

Energy partitioning and growth in mice selected for high and low body weight

BY S. K. STEPHENSON AND R. C. MALIK*

*Department of Animal Science, University of New England,
N.S.W. 2351, Australia*

(Received 3 December 1982 and in revised form 21 September 1983)

SUMMARY

The partitioning of digestible energy intake on an *ad libitum* diet of standard mouse nuts was investigated in mice selected for high and low body weight at eight weeks and in an unselected control population. In selected mice aged from four to six weeks and housed at a temperature of 24.5 °C, almost all their energy intake could be attributed to basic maintenance and the deposition of extra protein and fat. Control mice, however, had an energy intake considerably in excess of their apparent maintenance and growth requirements. It was concluded that the unaccountable energy loss of the control line could be used to increase growth efficiency in the selected lines. The result is analogous to those obtained from studies on normal and obese mouse genotypes and indicates genetic changes in mechanisms controlling the conversion of food energy to heat.

Provision of a nest to reduce thermoregulatory heat production caused a minor reduction in energy intake and a corresponding decrease in the energy discrepancy. There was no effect on growth.

1. INTRODUCTION

There have been numerous experiments in which mice have been selected for body weight at a specified age (e.g. Falconer, 1953; Hull, 1960; Baker *et al.* 1979), weight gain (e.g. Sutherland, Biondini & Ward, 1974) or efficiency defined as gain in relation to food intake (e.g. Hetzel & Nicholas, 1979; McPhee *et al.* 1980; Yüksel, Hill & Roberts, 1981). These three characteristics have shown genetic change in response to selection, but only limited attempts have been made to interpret responses in terms of the underlying biological control of growth and tissue deposition.

McCarthy and others (Hayes & McCarthy, 1976; McCarthy, 1978; Roberts, 1979) considered nutritional energy as a limitation to selection response. They proposed that selection for weight or gain imposed a demand for extra energy that might involve a general stimulation of appetite and the economic use of this energy up until the age of selection. A major concept was the idea that deposition of wet

* Present address: Department of Agriculture (UPNG), University of Technology, Lae, Papua New Guinea.

muscle was energetically more efficient than deposition of fat in meeting the selection criteria, and so growth prior to the selection age ought to involve mainly the laying down of extra bone and muscle. Growth after the age of selection is no longer constrained by an energy limitation and so post-selection weight gains would be expected to consist of a progressively greater deposition of energetically expensive fat. Support for this theoretical model was given by the results of Hull (1960), Hayes & McCarthy (1976) and Baker *et al.* (1979).

Nevertheless there is evidence that the same selection criterion (post-weaning rate of gain) can lead to different responses in terms of muscle or fat deposition (Biondini *et al.* 1968) suggesting that the genetic variability underlying different physiological systems can be the basis for the response to selection for body weight or weight gain. Further, there are at least two reported experiments where selection for efficiency of gain has resulted in an increase in body weight on restricted intake together with an increase in the proportion of fat in the body (McPhee *et al.* 1980; Yüksel *et al.* 1981). In terms of metabolic energetics these results may be explained if the unselected mice were inefficient in the use of their dietary energy and the selected lines can redirect this loss into tissue synthesis.

Additional evidence is provided by studies on obese mutants in rodents, particularly the *ob* gene in mice (James & Trayhurn, 1981). Energy used for heat production is related to the needs of thermoregulation (Rothwell & Stock, 1981). It may also result from the 'burning off' of excess energy intake through dietary thermogenesis (Rothwell & Stock, 1979; Trayhurn *et al.* 1982*a*) although there is argument over the existence of such an effect (e.g. Barr & McCracken, 1982; Hervey & Tobin, 1983). A biochemical system for converting dietary energy directly to heat appears to operate through the proton conductance pathway in brown adipose tissue (Nicholls, 1979). This ability seems to be largely or completely lost in obese (*ob/ob*) mice with the consequence that they store any excess food energy as fat and are more efficient at converting food energy to body weight gain. Such mice are, however, more susceptible to cold stress (Trayhurn, Thurlby & James, 1977).

Another possibility is that a difference between maintenance requirements on *ad libitum* and restricted feeding can be redirected to provide energy for growth in selected populations. Graham, Searle & Griffiths (1974) and Corbett, Furnival & Pickering (1982) in sheep and Rothwell & Stock (1982) in rats have found a difference in maintenance requirements on different planes of nutrition and a similar variation could be present in unselected mice.

The aim of the present work was to investigate the effects on energy partitioning and tissue deposition in mice selected for high and low body weight. Since heat production is an important component of growth models that include energy useage it was thought desirable to obtain some estimate of thermoregulatory energy cost. This was considered to be most easily achieved by providing mice with a cotton wool nest giving individuals the ability to create their own thermoneutral environment (Lynch & Hegmann, 1972; Lynch & Possidente, 1978). It was also considered that the work might make possible some evaluation of mice as a model for the genetic control of growth and the deposition of carcass tissues in livestock.

