard error of each line×age×feed sub-class mean

+ Line means followed by the same letter are not significantly different ( $P < 0.05$ )

combined were  $4.0 \pm 0.19$  g and  $12.8 \pm 0.49\%$  and for the F line,  $4.9 \pm 0.27$  g and  $17.2 \pm 0.67\%$ . Almost all the excessive fatness of the F line was expressed on free feeding, particularly in female mice. Average 9 week fat measurements of the F line on free feeding of  $6.7 \pm 0.38$  g and  $17.9 \pm 0.92\%$  were well above values of  $3.4 \pm 0.28$  g and  $10.7 \pm 0.68\%$  for the S and C lines combined.

#### Protein and water (Tables 2 and 3)

There was a very close parallel in the effects of line and feed on these two body components. All three lines had the same amounts of body protein and water at 3 weeks but, with increasing age, weights (but not percentages) of these components in the F and S lines increased above the levels in the C line. Average weights at 9 weeks for the C line and the F and S lines combined were  $5.7 \pm 0.07$  g and  $6.4 \pm 0.05$  g for protein and  $18.9 \pm 0.26$  g and  $21.0 \pm 0.18$  g for water, respectively.

**Table 3.** Body components expressed as percentages of total body weight of 3, 5 and 9 week-old mice from the selection and control lines grown on free and set feeding after 6 generations of selection

|                |      |  | F line<br>% | S line<br>% | C line<br>% | SE <sup>a</sup><br>% |
|----------------|------|--|-------------|-------------|-------------|----------------------|
| <b>Fat</b>     |      |  |             |             |             |                      |
| Free feed      | 3 wk |  | 9.1a +      | 7.5         | 8.9 a       | 0.35                 |
|                | 5 wk |  | 10.2 a      | 7.4 b       | 8.3 ab      | 0.74                 |
|                | 9 wk |  | 17.9        | 10.5 a      | 11.0 a      | 0.95                 |
| Set feed       | 5 wk |  | 10.0 a      | 8.9 a       | 8.7 a       | 0.74                 |
|                | 9 wk |  | 16.4 a      | 14.8 a      | 15.0 a      | 0.95                 |
| <b>Protein</b> |      |  |             |             |             |                      |
| Free feed      | 3 wk |  | 18.1 a      | 18.2 a      | 18.4 a      | 0.11                 |
|                | 5 wk |  | 19.5        | 20.2 a      | 20.4 a      | 0.17                 |
|                | 9 wk |  | 18.5        | 20.3 a      | 20.3 a      | 0.41                 |
| Set feed       | 5 wk |  | 19.2 a      | 19.0 a      | 19.4 a      | 0.17                 |
|                | 9 wk |  | 19.0 a      | 18.4 a      | 18.5 a      | 0.41                 |
| <b>Water</b>   |      |  |             |             |             |                      |
| Free feed      | 3 wk |  | 69.3 a      | 70.8        | 69.2 a      | 0.32                 |
|                | 5 wk |  | 66.7 a      | 68.4 b      | 67.6 ab     | 0.58                 |
|                | 9 wk |  | 59.9        | 65.1 a      | 64.6 a      | 0.72                 |
| Set feed       | 5 wk |  | 66.6 a      | 67.7 a      | 67.6 a      | 0.58                 |
|                | 9 wk |  | 61.6 a      | 62.9 a      | 62.5 a      | 0.72                 |
| <b>Ash</b>     |      |  |             |             |             |                      |
| Free feed      | 3 wk |  | 3.5 a       | 3.5 a       | 3.5 a       | 0.40                 |
|                | 5 wk |  | 3.5 a       | 3.7 b       | 3.6 ab      | 0.07                 |
|                | 9 wk |  | 3.6         | 4.0 a       | 4.0 a       | 0.11                 |
| Set feed       | 5 wk |  | 3.8         | 3.6 a       | 3.6 a       | 0.07                 |
|                | 9 wk |  | 3.6 a       | 3.7 a       | 3.8 a       | 0.11                 |

<sup>a</sup> Average standard error of each line×age×feed sub-class mean

+ Line means followed by the same letter are not significantly different ( $P < 0.05$ )

Interactions between line and feeding level were found for water ( $P < 0.01$ ) but fell short of significance for protein ( $P < 0.1$ ). These arose from a tendency for water and protein levels to be highest in the F line on free feeding and in the S line on set feeding. Percentages of protein and water, particularly the latter, declined with age. Significant line × feed interactions ( $P < 0.05$ ) were recorded for both components. These could largely be ascribed to the rapid increase in fatness with age of the F line on free feeding.

