

Effects of selection on growth, body composition, and food intake in mice

III. Correlated responses: growth, body composition, food intake and efficiency and catabolism

BY S. C. BISHOP AND W. G. HILL

*Department of Genetics, University of Edinburgh, West Mains Road,
Edinburgh EH9 3JN*

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SUMMARY

Weekly food intake and body weight were measured from 3 to 17 weeks of age on mice selected 14 generations for increased and decreased values of one of three criteria: appetite (A) as measured by 4- to 6-week food intake, adjusted by phenotypic regression to minimize change in 4-week body weight; fat percentage (F), using the ratio of gonadal fat pad weight to body weight at 10 weeks of age and total lean mass (protein, P), using the index body weight in 10-week males - $(8 \times \text{gonadal fat pad weight})$. Carcass composition analyses were undertaken on the 17-week-old mice, and are presented along with composition data for younger mice from earlier generations. The high intake A line mice are larger, eat more, have higher maintenance requirements and are slightly leaner than the low intake A line mice, but are no more efficient. The increased lean mass P line mice are much larger, eat more and are more efficient than the decreased lean mass P line mice, but show little difference in maintenance or carcass composition. The (much) fatter F line mice are larger, more efficient and eat more during the rapid growth period than their leaner F line counterparts, but show no difference in lean mass or maintenance requirements. These results provide implications about the relationships between the input (intake) and output (maintenance and lean and fat deposition) components of growth.

1. INTRODUCTION

Improving the efficiency of growth and reducing fatness in domestic animals are two of the most important problems that animal breeders face. In order to design breeding plans to meet these objectives, it is necessary to have detailed knowledge of the genetic interrelationships between the input and output components of growth. These components may be thought of as food intake, lean and fat deposition, and heat wastage (of which maintenance, i.e. heat produced by protein turnover, digestion, thermoregulation, activity and other bodily processes, forms the greater part) (Webster, 1980). Experiments on domestic animals are both costly and time consuming however, so the laboratory mouse has often been used to study growth and its components.

The properties of growth *per se* in the mouse are now quite well understood, as a result of many selection experiments, see reviews by Eisen (1974), Roberts (1981) and McCarthy (1982). Perhaps less well understood, however, are the properties of the components of growth in the mouse. Food intake (Sutherland *et al.* 1970) and muscle mass (McLellan & Frahm, 1973) in the mouse, and lean mass (Notter, Dickerson & Deshazer, 1976) in the rat have all responded to selection, however the genetic relationships between intake, carcass composition, maintenance and efficiency have still to be clearly resolved. It was with the aim of contributing more information to this problem area, that lines of mice selected for appetite, lean mass and fat content were set up by Sharp, Hill & Robertson (1984).

The aim of this study was to investigate correlated responses to selection in these lines. This paper attempts to describe the effects that changes in each of the components of growth have had on overall growth and efficiency, as well as on each of the other components of growth. Data on growth, food intake and carcass composition from weaning until maturity were collected, and from these data estimates of various related traits were also made.

2. MATERIALS AND METHODS

(i) *Selection lines*

Mice were selected for one of three criteria: appetite (A) measured as 4- to 6-week food intake, corrected by phenotypic regression for 4-week body weight; fat percentage (F), using the ratio of gonadal fat pad weight (GFPW) to body weight (BW) in 10-week-old males; and total lean mass (P), using the index $BW - (8 \times GFPW)$ in 10-week-old males.

For each selection criterion there were three contemporary lines, one selected for high (H) performance, one for low (L) performance and one unselected control (C). These lines were replicated three times (replicates 1, 2 and 3) for each of the three selection criteria. Thus there were 27 lines maintained in all: 3 selection criteria \times 3 replicates \times 3 directions (H, C, L). Sixteen pair matings were made in each line up to generation 8; subsequently 8 pair mating were used. A full account of the origins of the mice, selection procedures, and responses to the traits under selection, for the first 11 generations, is given by Sharp *et al.* (1984).

(ii) *Collection of data*

The mice used in this study were sampled from generation 14 of the selection experiment. From each of the 27 lines 4 full sib families were chosen at random, and from within each of these families 2 male and 2 female mice were sampled, giving a total of 432 mice. Each mouse was weighed weekly from birth until 17 weeks of age, whereupon it was slaughtered for carcass analysis. In addition, weekly food intake was measured on half of these mice after weaning at 3 weeks of age. These measurements were made on pairs of mice of the same sex and line, rather than individual mice, to reduce the feeding cage requirements. The remainder of the mice were housed in stock cages. The diet, offered *ad libitum*, was Beta Diets Rat and Mouse No. 1 Expanded Maintenance Diet (crude protein = 14.8%).

The carcass analyses comprised fat, protein and water content estimates made on batch samples of mice of the same line and sex. Water content was estimated by freeze drying the samples. Nitrogen was digested and extracted from minced freeze dried samples using a modified Kjeldahl technique (Crooke & Simpson, 1971) and protein was estimated as 6.25 times nitrogen content. Fat was extracted using standard soxhlet extraction techniques.

This paper also presents summary carcass composition data at three other ages, namely 26 and 44 days, on mice of generations 11, 12 and 13 (M. K. Nielsen, unpublished), and 10 weeks of age, on mice of generation 7 (Sharp *et al.* 1984). These analyses were carried out in the same way as those mentioned above. To enable composition data from mice of different generations to be compared, all line means were adjusted, 'standardized', to that expected after 14 generations of selection, assuming a linear regression of response of generation number.