2. MATERIALS AND METHODS

(A) *Selection lines.* Mice used in this study were from lines selected for high and low body weight at eight weeks of age (HBW and LBW respectively) and a random bred control line (C). The base population was constructed by crossing the following inbred lines: 101, CBA, C₃H and an unspecified albino stock. This base was the foundation of the control population and a high and low index line where selection was for leg length and body weight (Dawson, Stephenson & Fredline, 1972). The index lines were selected for 18 generations, at which point they were crossed with the control to give a gene pool containing 50% of the control, 25% of the high and 25% of the low index genotypes. From this gene pool the HBW and LBW lines had been selected for ten generations followed by two generations of relaxed selection. They showed respectively an increase and a decrease in the proportion of body fat, together with associated changes in the amount of protein, water and ash (Malik, 1984). Throughout the selection, mice were kept at a mean ambient temperature of 24–25 °C.

(B) *Experimental design.* Following weaning at 3 weeks of age, males and females of each litter were kept separately in cages with fresh sawdust and *ad libitum* access to water and mouse nuts. At 4 weeks, four females and four males from each litter were caged individually. Three litters were chosen at random from each line with the restriction that they provided four mice of each sex, consequently smaller litters were not included. This gave a total of 72 mice. Body weight and food consumption were recorded every 3 days for a 15 day trial period, the mice being fed from containers specially designed to prevent spillage and contamination (Hetzl & Nicholas, 1982). Two males and two females from each litter were provided with cotton wool inside a cardboard nest, while the other two were kept in standard cages without nesting material at the normal mouse colony temperature of 24.5 ± 1 °C. It was important to undertake all experimental work at this temperature because it was the one at which the selection work was carried out. If there was a temperature \times genotype interaction in energy partitioning, a different temperature would not necessarily have shown the nature of any genetically based metabolic changes that occurred.

(C) *Calculation of feed efficiency and energy parameters.* For each mouse the recorded measurements of body weight and food consumption were used to calculate the mean body weight, the weight gain and the total amount of food consumed for the experimental period. The amount of food eaten was converted to digestible energy intake (DEI) by the equation

$$\text{DEI} = \text{food consumption} \times \text{energy content of food (16.8 kJ/g)} \times \text{digestibility (0.806)}.$$

The energy content of the food was measured by combustion in a bomb calorimeter. Digestibility was estimated in the normal way from food intake and faecal output together with measurements of faecal energy content (Malik, 1984). There were no between-line differences in digestibility.

Mice from the three lines had been analysed for body composition at weekly intervals from 3 to 8 weeks (Malik, 1984), and this information was used to estimate

Table 1. *Least squares regressions of protein or fat weight on body weight calculated from the individual values of chemical composition at 4, 5 and 6 weeks*

Line	Sex†	Protein weight (Y_1) in grams		Significance of sex difference (F ratios)		Fat weight (Y_2) in grams		Significance of sex difference (F ratios)	
		$Y_1 = 0.190$ B. Wt. - 0.153 $Y_1 = 0.174$ B. Wt. - 0.038	$Y_1 = 0.209$ B. Wt. - 0.415 $Y_1 = 0.181$ B. Wt. - 0.051	Means	Slopes	$Y_2 = 0.160$ B. Wt. - 1.728 $Y_2 = 0.170$ B. Wt. - 1.267	$Y_2 = 0.131$ B. Wt. - 0.810 $Y_2 = 0.101$ B. Wt. - 0.059	Means	Slopes
HBW	♂♂ ($n = 30$)			12.8 ^{*,57}	0.8 NS			28.1 ^{*,57}	0.1 NS
	♀♀ ($n = 31$)								
C	♂♂ ($n = 31$)			7.4 ^{*,55}	3.1 NS			5.2 ^{*,55}	0.9 NS
	♀♀ ($n = 28$)								
LBW	♂♂ ($n = 33$)			6.3 ^{*,61}	4.1*			10.2 ^{*,61}	0.7 NS
	♀♀ ($n = 32$)								

Pullar & Webster (1977) give the total energy costs of tissue deposition as:

1 g fat = 53.4 kJ;
1 g protein = 52.9 kJ.

† Since there were significant sex differences, separate regressions were used for males and females: ^{***} $P < 0.001$; ^{**} $P < 0.01$; ^{*} $P < 0.05$; NS, $P > 0.05$.

the composition of gain from 4 to 6 weeks in terms of increases in the weight of protein and fat. The regression equations calculated from the body composition analyses and used to predict protein and fat increases from body weight, are shown in Table 1. To calculate the energy required for growth over the experimental period it was necessary to know the energy costs of protein and fat deposition. The figures estimated by Pullar & Webster (1977) and given in Table 1 were used for the present study.