#### Ash (Tables 2 and 3)

From levels which were the same for all lines at 3 weeks, body ash rose to  $1.15 \pm 0.02$  g in the C line and  $1.25 \pm 0.02$  g in the F and S lines combined at 9 weeks. A line × feed interaction ( $P < 0.01$ ) at 9 weeks arose from an unusually high level of ash in S line mice on set feeding. This mirrored a similar sharp increase with age in water level of the S line.

**Table 4.** Parameters of relationships  $Y = aX^b$  between the weight of body components (Y) and total body weight (X). Relationships were pooled over lines within each feeding level  $\times$  sex sub-class, except for free fed females

| Sex    | Feed   | Fat  |                 | Protein |                 | Ash  |                 | Water |                 |
|--------|--------|------|-----------------|---------|-----------------|------|-----------------|-------|-----------------|
|        |        | a    | b               | a       | b               | a    | b               | a     | b               |
| Male   | Set    | 0.01 | $1.67 \pm 0.08$ | 0.17    | $1.04 \pm 0.02$ | 0.04 | $1.00 \pm 0.03$ | 0.98  | $0.87 \pm 0.01$ |
|        | Free   | 0.05 | $1.18 \pm 0.09$ | 0.14    | $1.11 \pm 0.01$ | 0.03 | $1.04 \pm 0.02$ | 0.85  | $0.93 \pm 0.01$ |
| Female | Set    | 0.01 | $1.80 \pm 0.08$ | 0.21    | $0.95 \pm 0.02$ | 0.03 | $1.06 \pm 0.03$ | 1.01  | $0.86 \pm 0.01$ |
|        | Free   |      |                 |         |                 |      |                 |       |                 |
|        | Line F | 0.01 | $1.81 \pm 0.09$ | 0.20    | $0.97 \pm 0.02$ | 0.03 | $1.04 \pm 0.03$ | 1.09  | $0.83 \pm 0.02$ |
|        | Line S | 0.02 | $1.44 \pm 0.13$ | 0.14    | $1.11 \pm 0.02$ | 0.02 | $1.24 \pm 0.03$ | 0.94  | $0.89 \pm 0.02$ |
|        | Line C | 0.05 | $1.23 \pm 0.14$ | 0.16    | $1.07 \pm 0.02$ | 0.02 | $1.20 \pm 0.05$ | 0.84  | $0.92 \pm 0.02$ |

#### Allometry (Table 4)

The weight of each body component (Y), fat, protein, water and ash, was related in turn to total body weight (X) by fitting the allometric equation  $Y = aX^b$ . Correlation coefficients ranged from 0.85 to 0.99 indicating that the allometric equation described well the relationship between the body components and total body weight. No significant differences were found between the b values of the F, S and C lines for any component except in female mice grown under free feeding. Free fed females of the F line had a much higher rate of fat deposition per gram body weight than those of the S and C lines. Conversely F females deposited protein, water and ash at a lower rate than females of lines S and C.

#### Discussion

Responses to selection for body weight gain in mice have been explained in terms of changes in the intake of food energy (FE) and the way the metabolisable energy (ME) produced from it by digestion is divided into a component retained for tissue growth (RE) and a residual heat component (HE). The latter is used for the maintenance of body weight, the processes of protein and fat deposition and the functions of thermoregulation and dietary thermogenesis.

The mouse lines of Timon and Eisen (1970) are typical of many which show response to high body weight selection due to a increase in voluntary FE intake per unit of body weight. In the present study there was no clear association between growth rate responses and intake changes in the selection lines. Intake was actually lower in the S than the C line when measured on free feeding in generation 7.

The efficiency with which FE was digested to produce ME was not measured but neither Fowler (1962) nor Stanier and Mount (1972) found any difference between strains of mice differing in growth habit and food conversion efficiency.

Stephenson and Malik (1984) examined closely the utilization of FE in mouse lines which differed in growth rate. They

found differences in that portion of HE which was not used for body weight maintenance. In the present study also, selection apparently reduced the HE requirements of the F and S lines. For each gram of food eaten between 3 and 9 weeks, the energy values of the F, S and C lines mice, averaged over both feeding levels, rose by an estimated 1.06, 0.90 and 0.70 KJ, respectively. It is not known which of the components of HE were reduced, but the body weights maintained over the period were the same in the F and S lines and were both higher than in the C line.