(iii) *Derived traits*

From the data on growth, food intake, and carcass composition several traits pertinent to the study of the components of growth were derived. Firstly, in addition to considering food intake *per se*, an attempt was made to remove body size effects by scaling intake by both body weight (BW), and metabolic body weight ($BW^{0.75}$). Metabolic body weight is a concept derived from interspecies comparisons of heat production and energy requirements (Blaxter, 1962), and may be thought of as an empirical means of removing metabolic differences between animals caused by size alone.

Maintenance requirements for all individuals on which food intake was measured have been estimated, and are defined here as catabolism. These estimates are presented scaled by both metabolic body weight and metabolic lean mass (lean mass^{0.75}), in order to investigate the effects that carcass composition have on catabolism. Lean mass was estimated as body weight minus fat mass and catabolism was calculated as metabolizable energy intake less the energy cost of fat and protein accretion. The rates of fat and protein accretion were estimated separately for each line from regressions of fat (%) and protein (%) on age. The metabolizable energy content of the diet was assumed to be the same for all lines, and was estimated from the manufacturer's specifications as 10.636 kJ/g. The energy requirements to deposit fat and protein (net efficiency of growth) were assumed to be 53.4 and 52.9 kJ/g respectively, for all lines (Pullar & Webster, 1977).

The efficiency of growth, defined as gain (g)/food intake (g), was calculated and is presented below as cumulative efficiency, i.e. total gain/total intake from weaning onwards. An allied trait – the ratio of intake (kJ) to maintenance requirements (kJ) – was also calculated, to enable easier interpretation and extrapolation of the results to other species. This trait will be called the 'intake ratio', hereafter.

(iv) *Statistical analysis*

For the analysis of all traits except body weight and carcass composition the observations were split into four time periods, namely 3–4, 4–6, 6–10 and 10–17 weeks. These correspond to an immediate postweaning period, a period of rapid growth, a period of decelerating growth, and a period approaching maturity, respectively, as well as corresponding to the ages at selection. The mean values from each of these periods were analysed assuming the following model:

$$Y_{ijklm} = U + T_i + D_{ij} + R_{ik} + L_{ijk} + S_l + (DS)_{ijl} + (RS)_{ikl} + e_{ijklm},$$

where

- Y_{ijklm} observation from the m th feeding cage,
 T_i i th selection criterion (A, F or P),
 D_{ij} j th direction of selection (H, L or C) in the i th criterion,
 R_{ik} k th replicate in the i th criterion,
 L_{ijk} ijk th line,
 S_l l th sex,
 e_{ijklm} random error for the m th feeding cage.

Linear contrasts were used to test the correlated response to selection (H–L) and the symmetry of response ((H+L)/2–C) for each criterion, with the line component of variance being used as the error term.

3. RESULTS

In the results presented below, the following conventions will be used. Selection criterion will refer to the separate A, P and F lines. Selection direction will refer to the direction of selection (H, L or C) within each selection criterion; therefore there are nine distinct selection directions. Each selection direction consists of three replicate lines, and these lines are pooled in the results presented below.

(i) *Growth curves*

The observed growth curves for the nine selection directions are shown in Fig. 1. All the A lines have similar body weights until 4 weeks of age, as was the intention with the selection index used, whereupon they diverge in weight – with the high intake (AH) lines becoming larger and the low intake (AL) lines becoming smaller than their controls. The P lines show much larger divergences in body weight than either the A or F lines, with the increased lean mass (PH) lines being larger, and the decreased lean mass (PL) lines smaller, throughout their entire growth period. The F lines show similar magnitudes of body weight change to the A lines; however, by 17 weeks of age the increased fat (FH) lines still appear to be growing rapidly whilst the decreased fat (FL) lines have only very slow growth.

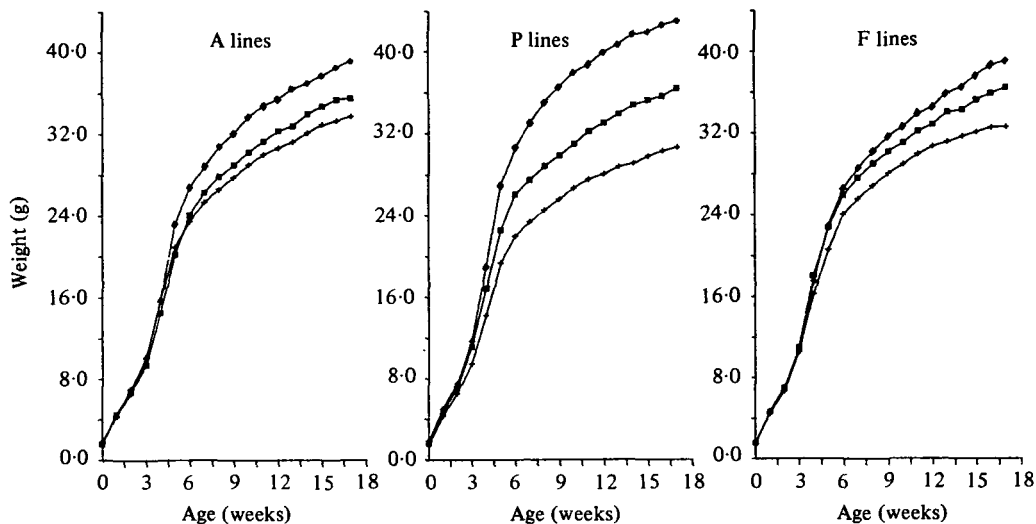


Fig. 1. Observed weights vs. age (◆—◆, high lines; ■—■, control lines; +—+, low lines).