The energy cost of maintenance in young mice was obtained by restricting food intake so that body weight was maintained without growth (Malik, 1984). Restricted feeding was started at 4 weeks of age and for the initial 3 weeks, adjustments were made to prevent weight gains or losses. Maintenance requirements appeared to vary over this period since the mice were adapting to the restricted intake. For the next 3 weeks however, a fixed level of intake maintained a constant body weight. The maintenance requirements estimated as the fixed levels of intake were 1.25, 1.35 and 1.5 g of feed per gram of body weight per week respectively in the HBW, C and LBW lines and there were no sex differences ($P > 0.7$). These maintenance figures were 12–20 % higher than the requirements of adult mice with constant body weight fed *ad libitum* (Malik, 1984). They were taken as representing a minimal basic maintenance requirement *under conditions of restricted feeding* for the young growing mice used in the present work.

Finally, the energy required for maintenance and growth was compared with the digestible energy intake (DEI). The difference, henceforth termed 'energy discrepancy', represented energy losses from the following possible sources.

(a) Energy used optionally for thermoregulation under conditions of *ad libitum* feeding, assuming that on a maintenance ration the animal can lower its heat production to some extent to conserve energy.

(b) Dietary thermogenesis or the burning off of excess energy intake as waste heat. Since this possibility has been reported in rats and mice whose appetite was stimulated by a 'cafeteria diet', it may also be used to eliminate excess energy intake on a standard diet.

(c) Some other adaptive depression in measured maintenance on restricted feeding.

(d) Extra energy used for alternative unspecified maintenance requirements (e.g. physical activity) when a young animal is fed *ad libitum*.

(e) In addition, errors in the estimation of maintenance or growth requirements will affect the energy discrepancy and these effects will be considered later in the discussion.

(D) *Statistical analyses.* The results were analysed according to the mixed model shown in Table 2 using Harvey's (1979) computer programme.

Line, sex and treatment were considered as fixed effects and litters within lines as a random component. A preliminary analysis showed the second order interaction, line \times treatment \times sex to be of no significance. Interactions involving the litter classification were examined and, as in only one case was significance reached at the 5 % level, these components were pooled into the residual error term in the model.

The variables analysed in this way were body weight (for each individual

averaged over 4–6 weeks), maintenance energy cost, energy used for growth, total energy accounted for by maintenance and growth, DEI, and energy discrepancy. Body weight was used as the covariate in an analysis of covariance because, with the exception of growth, the energy variables might be expected to be a linear function of the body weight of the individual.

Table 2. *Model for the analyses of variance and covariance using Harvey's (1979) computer programme and the expectations for the mean squares in the analysis*

(1) Model

$$Y_{ijklm} = \mu + \alpha_i + e_{ij} + \beta_k + \gamma_l + \beta\gamma_{kl} + \alpha\beta_{ik} + \alpha\gamma_{il} + \xi_{ijklm},$$

where α_i is the effect of the i th line,

e_{ij} is the effect of the j th litter nested within the i th line,

β_k is the effect of the k th treatment,

γ_l is the effect of the l th sex,

m is the within cell residual – each cell containing two individuals.

(2) Analysis of variance

Source	D.F.	Expectations for the mean square
Lines (ln)	2	$\sigma_w^2 + 8\sigma_{li:ln}^2 + 12 \sum_{i=1}^3 \alpha_i^2$
Between litters within lines (li:ln)	6	$\sigma_w^2 + 8\sigma_{li:ln}^2$
Treatments (T)	1	$\sigma_w^2 + 36 \sum_{k=1}^2 \beta_k^2$
Sex (S)	1	$\sigma_w^2 + 36 \sum_{l=1}^2 \gamma_l^2$
T × S	1	$\sigma_w^2 + 18 \sum (\beta\gamma_{kl})^2$
ln × T	2	$\sigma_w^2 + 6 \sum (\alpha\beta_{ik})^2$
ln × S	2	$\sigma_w^2 + 6 \sum (\alpha\gamma_{il})^2$
Residual	56	σ_w^2

Table 3. *Male and female values of each line for the variables showing a line × sex interaction*

(Energy costs are in kJ/24 h.)

Variable	Line						F ratio
	HBW		C		LBW		
	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	
Body weight (g)	25.0	29.7	17.4	20.3	14.2	15.8	6.06**
Maintenance energy cost (kJ/d)	60.1	71.8	45.5	52.9	41.2	45.8	4.52*
Energy used for growth (kJ/d)	7.96	14.21	5.07	8.89	3.97	6.75	10.56***

Sex differences did not affect the other classifications and will be considered elsewhere. Line × sex was the only significant first order interaction. The variables showing this effect were body weight, maintenance energy cost and energy used for growth, a result arising from the increasing difference in size and growth rate between males and females with increasing mean body weight of the different lines.

Details of this interaction are given in Table 3 but it was considered unlikely to have a significant influence on the conclusions regarding lines, treatments and litters nested within lines.

The line \times treatment interaction did not remove a significant amount of variation in the analysis.