The main aim of the present study was to expose to selection, variation in growth rate which reflected the way RE was partitioned between lean and fat deposition. According to Webster (1977) fat and protein both require about 55 KJ/g to deposit but most protein is deposited with water as lean tissue and this takes only 20% as much energy per gram to lay down as fat. A unit increase in RE should therefore give a higher body weight gain in lean than in fat animals.

The set feeding regimen was designed to eliminate the contribution of FE intake to variation in growth rate. Similar studies have been carried out in lines of mice selected for 6 week weight on restricted feeding by Falconer and Latyszewski (1952), 3 to 6 week gain by Hetzel and Nicholas (1986) and 5 to 9 week gain by McPhee et al. (1980). All lines responded to selection but only those of McPhee et al. failed to display the expected improvement in the rate of lean deposition. It seems likely that the latter's mice were too old for RE partitioning to make a major contribution to variation in weight gain. There is some evidence that RE partitioning comes under greatest selection pressure if the growth period chosen follows puberty (Hayes and McCarthy 1976). At this age the difference between the rates of lean and fat deposition is expected to be largest. The present study with younger mice from the same genetic base as that of McPhee et al. (1980) supports this.

The objective of the set feeding regimen was to provide a diet and ration which was the same for all mice and satisfied their requirement for maximum protein deposition. In fact, as measured in generation 7, set

feeding reduced protein deposition to about 80% of that on free feeding. The coefficient of variation of food intake between mice achieved on set feeding was 2%. This is almost negligible when compared with 16%, the coefficient of variation of the selection criterion, 3 to 6 week gain.

In all generations the negative regressions of 3 to 6 week gain on 3 week weight, higher in the S than the F line, suggested that more FE was used for maintenance and less was available for RE in the initially heavy than in the light mice. Although the full sib heritability estimates indicated that much of the variation in 3 week weight was of maternal origin, the removal by regression of its influence on 3 to 6 week gain was justified by the satisfactory response obtained and the absence of change in 3 week weight. In Hetzel and Nicholas' (1986) similar study, they selected for actual 3 to 6 week gain on restricted feeding and observed a decline in 3 week weight. It may be concluded that some of their gains at least derived from a reduced HE demand due to a lowering in maintenance requirement over the 3 to 6 week growth period.

As indicated in Table 5, selection on set feeding did apparently change the rates of tissue deposition toward protein and away from fat as expected.

The ratios of protein to fat gain from 3 to 9 weeks and the gains in protein per unit of food eaten were highest in the S line on both levels of feeding. Protein to fat gain was particularly low in the F line on free feeding due to the very high rate of fat accretion, particularly in females, in that line. These observations agree with Hetzel and Nicholas' (1986) results. Their S and F equivalent lines had protein to fat gain ratios from 3 to 6 weeks of 2.2 and 1.7, respectively.

After 6 generations of selection, the energy utilization in the F and S lines could be summarised as follows. The voluntary intake of FE per gram body weight remained unchanged but those components of HE not associated with the maintenance of body weight were apparently reduced. There was an increase in RE per unit of FE in both lines but RE partitioning was altered toward increased deposition of protein relative to fat in the S line on both feed levels and toward reduced pro-

tein relative to fat deposition in the F line on free feeding.

Although mice as a species expend an unusually high proportion of FE in HE production, the results of the study may have relevance for selection in such meat producing livestock as pigs for which growth rate, food conversion efficiency and protein and fat deposition have considerable commercial importance. Where economy dictates that growth rate be the sole selection criterion, the most appropriate feeding regimen for performance testing to improve the rate and efficiency of growth may be the one on which production will be carried out. However where the breeding objective is to improve the efficiency and rate of lean deposition on a range of feeding levels, a restricted level of feeding may be the best performance testing regimen.

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**Table 5.** Three to 9-week fat and protein gains and food intakes expressed as ratios, measured in generation 7

| Feed<br>Line   | Free |      |      | Set  |      |      |
|----------------|------|------|------|------|------|------|
|                | F    | S    | C    | F    | S    | C    |
| Protein/fat    | 0.82 | 1.78 | 1.67 | 0.89 | 0.96 | 0.88 |
| (Protein/food) | 1.54 | 1.62 | 1.22 | 1.51 | 1.64 | 1.21 |
| $\times 10^2$  |      |      |      |      |      |      |
| (Fat/food)     | 1.88 | 0.91 | 1.73 | 1.69 | 1.72 | 1.38 |
| $\times 10^2$  |      |      |      |      |      |      |