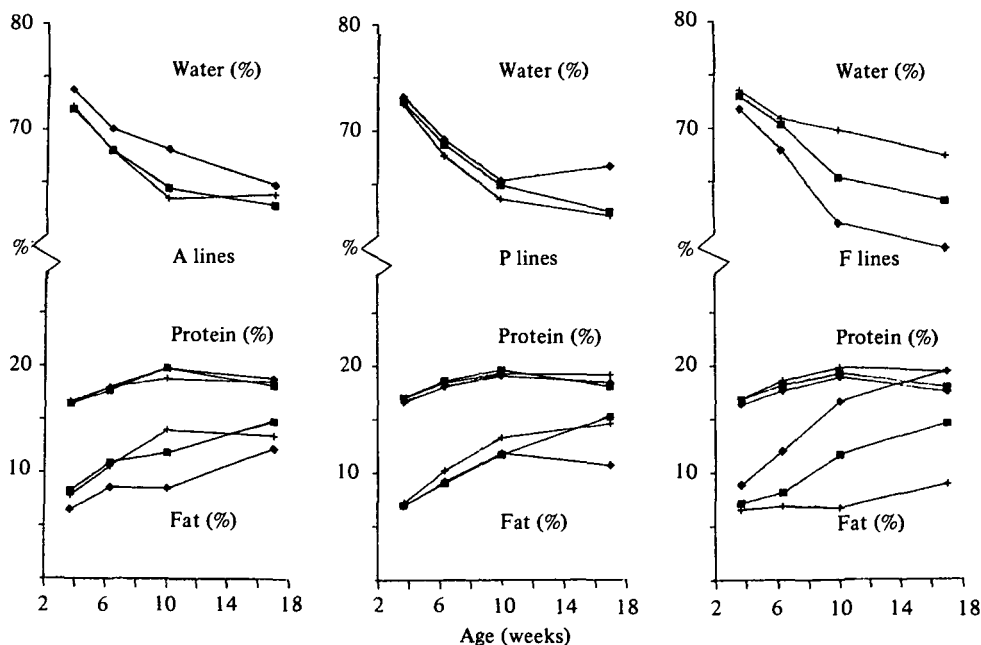


Fig. 2. Carcass composition vs. age (◆—◆, high lines; ■—■, control lines; +—+, low lines).

(ii) Carcass composition

Shown in Fig. 2 are water, fat and protein percentages for all selection directions, adjusted to that expected after 14 generations of selection. For all three criteria the changes in fat (%) over time are mirrored by the changes in water (%).

Table 1. Linear contrasts for differences between high and low selected lines (H-L) and males and females (M-F), and analyses of variance for total food intake (g/pair/day), food intake scaled by body weight (BW) (g/g/week), and food intake scaled by metabolic body weight ($BW^{0.75}$) (g/g^{0.75}/week), for the four age periods

		Period			
		1	2	3	4
Contrast	D.F.	Total food intake			
A: H-L	1	0.66*	1.97**	2.40**	1.70*
P: H-L	1	1.47**	2.25**	2.57**	2.35**
F: H-L	1	0.34	1.19*	0.69	0.32
Sex: M-F	1	0.04	0.62**	0.60**	0.14
Mean squares					
Replicates	6	1.348†	2.746†	5.035	2.319
Lines	12	0.520	1.055*	2.270**	4.146**
Residual	58	0.383	0.462	0.531	0.546
Contrast		Food intake/BW			
A: H-L	1	0.104*	0.162**	0.125*	0.020
P: H-L	1	-0.031	-0.111**	-0.105**	-0.156**
F: H-L	1	0.040	0.070*	-0.060	-0.103†
Sex: M-F	1	-0.040*	-0.037**	-0.103**	-0.158**
Mean squares					
Replicates	6	0.0266†	0.0364**	0.0314	0.0355†
Lines	12	0.0110	0.0062	0.0117**	0.0140*
Residual	58	0.0085	0.0050	0.0033	0.0044
Contrast		Food intake/ $BW^{0.75}$			
A: H-L	1	0.228**	0.436**	0.389**	0.145
P: H-L	1	0.140†	0.017	-0.001	-0.131
F: H-L	1	0.099	0.218*	-0.052	-0.162
Sex: M-F	1	-0.052	-0.005	-0.134**	-0.274**
Mean squares					
Replicates	6	0.1269*	0.1660*	0.2086†	0.2185†
Lines	12	0.0280	0.0363	0.0766*	0.0812**
Residual	58	0.0336	0.0200	0.0183	0.0225

† $P < 0.1$; * $P < 0.05$; ** $P < 0.01$, otherwise $P > 0.1$.

Tests are: selection criterion, contrasts and (pooled) replicates against (pooled) lines. Sex against (pooled) replicates by sex interaction. Lines against residual.

Although the protein (%) changes are also negatively related to the fat (%) changes, the magnitudes of these changes are much smaller.

The A lines show distinct changes in fatness, the AH lines being less fat, and these changes are apparent in 26 days of age and possibly do not increase thereafter. In general the P lines show little change in carcass composition, except for decreased fatness of the PH lines at 17 weeks. There is some doubt as to the validity of this result, however, as problems were experienced in thoroughly drying some of the largest PH mice, and no replication of the samples analysed was possible. The F lines show large and consistent changes over age in fat (%) and water (%), with the FH lines becoming very fat and the FL lines remaining very lean