3. RESULTS

(A) *Body weight.* Table 4 shows that the body weight means of the HBW, C and LBW lines decreased, as expected, in that order. There was no significant treatment effect. The significant within-line litter differences can be attributed to maternal or other pre-weaning influences that were common to a litter and which affected weaning weight and the subsequent mean body weight.

(B) *Maintenance energy cost.* Within each line, maintenance energy cost was calculated as a function of body weight so that any differences merely reflected body weight variations. Since the maintenance cost per unit of body weight increased respectively in the HBW, C and LBW lines the total maintenance energy requirements were proportionally less than the corresponding line differences in body weight. These energy costs (kJ per 24 h) are shown in Table 5. The results of the covariance analysis were consistent with the predicted pattern as they showed that, after adjustment for body weight, the HBW line had the lowest maintenance requirements followed by C and LBW in that order.

(C) *Energy used for growth.* The mean values for the three lines (Table 6) showed that HBW, C and LBW used progressively less energy for depositing additional protein and fat tissue from 4 to 6 weeks of age. Over this period, therefore, between-line differences in mean body weight were positively correlated with the energy used for growth and with growth rate. The differences between litters within lines, however, showed the inverse relationship in that higher mean body weights were associated with smaller amounts of energy utilized for growth. The non-significant regression of energy used for growth on body weight showed that it was unnecessary to apply a covariance correction.

(D) *Total energy accounted for by maintenance and growth.* This character is a compound effect of maintenance and growth. The mean values for the three lines have been given in Table 7 as they are needed for comparisons with DEI and the energy discrepancy. Since the maintenance energy requirement per unit of body weight increased and energy used for growth decreased in the order HBW, C and LBW, there was an accompanying increase in the percentage of the total energy used for maintenance and a decrease in the growth component.

(E) *Digestible energy intake, DEI.* As expected, there was a broad general relationship of DEI to the total energy accounted for by maintenance and growth (Table 8). There was also a significant treatment effect as mice provided with a nest had a lower energy intake.

Between litters within lines, higher mean body weights were associated with a greater DEI. This result was confirmed by the correlations between body weight and DEI shown in Table 9. The regression of DEI on body weight was not significant.

Table 4. *Mean body weights (g) and F values for line and litter-within-line effects*
(Treatment effects and other interactions which were not significant
have not been included.)

Effect	Mean values for each classification			F value and significance‡
	HBW	C	LBW	
Lines ...				
Mean energy usage	27.36	18.85	14.99	22.32**
Between litters within lines				
A†	24.94	15.13	14.93	17.47***
B†	27.86	19.84	15.32	
C†	29.29	21.58	14.72	
	† Litter.			

Table 5. *Maintenance energy costs (kJ per 24 h) in the three lines*

Effect	Mean values for each classification			F value and significance‡
	HBW	C	LBW	
Lines ...				
Mean maintenance energy cost (kJ)	66.02	49.23	43.49	11.39**
Mean maintenance cost adjusted for body weight (kJ)	48.00	53.24	57.50	82.69***
Within cells regression coefficient	2.598			3451.16***

Table 6. *Energy used for growth (kJ per 24 h)*

Effect	Mean values (kJ) for each classification			F value and significance‡
	HBW	C	LBW	
Lines ...				
Mean energy usage	11.08	6.98	5.36	11.79**
Between litters within lines				
A†	12.69	9.09	6.42	9.83***
B†	10.87	6.13	5.21	
C†	9.69	5.72	4.45	
Within cells regression coefficient	—	-0.134	—	1.39 NS

† Litter.

‡ In tables 4, 5 and 6 ***, **, * indicate $P < 0.001$, $P < 0.01$, $P < 0.05$.

(F) *Energy discrepancy*. The analysis of variance showed a large energy discrepancy as a feature of the C line (Table 10). HBW mice used almost all their intake for maintenance and growth while LBW mice showed only a small unaccountable energy loss. Although the treatment effect was non-significant, the difference accounted for most of the energy difference in the DEI of the two groups and mean values have been included for comparative purposes. Mice provided with a nest tended to have a lower energy discrepancy.

The regression in the covariance analysis was negative in relation to body weight. It appears likely, therefore, either that a relatively larger appetite in mice

Table 7. Total energy (kJ per 24 h) accounted for by maintenance and growth

Effect	Mean values for each classification			F value and significance‡
	HBW	C	LBW	
Lines ...				
Mean energy usage	77.11	56.20	48.85	27.34**
% of total due to maintenance	86	88	89	—
% of total due to growth	14	12	11	—

Table 8. Digestible energy intake (kJ per 24 h)

Effect	Mean values for each classification			F value and significance‡
	HBW	C	LBW	
Lines ...				
Mean energy intake	77.33	68.01	52.16	22.98**
Between litters within lines				
A +	76.62	65.76	50.17	4.66***
B +	74.50	68.41	59.91	
C +	80.88	69.85	46.40	
Within cells regression coefficient	0.799			2.49 NS
DEI				
Body weight	2.83	3.61	3.48	—
Treatment ...	No nest	Nest		
Mean energy intake	67.69	63.98		6.85*

† Litter.

