SECTION 3

A COMPARISON OF THE LINES SELECTED FOR INCREASED AND DECREASED EIGHT WEEK BODY WEIGHT

II. FEED AND ENERGETIC EFFICIENCY

3.1 INTRODUCTION

Many selection experiments with mice using body weight or weight gain as the selection criterion report that the differences between the selected and unselected lines in growth characteristics are associated with changes in food consumption and efficiency of feed conversion. The general pattern seems to be that, compared to the control line mice, mice of the lines selected for high body weight or increased growth rate consume more food per unit of time and grow at a faster rate per unit of food consumed over a given time period. The lines selected for low body weight or decreased growth rate show decreases both in feed intake and feed efficiency (Fowler, 1962; Lang and Legates, 1969; Sutherland *et al.*, 1970; Timon and Eisen, 1970; Timon *et al.*, 1970; Brown and Frahm, 1975; Eisen *et al.*, 1977; Kownacki *et al.*, 1977; Hetzel, 1978; Roberts, 1981).

Gross feed efficiency is calculated as a ratio of gain to feed intake, whereas energetic efficiency is calculated by transforming feed consumption and body tissue deposition into units of energy. Gross and energetic efficiencies are influenced by: (1) the level of feed intake, (2) digestibility, (3) the partitioning of feed intake between maintenance and growth requirements and (4) composition of body weight gain in terms of lean and fat. Almost all the energy in the body is stored as fat and protein. The energy content of protein is about 60 percent that of fat. But, as tissue protein is combined with about 80 percent water in the lean, the energy density of fat is about eight times that of lean (Webster, 1980). Therefore, differences between animals in the composition of gain may lead to large differences in their body energy contents. Because feed efficiency in terms of gain in body weight per unit of feed intake does not take account of differences in the energetic composition of the body weight gain, the animals that show high feed efficiency are not necessarily those with a high energetic efficiency.

There are a number of reports showing that the increased feed intake of mice selected for high body weight or faster growth resulted in higher weight gain and efficiency (Fowler, 1962; Timon and Eisen, 1970; Roberts, 1981). Only minor variations in digestibility in the mice (Flowler, 1962; Sutherland *et al.*, 1970; Stanier and Mount, 1972) and even between species (Blaxter, 1968) have been reported.

Between-line differences in feed and energy requirement for maintenance have been reported. Except for one study in mice (Canolty and Koong, 1977) in which selection for larger size did not alter maintenance requirements of selected mice, evidence from other reports suggests that larger mice have less maintenance requirement on a per unit of body weight basis. Canolty and Koong (1977) assumed that the maintenance requirements of their lines of mice were proportional to 0.75 power of bodyweight. This assumption is common but of questionable accuracy in growing animals (Brody, 1945; Park, 1982). Stephenson and Malik (1984) using mice selected for high and low eight week body weight and an unselected line reported significant differences for maintenance energy requirement between the three lines. Trayhurn (1980) found that the maintenance energy requirement in a genetically obese line of mice was significantly influenced by the temperature. Similar observations were made by McCarthy (1980) on his selected large and small mice. Lynch and Roberts (1984) related the thermoregulatory advantage of large size to lower thermo-regulatory heat production.

There are disagreements between the availabe reports on the efficiency of energy utilization for growth between lines. Timon *et al.* (1970) observed no differences between a line selected for postweaning weight gain and a control line in the efficiency of tissue growth after adjusting for maintenance requirements. Canolty and Koong (1977) in a comparison between a line selected for faster postweaning gains and the control line and Stephenson and Malik (1984) between the body weight selection lines and the control line reported significant differences for energy used for growth.

This section presents a comparison between lines of mice selected for high and low eight week body weight and a randombred control line for postweaning feed consumption, weight gain, feed efficiency and energetic efficiency. The results are presented in relation to four experiments for the determination of: (1) feed and energetic efficiencies, (2) maintenance feed requirements of growing mice, (3) maintenance feed requirements of adult mice and (4) digestibility of feed in the three lines of mice.

3.2 EXPERIMENT 1: Efficiency of feed and energy utilization

3.2.1 MATERIALS AND METHODS

The origin, selection procedure, breeding, feeding and management of the low body weight line (L), high body weight line (H) and the randombred line (R) used in this study have been described in detail in Section 2.2.