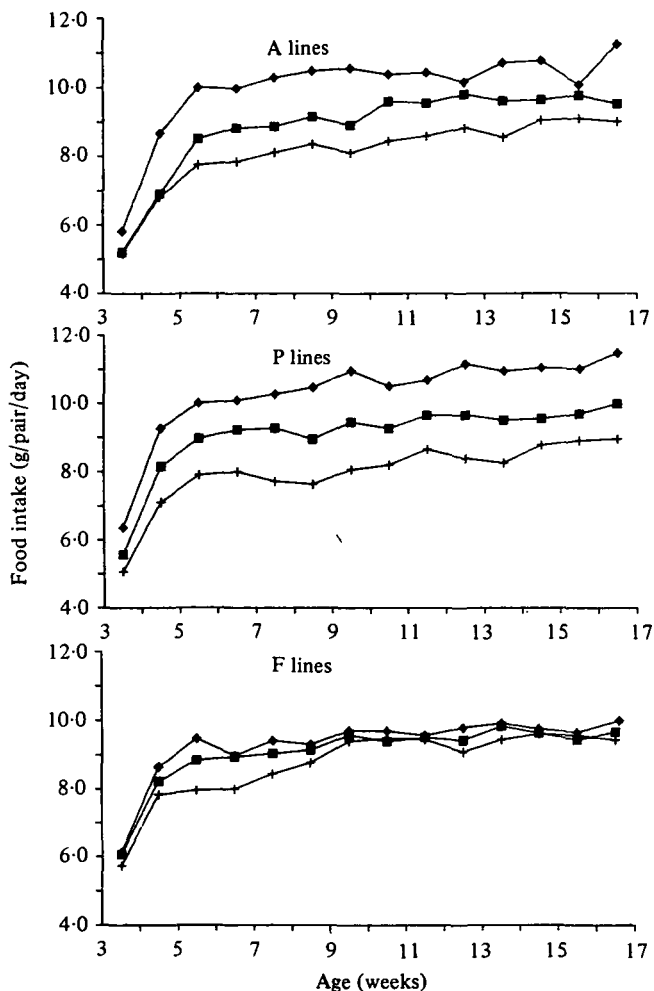


Fig. 3. Food intake vs. age (◆—◆, high lines, ■—■, control lines; +—+, low lines).

throughout their lifetime. Small but consistent changes in protein (%) in the F lines can also be seen, with these divergences being in the opposite direction to the changes in fatness. It can be shown from these results that the H, C and LF lines have very similar lean masses throughout the entire measurement period, the body weight differences being due to fat alone.

(iii) Food intake traits

Fig. 3 shows unadjusted food intake, and Figs. 4 and 5 the ratio of food intake to body weight and metabolic body weight, respectively. Linear contrasts and components of the analyses of variance are shown in Table 1. Not shown are the components due to selection criterion, the sex by replicate and sex by direction

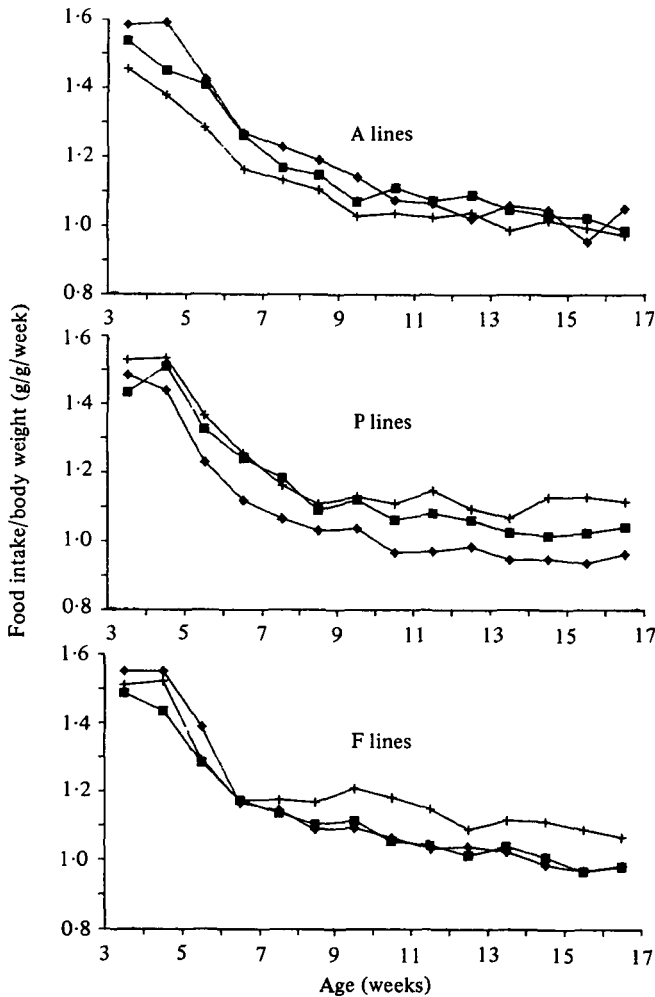


Fig. 4. Food intake scaled by body weight vs. age (◆—◆, high lines; ■—■, control lines; +—+, low lines).

interactions, and the symmetry of response $((H+L)/2-C)$ contrasts, as these components were nearly always non-significant.

For food intake *per se*, there are large H–L divergences in the A and P lines at all ages, with the magnitude of the divergence being slightly larger in the P lines. There is considerable variation between weeks in the AH lines in the 10–17 week period, however the large ‘line’ component of variation (Table 1) suggests measurement error. The F lines show significant divergences during the fast growing period, with the FH lines eating more; as the lines approach maturity, however, the differences in food intake disappear.