‡ Significance levels as for Tables 4–6.

Table 9. Correlations between body weight and energy used for growth or digestible energy intake

	Body weight and energy used for growth	Body weight and DEI
Correlation excluding line and sex, but including litter effects, $\nu = 62$	-0.54	0.42
Correlation (within litter residual variation), $\nu = 56$	-0.16	0.21

eating to compensate for a pre-weaning handicap was more extravagant in energy, or that smaller mice within a line used more energy for thermoregulation. The line differences appeared to be over-corrected in this analysis, particularly HBW and LBW. The treatment differences should not have been subjected to the same bias, however, and the energy discrepancy corrected for body weight was lower when mice were provided with a nest.

(G) *Interrelationships among the energy variables.* The more important of these relationships are summarized in Table 11 which gives the ratios of energy useage to DEI in the three lines and the ratio of growth to maintenance costs.

The HBW line mice had a high total DEI and growth rate; maintenance and

Table 10. *Energy discrepancy (kJ per 24 h)*

Effect	Mean values for each classification			<i>F</i> value and significance†
	HBW	C	LBW	
Lines . . .				
Mean energy discrepancy	0.23	11.80	-3.31	11.59**
Discrepancy adjusted for body weight	7.42	10.20	-2.28	10.98**
Within cells regression coefficient		-1.665		11.75**
Treatment . . .	No nest	Nest		
Mean energy discrepancy	6.33	3.89		2.75 NS
Discrepancy adjusted for body weight	6.60	3.63		4.82*

† Significance levels as for Tables 4-6

Table 11. *Ratios summarizing the partitioning of energy intake in the three selection lines*

Ratios	HBW	C	LBW
Energy cost of maintenance/DEI	0.854	0.724	0.834
Energy used for growth/DEI	0.143	0.103	0.103
Energy used for growth + maintenance/DEI	0.997	0.826	0.937
Energy used for growth/Energy cost of maintenance	0.168	0.142	0.123

growth accounted almost completely for their energy intake. Also, a relatively high proportion of their intake was used for growth, and the growth-to-maintenance ratio was increased in comparison to the other lines. These effects resulted in part from a lower maintenance cost per unit of body weight and in part from the increased rate of growth.

The C line mice had an intermediate DEI and growth rate. Their maintenance and growth utilization were, however, both low in relation to intake. Consequently there was a large energy discrepancy and a low conversion of food energy to new body tissue. The partitioning of energy between growth and maintenance for the C line was intermediate between the other two lines.

The LBW line mice had an overall low DEI and growth rate. Relative to intake they had a high energy maintenance cost and low energy utilization for growth. This effect resulted from their high maintenance requirement per unit of body weight and low growth rate. Maintenance and growth accounted for about 94 % of intake and there was a minor energy discrepancy. The growth to maintenance ratio was decreased in comparison with the other two lines.

When a nest was provided there was a reduction in DEI of about 3.6 kJ and the energy discrepancy was lower by approximately 2.5 kJ. There were no other significant effects and the difference represented the extra energy required for thermoregulation without a nest in the mouse house temperature of 24.5 °C.

4. DISCUSSION

There are no obvious sources of bias in the line estimates of digestible energy intake and energy used for growth. Calculations of protein and fat deposition were based on independent regressions for males and females, which showed regular and repeatable patterns within each line. Although there is some variation in different estimates of energy required for protein deposition, Pullar & Webster (1977) stress that their figure is almost identical to the preferred value suggested earlier by Kielanowski (1976). Any slight error would be applied equally to all genotypes and sexes and would have a negligible effect on comparisons between lines. In addition, growth energy was a small proportion of the total budget so any minor inaccuracies should not have a marked effect on the estimated patterns of useage.

The figures for maintenance energy costs were critical for the accuracy of the analysis. They were derived from only one estimation for each line and in particular, with the C line an underestimation of maintenance needs would have given an overestimation of the energy discrepancy. This aspect was investigated by analysing the weight changes of the lines over the three-weekly, fixed intake test period. The C line showed a slightly higher weight gain (0.07 g compared with 0.05 g in the selection lines) suggesting that 1.35 g of feed per gram of body weight might have been a slight *over*-estimate of maintenance requirements. The line differences in this analysis were, however, completely non-significant.

Also, it is arguable that food intake should have been related to a theoretical metabolic body weight such as $W^{0.75}$, rather than to absolute body weight. Figures obtained from experimental feeding trials were, however, used for the basic maintenance requirements of the three lines. These figures represented maintenance energy on restricted feeding together with a fraction required for thermoregulatory heat production at the experimental temperature. Since a different figure was used for each line this approach has corrected for between-line differences in body weight.