The mice sampled from each line in this experiment were those used for body composition analysis presented in the preceding section. The number of mice allotted to each line-age subclass is given in Table 3.1. The numbers decreased in successive ages due to serial slaughter of mice at different ages for body composition analyses. Body weight and feed consumption measurements on individually caged mice were recorded to the nearest 0.1 g at weekly intervals between the ages of 3 and 8 weeks. The mice had *ad libitum* access to water and food. The food container, originally used by Hetzel (1978), consisted of a shoe cream glass jar of 25 g capacity with a perforated metal disc placed over the feed and a lid to minimize spillage. Mice were fed three times weekly and weekly feed intake and body weight gain were recorded. At every feeding time the left-over food was weighed and feed consumption measured from the difference between the food offered and the food left over. No bedding was provided, so that any spilled food could be detected. There was very little spillage however and the amount was not recorded. Any spilled food was carefully

isolated from the excreta and replaced in the feeding jar before weighing. Weekly feed efficiency was calculated as the ratio of weight gain to feed intake (G/F) during 3 to 8 weeks of age.

Table 3.1 Number of mice available from each line for weight gain, feed intake, feed efficiency and energetic efficiency analyses at different age intervals.

Trait		Age in Weeks[1]					Age in Weeks[2]	
Line	Sex	3-4	4-5	5-6	6-7	7-8	3-5	5-8 and 3-8
L	M	62	52	43	29	20	10	20
	F	55	44	34	24	16	11	16
H	M	57	47	37	27	16	10	16
	F	56	46	36	25	14	10	14
R	M	61	51	41	30	19	10	19
	F	63	54	44	35	26	9	26

Traits: 1 Weight Gain, Feed Intake, Feed Efficiency
2 Energetic Efficiency

Energy content of the whole body of each mouse was obtained from the body composition analyses. Total body energy (BE) was determined as (fat weight x 39.3 kJ) + (protein weight x 23.5 kJ), where 39.3 and 23.5 kJ respectively refer to the energy content per gram of fat and protein (Pullar and Webster, 1977). Three-week body composition and body weight data were used for obtaining regression equations to express fat weight and protein weight as a function of body weight at this age separately for each line. These equations were then utilised to predict BE at 3-week body weight of the mice slaughtered at 5 and 8 weeks of age. This technique has been used earlier by Eisen *et al.* (1977) and Bandy and Eisen (1984). A similar procedure was adopted for calculating BE at 5 weeks of age for mice slaughtered at 8 weeks of age (Table 3.2). The difference between the individual's measured BE at 5 weeks of age and predicted BE at 3 weeks, and between measured BE at 8 weeks

and predicted BE at 5 weeks provided the estimates of change in BE (ΔBE) during 3 to 5, 5 to 8, and 3 to 8 weeks of age.

Table 3.2 Regression equations for predicting fat and protein weights at 3 and 5 weeks as a function of body weight at these ages.

Line	Fat Weight	r	Protein Weight	r
		Three weeks		
L	0.122 BW*- 0.326 ±0.016 ±0.133	0.85	0.157 BW + 0.121 ±0.014 ±0.121	0.92
H	0.090 BW + 0.118 ±0.036 ±0.476	0.49	0.142 BW + 0.346 ±0.010 ±0.137	0.95
R	0.079 BW + 0.198 ±0.016 ±0.172	0.77	0.148 BW + 0.213 ±0.012 ±0.138	0.94
		Five weeks		
L	0.110 BW - 0.497 ±0.029 ±0.451	0.67	0.171 BW - 0.039 ±0.015 ±0.232	0.94
H	0.132 BW - 0.930 ±0.018 ±0.461	0.69	0.205 BW - 0.913 ±0.019 ±0.479	0.93
R	0.119 BW - 0.602 ±0.033 ±0.682	0.65	0.183 BW - 0.258 ±0.016 ±0.332	0.94

* Body weight

All regression coefficients for slopes were significant.

Energetic efficiency was measured as a ratio of gain in body energy to digestible energy intake in percentage terms (100 x ΔBE/DEI).