In addition to having a larger intake *per se*, the AH lines also eat more in relation to their body weight (Fig. 4) and metabolic body weight (Fig. 5) than the AL lines,

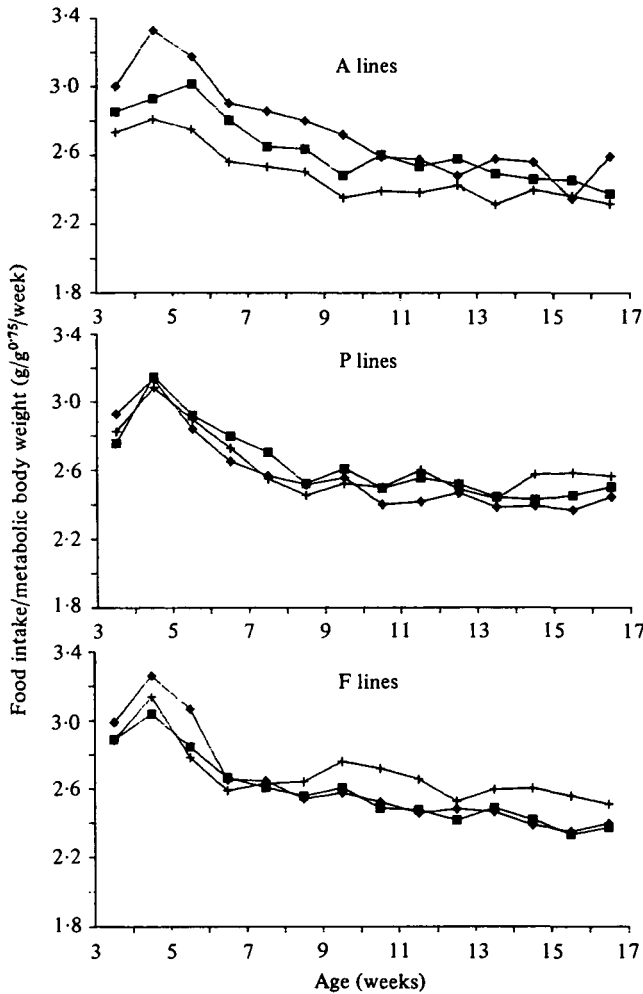


Fig. 5. Food intake scaled by metabolic body weight ($BW^{0.75}$) vs. age (◆—◆, high lines; ■—■, control lines; +—+, low lines).

until 10 weeks of age – after which the trends become less clear. The H–L divergences are larger when scaled by $BW^{0.75}$ than when scaled by BW. The PH lines eat less in relation to their body weight than the PL lines, and this divergence appears to increase with age. When scaled by metabolic body weight, however, the H–L divergences become consistently very small throughout the entire measurement period. For the F lines, the choice of either body weight or metabolic body weight as the scaling factor makes little difference to the trends. During the faster growth period (4–6 weeks) the FH lines eat slightly more, however as the rate of growth slows down, the FL lines have the higher relative intake.

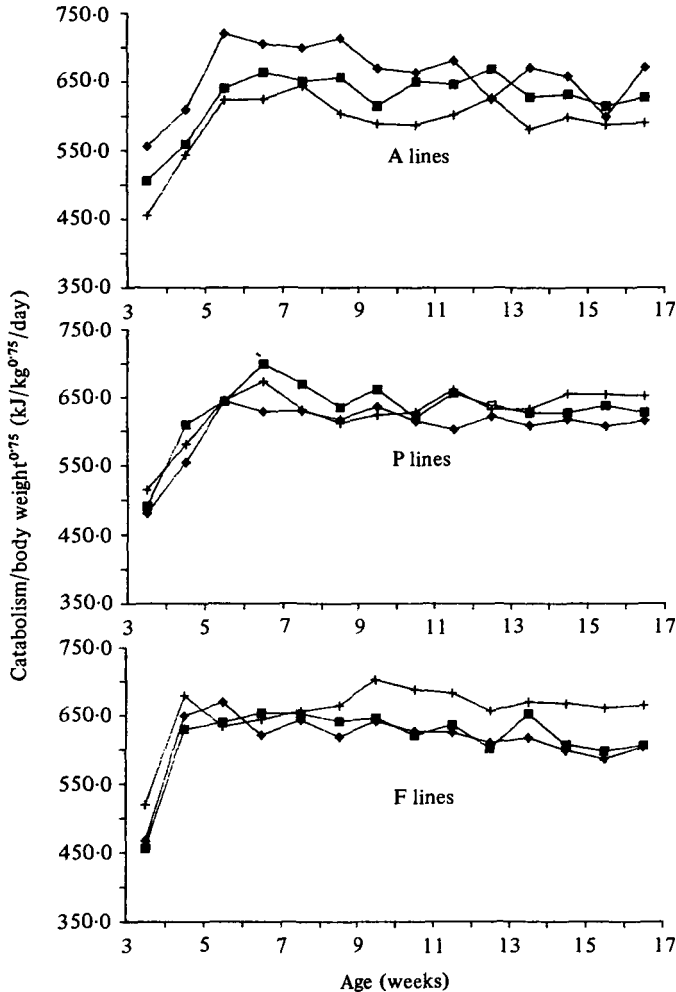


Fig. 6. Catabolism scaled by metabolic body weight ($BW^{0.75}$) vs. age (◆—◆, high lines; ■—■, control lines; +—+, low lines).

(iv) *Catabolism*

Catabolism is shown relative to metabolic body weight in Fig. 6 and metabolic lean mass in Fig. 7. Linear contrasts and the analyses of variance are shown in Table 2.

Large H—L divergences in catabolism/ $BW^{0.75}$ exist in the A lines, until 10 weeks of age. When scaled by lean mass^{0.75} the trends are similar, but the divergences are slightly smaller. In the P lines there is little differentiation between selection directions for either trait. The F lines show no divergence in catabolism/ $BW^{0.75}$ over the fast growing periods, but have an increasing divergence with age as the lines become more differentiated in degree of fatness. When scaled by lean mass, however, the H—L divergences disappear in the F lines.