A second possible source of bias is that the within-line variance might be altered if maintenance energy requirements were calculated as a function of $W^{0.75}$ rather than as a function of $W^{1.0}$. A detailed discussion of the exponential relating metabolic requirements to body weight (Mount, 1968) indicates that, in young growing mammals as opposed to adult mammals of different body weight the exponential coefficient may be near unity. In general, the coefficient is found to be lower in older mammals and in those on a lower plane of nutrition. Since mice on restricted feeding were used to calculate our maintenance energy requirements, the exponential applying to that group could be lower than for the growing mice on *ad libitum* feeding used in the present work. Even on restricted feeding however, there were no positive within-line correlations between body weight at the beginning of the trial period and any subsequent weight change. Such a relationship would be predicted if absolute body weight gave an above-maintenance allowance to larger mice and vice versa; consequently the lack of any correlation suggests an exponential close to unity.

Calculations of energy balance did not allow for urinary losses (Rothwell & Stock, 1981) but this effect has been neglected in other studies (e.g. Trayhurn *et al.* 1982*a*)

and was considered unlikely to have made any significant contribution to the line differences.

It is evident that at a temperature of 24.5 ± 1 °C the three lines used their food energy in different ways. C mice on *ad libitum* feeding apportioned 72 % of their DEI for maintenance and a further 10 % for body tissue deposition. Included in the 'energy discrepancy' was 18 % which indicates a major loss through extra heat production on an unrestricted diet. At present it is not known whether this results from thermoregulatory stimulation that could be conserved on a maintenance ration, from dietary thermogenesis or from some other factor causing a relatively large increase in maintenance requirements on *ad libitum* feeding.

HBW mice were larger, ate more and grew faster, but almost all their DEI was used for basic maintenance and growth. The proportions of their food energy used for maintenance (85 %) and for growth (14 %) were both higher than with C mice. Since the HBW mice appeared to divert practically all their energy intake above maintenance needs into growth they were similar in this respect to obese (*ob/ob*) mutants (James & Trayhurn, 1981). At present it is not possible to decide whether the genetic difference between C and HBW operates through the same system as the *ob/ob* genotype, nor whether it results from the effects of one or several major 'obese type' genes, from a quantitative polygenic control or from a combination of both these systems.

LBW mice were the smallest, their total intake was lower and they grew more slowly; also they had the least fat and a consistent tendency for more protein in the body (Malik, 1984). Compared with the C line their basic maintenance requirements were high in relation to body weight, but they had a low energy discrepancy and diverted a similar proportion of their DEI to tissue deposition and growth. The low energy discrepancy suggested that in this line too the energy intake above maintenance was largely diverted to growth and away from unaccountable losses. When compared with HBW however, there was less fat synthesis and more protein deposition, suggesting a fundamental alteration in the growth hormone-insulin balance with possible involvement of the thyroid system. Growth hormone promotes general growth, but it is thought to have an intrinsic lipolytic activity (Hart *et al.* 1978; Paladini, Pena & Retegui, 1979) although the effects may result in part from impurities such as thyroid stimulating hormone (Lee, Ranachandran & Li, 1974). Conversely, insulin stimulates lipogenesis but inhibits lipolysis (Bassett, 1975). The results therefore indicate that a more effective conservation of energy intake may be accompanied by different patterns of growth that depend on changes to the various hormone systems affecting appetite and tissue deposition.

This work does not support a simple model to explain the results of selection for body weight or weight gain in terms of the energy cost of laying down new muscle or fat. The C line mice had a discrepancy energy cost that exceeded their growth requirements, but genetic change in HBW and LBW appeared to enable this energy to be utilized for tissue deposition. Alternatively, selected mice that have a less wasteful energy budget may fit the model proposed by Hayes & McCarthy (1976) and Roberts (1979). The exceptions to this model found by McPhee *et al.* (1980) and Yüksel *et al.* (1981) could have resulted from redirection

of excess energy to tissue synthesis which allowed an increase in both growth and the proportion of body fat on a fixed dietary intake. The present studies therefore, support the concept that growth efficiency can be increased by diverting a greater amount of digestible energy into tissue synthesis. In addition, the results showed that maintenance required from 72 to 85% of the total food energy. Since only a small proportion of DEI was used for growth, minor savings would be expected to have a large effect on the rate and pattern of tissue deposition.

The validity of experiments using mice as a model for growth and carcass composition of livestock would appear to depend on the physiological systems that partition the DEI into different end uses and the relative extent of genetic variation in each system. These aspects are largely unknown although it has been thought that livestock where past artificial selection has placed at least some emphasis on feed efficiency, may be more efficient in their energy usage. The results of Frisch & Vercoe (1981) who compared growth in relation to level of nutrition in British and Brahman crossbred beef cattle can be explained by variations in DEI relative to the needs of basal maintenance, the genetic potential for tissue deposition and susceptibility to disease. Corbett *et al.* (1982) however, reported a variation in the basal maintenance requirement of sheep with level of feed intake. In addition, Graham *et al.* (1974) have inferred that growing ruminants have an appreciable energy expenditure which is associated with the nutritional and growth state of the individual.