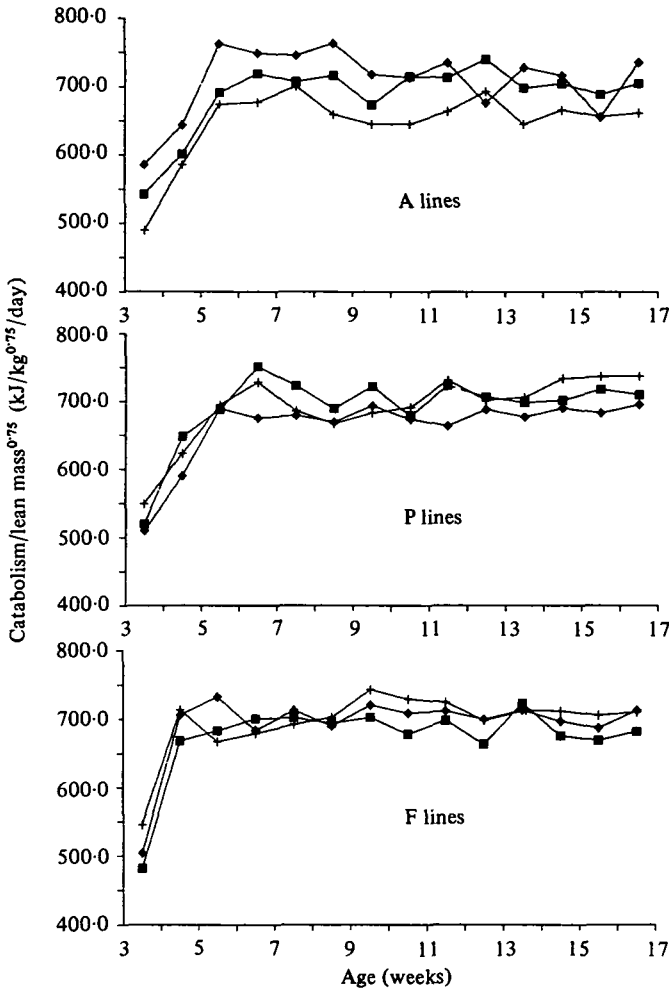


Fig. 7. Catabolism scaled by lean mass^{0.75} vs. age (◆—◆, high lines; ■—■, control lines; +—+, low lines).

(v) *Efficiency and the intake ratio*

Cumulative efficiency up to each age and the intake ratio are shown in Figs. 8 and 9, respectively. Linear contrasts together with the analyses of variance are presented in Table 2.

The AL lines are slightly more efficient than the AC and AH lines during period 1, due to a much higher intake ratio, however during period 2 (4–6 weeks, the period of selection) they are slightly less efficient. These two effects cancel each other out, and after 5 weeks of age the A lines show almost identical efficiency until maturity. The A lines also display no divergence in the intake ratio after 5 weeks of age. The PH lines always have a much higher cumulative efficiency than the PL and PC lines, as well as having a greater intake ratio in periods 1 and 3. In the F lines,

Table 2. *Linear contrasts for differences between high and low selected lines (H-L) and male and females (M-F), and analyses of variance for catabolism/BW^{0.75} (kJ/kg^{0.75}), catabolism/lean mass^{0.75} (kJ/kg^{0.75}), and the intake ratio (food intake (kJ)/catabolism (kJ)) for the four age periods, and cumulative efficiency (g/g) up to the end of each period*

		Period			
		1	2	3	4
Contrast	D.F.	Catabolism/BW ^{0.75}			
A: H-L	1	86.31**	93.11**	94.72**	41.13
P: H-L	1	-30.46	-13.36	-15.84	-41.28
F: H-L	1	-55.30*	-1.43	-41.86	-67.92†
Sex: M-F	1	-40.71**	-37.36**	-45.46**	-74.70**
Mean squares					
Replicates	6	13809.7**	12834.3**	13142.7	16719.1†
Lines	12	2840.8	2053.6	48240.0**	6340.2**
Residual	58	2953.5	1676.6	1377.7	1614.3
Contrast		Catabolism/lean mass ^{0.75}			
A: H-L	1	84.92**	86.51**	87.35*	30.54
P: H-L	1	-34.93	-18.74	-20.75	-47.60
F: H-L	1	-48.91*	24.01	-8.68	-16.74
Sex: M-F	1	-43.24**	-39.85**	-49.21**	-87.75**
Mean squares					
Replicates	6	15652.8*	14693.6**	15424.4†	20583.1†
Lines	12	3247.6	2386.2	5694.4**	7851.5**
Residual	58	3358.9	1912.7	1616.8	1974.0
Contrast		Intake Ratio (food intake/catabolism)			
A: H-L	1	-0.2008*	0.0031	0.0026	-0.0055
P: H-L	1	0.1784†	0.0381	0.0265*	0.0116
F: H-L	1	0.2541*	0.1033**	0.0470**	0.0460**
Sex: M-F	1	0.1089**	0.0768**	0.0212**	0.0068*
Mean squares					
Replicates	6	0.1856*	0.0075	0.0017†	0.0005
Lines	12	0.0426	0.0044	0.0006	0.0003*
Residual	58	0.0335	0.0046	0.0004	0.0001
		Week			
		4	6	10	17
Contrast		Cumulative Efficiency			
A: H-L	1	-0.0229	0.0002	0.0018	0.0005
P: H-L	1	0.0674*	0.0302*	0.0194**	0.0112**
F: H-L	1	0.0249	0.0135†	0.0094†	0.0073
Sex: M-F	1	0.0321*	0.0305**	0.0179**	0.0101**
Mean squares					
Replicates	6	0.01576**	0.00022	0.00013	0.00006
Lines	12	0.00307	0.00025	0.00011	0.00006*
Residual	58	0.00286	0.00033	0.00008	0.00002

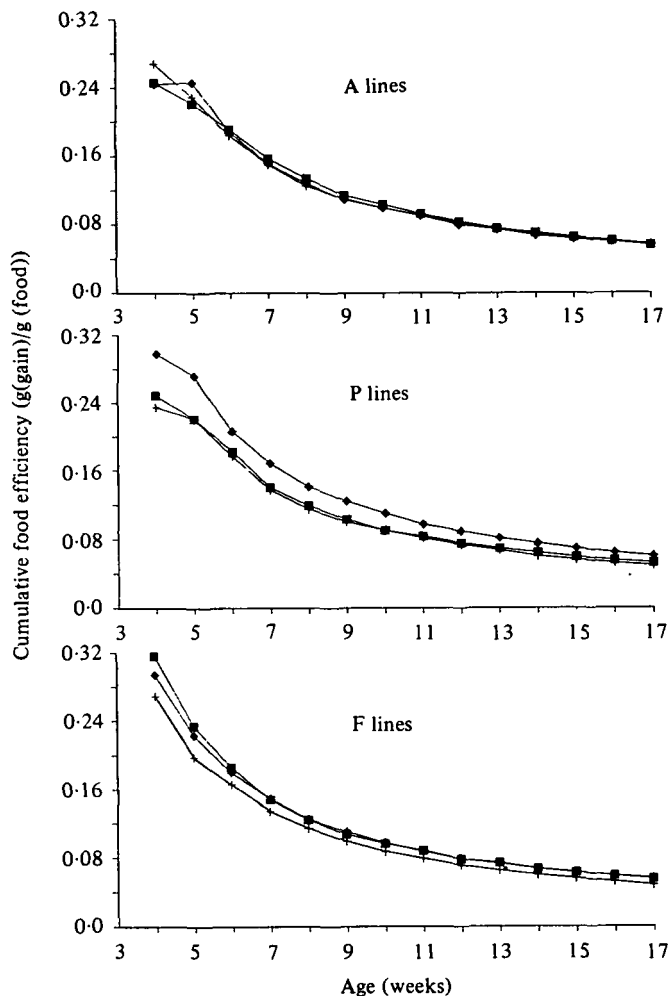


Fig. 8. Cumulative food efficiency vs. age (◆—◆, high lines; ■—■, control lines; +—+, low lines).

there are large significant divergences in both cumulative efficiency and the intake ratio, with the fatter FH lines always having larger values for both traits than the leaner FL lines.

4. DISCUSSION

(i) *A lines*

Changing the input component of growth over and above that explicable by subsequent body weight changes has been successfully achieved, as scaling intake by $BW^{0.75}$ rather than BW is normally expected to reduce rather than increase intake differences (Blaxter, 1962). The selection index used, 4-to 6-week intake corrected for 4-week weight, was intended to restrict 4-week body weight change,

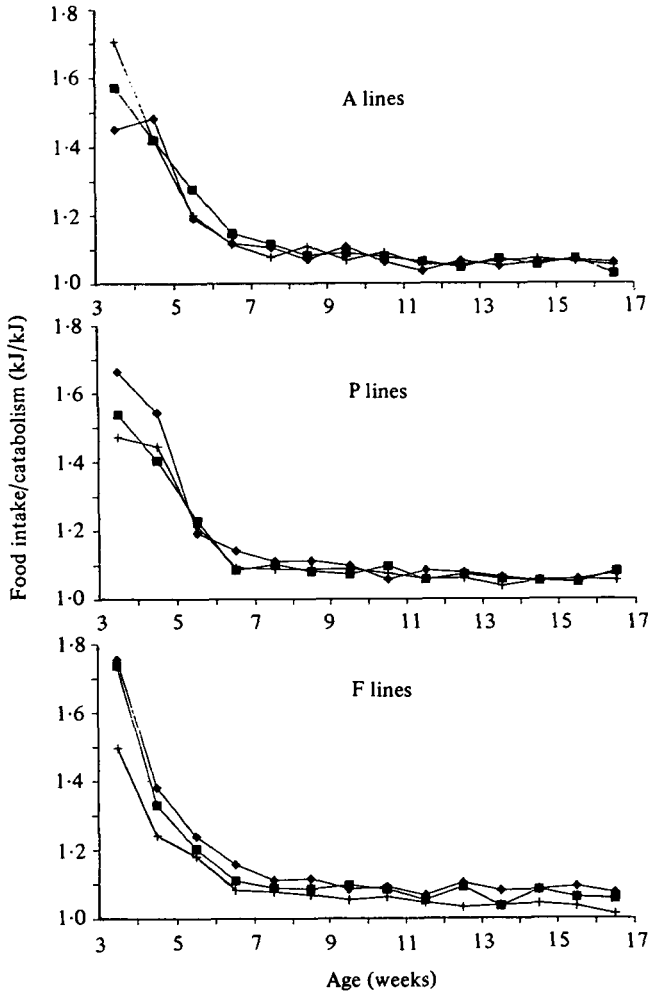


Fig. 9. Intake ratio (food intake/catabolism) vs. age (◆—◆, high lines; ■—■, control lines; +—+, low lines).

and Fig. 1 indicates that this intention has been realized. Subsequently, however, there are divergences in body weight, but this is the expectation from selection for food intake (Sutherland *et al.* 1970; Pym & Nicholls, 1979). The decreasing divergences in intake/BW and intake/BW^{0.75} as the mice mature result from these body weight divergences.

Increasing intake relative to metabolic body weight has also increased catabolism, or energy used for maintenance, which agrees with the finding of Pym & Farrell (1977), in chickens. Kownacki, Keller & Gebler (1975), Kownacki & Keller (1978), and Stanier & Mount (1972) have found evidence of decreases in heat production and maintenance, after selection for growth in mice, although Canolty & Koong (1976) were unable to do so. The genetics of maintenance requirements in mice clearly warrants more study.