Within each line the between-litter differences in mean body weight appear likely to be related mainly to the milk production of the dams. Following weaning there was marked compensatory growth. Such effects are well documented in livestock (Wilson & Osbourn, 1960) and appear to result from an intake that is high in relation to the body weight of handicapped individuals (Williams & Senior, 1979).

The only effect of reducing thermoregulatory energy cost by providing a nest was to lower DEI by approximately 3.6 kJ. The saving in thermogenesis appeared as a reduction in energy discrepancy of about 2.5 kJ. These minor differences contrast with the major thermoregulatory energy cost reported by Trayhurn *et al.* (1982*b*) when virgin female mice aged three months were kept at 21 °C compared with a thermoneutral temperature of 33 °C. Provision of a nest, however, does not appear to have provided adequate insulation against cold. Also the temperature of 24.5 °C used in the present study would have been less stressful to mice than 21 °C.

Our results need confirmation with a more rigorous cold stress since the energy usage of the lines may alter significantly when survival requires increased body heat production. In addition, the precise nature of the 'energy discrepancy' components that produce the differences between the HBW, C and LBW lines is unknown, but will be the subject of future investigations.

The authors wish to acknowledge the technical help provided by Mr D. K. Fredline and the statistical advice given by Dr V. J. Bofinger, Department of Mathematics. This work was supported by a research grant from the University of New England.

REFERENCES

- BAKER, R. L., CARTER, A. H. & COX, E. H. (1979). The effects of selection for body weight at different ages on fat deposition in mice. *New Zealand Society of Animal Production* **39**, 118–128.
- BARR, H. G. & McCRACKEN, K. J. (1982). Energy balance and body composition changes in growing rats kept at 24 °C and offered a varied diet. In *Energy Metabolism of Farm Animals* (ed. A. Ekern and F. Sundstøl), pp. 160–163. EAAP Publ. no. 29.
- BASSETT, J. M. (1975). Dietary and gastro-intestinal control of hormones regulating carbohydrate metabolism in ruminants. In *Digestion and Metabolism in the Ruminant* (ed. I. W. McDonald and A. C. I. Warner), pp. 383–398. Armidale: University of New England Publishing Unit.
- BIONDINI, P. E., SUTHERLAND, T. M. & HAVERLAND, L. H. (1968). Body composition of mice selected for rapid growth rate. *Journal of Animal Science* **27**, 5–12.
- CORBETT, J. L., FURNIVAL, E. P. & PICKERING, F. S. (1982). Energy expenditure at pasture of shorn and unshorn Border Leicester ewes during late pregnancy and lactation. In *Energy Metabolism of Farm Animals* (ed. A. Akern and F. Sundstøl), pp. 34–37. EAAP Publ. no. 29.
- DAWSON, N. J., STEPHENSON, S. K. & FREDLINE, D. K. (1972). Body composition of mice subjected to genetic selection for different body proportions. *Comparative Biochemistry and Physiology* **42 B**, 679–691.
- FALCONER, D. S. (1953). Selection for large and small size in mice. *Journal of Genetics* **51**, 470–501.
- FRISCH, J. E. & VERCOE, J. E. (1981). Animal breeding for improved productivity. In *Nutritional Limits to Animal Production from Pasture* (ed. J. B. Hacker). Proceedings of International Symposium (Brisbane, Aust.). Commonwealth Agricultural Bureaux.
- GRAHAM, N. MCC., SEARLE, T. W. & GRIFFITHS, D. A. (1974). Basal metabolic rate in lambs and young sheep. *Australian Journal of Agricultural Research* **25**, 957–971.
- HART, I. C., BINES, J. A., MORANT, S. V. & RIDLEY, J. L. (1978). Endocrine control of energy metabolism in the cow: Comparison of the levels of hormones (prolactin, growth hormone, insulin and thyroxine) and metabolites in the plasma of high and low yielding cattle at various stages of lactation. *Journal of Endocrinology* **77**, 333–345.
- HARVEY, W. R. (1979). Users guide for LSML76: mixed model least squares and maximum likelihood computer program. Ohio State University (Mimeo.).
- HERVEY, G. R. & TOBIN, G. (1983). Luxuskonsumption, diet-induced thermogenesis and brown fat: a critical review. *Clinical Science* **64**, 7–18.
- HAYES, J. F. & MCCARTHY, J. C. (1976). The effects of selection at different ages for high and low body weight on the pattern of fat deposition in mice. *Genetical Research* **27**, 389–403.
- HETZEL, D. J. S. & NICHOLAS, F. W. (1979). Selection of mice for growth rate under *ad libitum* or restricted feeding. *Proceedings – Australian Association of Animal Breeding and Genetics* **1**, 35–36.
- HETZEL, D. J. S. & NICHOLAS, F. W. (1982). Direct and correlated responses to selection for post weaning weight gain on *ad libitum* or restricted feeding in mice. *Theoretical and Applied Genetics* **63**, 145–150.
- HULL, P. (1960). Genetic relations between body weight and carcass fat in mice. *Journal of Agricultural Science* **55**, 317–321.
- JAMES, W. P. T. & TRAYHURN, P. (1981). Thermogenesis and obesity. *British Medical Bulletin* **37**, 43–48.
- KIELANOWSKI, J. (1976). Energy cost of protein deposition. In *Protein Metabolism and Nutrition* (ed. D. J. A. Cole, K. N. Boorman, P. J. Buttery, D. Lewis, R. J. Neale and H. Swan), pp. 207–215. EAAP Publ. no. 16.
- LEE, V., RANACHANDRAN, J. & LI, C. H. (1974). Does bovine growth hormone possess rapid lipolytic activity? *Archives of Biochemistry and Biophysics* **161**, 222–226.
- LYNCH, C. B. & HEGMANN, J. P. (1972). Genetic differences influencing behavioural temperature regulation in small animals. I. Nesting by *Mus musculus*. *Behavioral Genetics* **2**, 43–53.
- LYNCH, C. B. & POSSIDENTE, B. P. (1978). Relationships of maternal nesting to thermoregulatory nesting in house mice (*Mus musculus*) at warm and cold temperatures. *Animal Behaviour* **26**, 1136–1143.
- MCCARTHY, J. C. (1978). In *Genetic Models of Obesity in Laboratory Animals*. Symposium of the Medical Research Council Laboratory Animals Centre. Great Britain.

- MCPHEE, C. P., TRAPPETT, P. C., NEILL, A. R. & DUNCALFE, F. (1980). Changes in growth, appetite, food conversion efficiency and body composition of mice selected for high post weaning gain on restricted feeding. *Theoretical and Applied Genetics* **57**, 49–56.
- MALIK, R. C. (1984). Genetic and physiological aspects of growth, body composition and feed efficiency in mice. Ph.D. thesis, University of New England.
- MOUNT, L. E. (1968). *The Climate Physiology of the Pig*, pp. 202–211. London: Arnold.
- NICHOLLS, D. G. (1979). Brown adipose tissue mitochondria. *Biochimica et Biophysica Acta* **549**, 1–29.
- PALADINI, A. C., PENA, C. & RETEGUI, L. A. (1979). The intriguing nature of the multiple actions of growth hormone. *Trends in Biochemical Sciences* **4**, 256–260.
- PULLAR, J. D. & WEBSTER, A. J. F. (1977). The energy cost of protein and fat deposition in the rat. *British Journal of Nutrition* **37**, 355–363.
- ROBERTS, R. C. (1979). Side effects of selection for growth in laboratory animals. *Livestock Production Sciences* **6**, 93–104.
- ROTHWELL, N. J. & STOCK, M. J. (1979). A role for brown adipose tissue in diet-induced thermogenesis. *Nature* **281**, 31–35.
- ROTHWELL, N. J. & STOCK, M. J. (1981). Regulation of energy balance. *Annual Review of Nutrition* **1**, 235–256.
- ROTHWELL, N. J. & STOCK, M. J. (1982). Effect of chronic food restriction on energy balance, thermogenic capacity, and brown-adipose-tissue activity in the rat. *Bioscience Reports* **2**, 543–549.
- SUTHERLAND, T. M., BIONDINI, P. E. & WARD, G. M. (1974). Selection for growth rate, feed efficiency and body composition in mice. *Genetics* **78**, 525–540.
- TRAYHURN, P., THURLBY, P. L. & JAMES, W. P. T. (1977). Thermogenic defect in pre-obese ob/ob mice. *Nature* **266**, 60–62.
- TRAYHURN, P., JONES, P. M., MCGUCKIN, M. M. & GOODBODY, A. E. (1982a). Effects of overfeeding on energy balance and brown fat thermogenesis in obese (ob/ob) mice. *Nature* **295**, 323–325.
- TRAYHURN, P., DOUGLAS, J. B. & MCGUCKIN, M. M. (1982b). Brown adipose tissue thermogenesis is 'suppressed' during lactation in mice. *Nature* **298**, 59–60.
- WILLIAMS, V. J. & SENIOR, W. (1979). Changes in body composition and efficiency of food utilization for growth in young adult female rats before, during and after a period of food restriction. *Australian Journal of Biological Sciences* **32**, 41–50.
- WILSON, P. N. & OSBOURN, D. F. (1960). Compensatory growth after undernutrition in mammals and birds. *Biological Reviews* **35**, 324–363.
- YÜKSEL, E., HILL, W. G. & ROBERTS, R. C. (1981). Selection for efficiency of feed utilisation in growing mice. *Theoretical and Applied Genetics* **59**, 129–137.