The A lines show no divergence in efficiency after 5 weeks of age, in contrast

to the high appetite line of Sutherland *et al.* (1970), where efficiency did increase. The A line result can be seen to be due to the lack of divergence in the intake ratio, as efficiency is a function of proportion of an animal's intake available for growth, i.e. the intake ratio. Therefore the maintenance requirements of the A lines appear to have changed proportionately to their intakes. The AL lines have a greater intake ratio and efficiency in period 1 than the AH lines, yet lesser values in period 2. This is simply due to both groups of lines having similar body weights at 4 weeks of age, despite having different levels of intake and catabolism.

The AH lines have become slightly leaner. This appears to conflict with the previous experiments in mice (Sutherland *et al.* 1970) and chickens (Pym & Solvens, 1979), where animals selected for intake became fatter, and the usual finding of a positive correlation between fatness and intake in mice (Hayes & McCarthy, 1976) and pigs (Fowler, Bichard & Pease, 1976). The A lines were not selected for food intake *per se*, however, but intake corrected for 4-week body weight. This, together with the fact that the composition differences are apparent by 4 weeks of age, and do not increase greatly subsequently, implies that the 4-week weight restriction has caused these composition changes. If maintenance requirements are a function of lean mass (see F line discussion) rather than body weight, then these changes are explicable: since maintenance forms the greater part of a mouse's intake, those mice with the greater intake and hence maintenance requirements, at the same body weight, will tend to be the leaner mice. These will be the mice selected by the A line criterion. This hypothesis needs experimental verification, however.

(ii) P lines

Possibly the most important feature of the P lines is the increased efficiency of the PH lines, which accompanies their increased body size. This efficiency change results from the intake ratio changes in periods 1 and 3, as there is little difference in carcass composition at these ages. It is not possible to ascribe these changes definitely to either increased (or decreased) intake, or decreased (or increased) catabolism, however, as the observed changes are very small. Most probably both factors contribute. Selection for increased protein gain in rats has been shown to result in a small and nonsignificant decrease in heat production (Notter *et al.* 1976; Wang *et al.* 1980), in agreement with the P line results.

Selection for body weight usually results in an increase in fatness, although this effect decreases with increasing age at selection (Clarke, 1969). In this study selection for estimated lean mass, instead of body weight, appears to have overcome this problem.

In summary, the observed P line differences appear to be solely a function of body size, with all components of growth changing proportionately.

(iii) F lines

The F lines appear to be the only reported selection experiment for carcass composition in laboratory animals. The outstanding feature of these lines is the

large difference in fatness, yet an equivalence of lean mass in the H, C and L lines. This shows a lack of correlation between fatness and lean mass, which is backed by the finding of no correlation between estimated lean mass and fat percentage in the P lines.

The trends for food intake scaled by body weight and metabolic body weight are slightly confusing, although the similar total food intakes of the lines as they mature indicate similar total maintenance requirements. The fact that catabolism differences between the lines disappear when scaled by lean mass, provides evidence that maintenance requirements are more closely related to the lean portion of the body mass, than to body mass *per se*. The same result has been found in comparisons of 'old' fat and lean sheep, and 'fatty' and lean rats (Webster, 1981).

The FL lines have become less efficient than their FC and FL counterparts, despite the fact that it is less efficient to deposit fat than lean. This result is explicable, however, by their much reduced intake ratio as compared to the FC and FL lines.

In summary, selection designed to change fat (%) has resulted in lines of mice with the same 'lean mass frame', but varying fat adjuncts on this frame. Metabolism appears to be a function of this lean mass frame, rather than total body weight.

(iv) *General*

Several implications towards the relationships between the components of growth may be drawn from this study.

Firstly, there appears to be variation in maintenance requirements as well as intake eaten in excess of maintenance, the latter being a necessity to get variation in body size and growth rate.

Secondly, results from the F lines suggest that maintenance may be more closely related to lean mass than body weight. In other words, animals maintain lean, rather than total body mass. In support of this, the A lines show a reduced divergence in catabolism when scaled by lean mass rather than body weight, and the P lines show little divergence in either catabolism or carcass composition. If this model is true, then the phenomenon of the AH lines becoming leaner than their controls, instead of fatter, can be explained. Finally, it may be speculated that if the slightly decreased heat production of lines of mice selected for body size (Kownacki *et al.* 1975), (Kownacki & Keller, 1978) was expressed relative to metabolic lean mass, then these differences might also be reduced, as the selected mice were most probably fatter than their controls (Clarke, 1969).

Thirdly, two interesting lacks of correlation between various components of growth are implied by these results. Firstly, the F and P lines indicate a lack of relationship between lean mass and carcass composition at any age, and secondly, the F lines indicate no correlation between an animals maintenance requirements and its intake available for growth (i.e. intake in excess of maintenance), at any given age. This latter observation is backed by the finding of a phenotypic correlation of zero between these traits in a separate study (S. C. Bishop, unpublished).

Fourthly, the A, P and F lines all support the importance of the intake ratio in defining efficiency, despite their differing carcass composition and utilization of food ingested. It can be shown that depositing 1 g more of tissue will always improve a mouse's efficiency, no matter whether it is deposited as lean or fat. This will be true for any animal whose efficiency is less than 1 g tissue/53 kJ metabolizable intake – the cost of depositing the more expensive tissue, i.e. fat. For more efficient species which have larger intake ratios, e.g. 3.0 for pigs (Davies & Lucas, 1972), excess fat deposition can be shown to reduce efficiency towards the figure of 1 g/53 kJ.

Finally, several implications have come from this study, but further experimental verification is needed for each one in turn. When extrapolating these results to domestic animal species, it is necessary to take account of such factors as the intake ratio and the differing patterns of fat and lean growth for each species considered.

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