Data for weight gain, feed intake and feed efficiency collected at weekly intervals from 3 to 8 weeks were analysed by least-squares procedures using the following model:

$$Y_{ijkl} = \mu + L_i + S_j + A_k + (LS)_{ij} + (LA)_{ik} + (SA)_{jk} + e_{ijkl}$$

where Y_{ijkl} = l^{th} observation of the ijk^{th} subclass

μ = Overall mean

L_i = Fixed effect of the i^{th} line (i = 1,3)

S_j = Fixed effect of the j^{th} sex (j = 1,2)

A_k = Fixed effect of the k^{th} age period (k = 1,5)

$(LS)_{ij}$, $(LA)_{ik}$ and $(SA)_{jk}$ are two-way interactions involving line, sex and age

e_{ijkl} = Random error (NID, O, σ^2)

The data for ΔBE, DEI and Energetic efficiency were summarised into time intervals of 3-5, 5-8 and 3-8 weeks of age to represent early postweaning period, late postweaning period and total postweaning period upto 8 weeks of age , respectively. Statistical analyses of these data were carried out by using the following model:

$$Y_{ijk} = \mu + L_i + S_j + (LS)_{ij} + e_{ijk}$$

Where Y_{ijk} = k^{th} observation of the ijk^{th} subclass

μ = Overall mean

L_i = Fixed effect of the i^{th} line (i = 1,3)

S_j = Fixed effect of the j^{th} sex (j = 1,2)

$(LS)_{ij}$ = is two way interaction involving line and sex

e_{ijk} = Random error (NID, O, σ^2)

The efficiency of energy utilization for growth was estimated by regression analysis using the following equation:

$$\Delta BE = bo + b_1 DEI$$

The slope of the regression line (b_1) describes the efficiency of utilization of DEI above maintenance requirement. Differences in the slopes of the regression lines were tested to compare the efficiency of energy utilization of the L, H and R mouse lines and between sexes within each line. Maintenance energy requirements of the three lines can be calculated by extrapolation of the regression line to zero gain, but this procedure was considered unsatisfactory because of the extrapolation involved and was not used.

The maintenance energy requirements (kJ) per gram of body weight per week were estimated for each mouse separately by subtracting the energetic cost of lean and adipose tissue deposition from the total digestible energy intake. The following formula was used for the calculation of maintenance requirements based on the assumption that in mice, energy not required for depositing protein and fat is used for maintenance (Trayhurn, 1980).

$$\text{Maintenance requirement} = \frac{\text{DEI} - 53.4\ \text{kJ} \times \text{fat gained (g)} - 52.9\ \text{kJ} \times \text{protein gained (g)}}{5 \times \text{Body weight}}$$

where, 53.4kJ and 52.9kJ refer to the energy costs of depositing 1 gram of fat and protein respectively (Pullar and Webster, 1977), and 5 is the number of weeks in the 3 to 8 week period of this study. The body weight is the mean weight of the individual mouse over the 3 to 8 week period. The analyses of variance were carried out for line and sex difference.

3.2.2 RESULTS

The least-squares averages for weekly weight gain, feed intake and gross efficiency of the L, H and R lines are shown in Figure 3.1 and in Table 3.3. Sex differences are presented in Appendix T. Analyses of variance are presented in Table 3.4.

Line comparisons for average weekly gains were significant from 3 to 7 weeks with the H line growing faster than the R and L lines during this period. The differences between the R and L lines were significant for 3-4 and 6-7 weeks. Sex effects were important up to 7 weeks of age with males showing faster gains than the females and this contributed to a significant sex x age interaction. Line x sex interaction was significant and was caused by comparatively larger sex differences in the weight gain of the H line than the R and L lines. Line x age interaction resulted from rapid gains in the early period of postweaning growth which were more rapid in the H line.

Weekly feed consumption curves of the three lines are characteristic, rising almost linearly to about 6 weeks of age after which the changes in mean intake of the lines were small. Line differences were significant at every age of measurement. Over a period of 3 to 8 weeks, the H line mice consumed 14 and 24 percent more food and gained 33 and 73 percent more weight

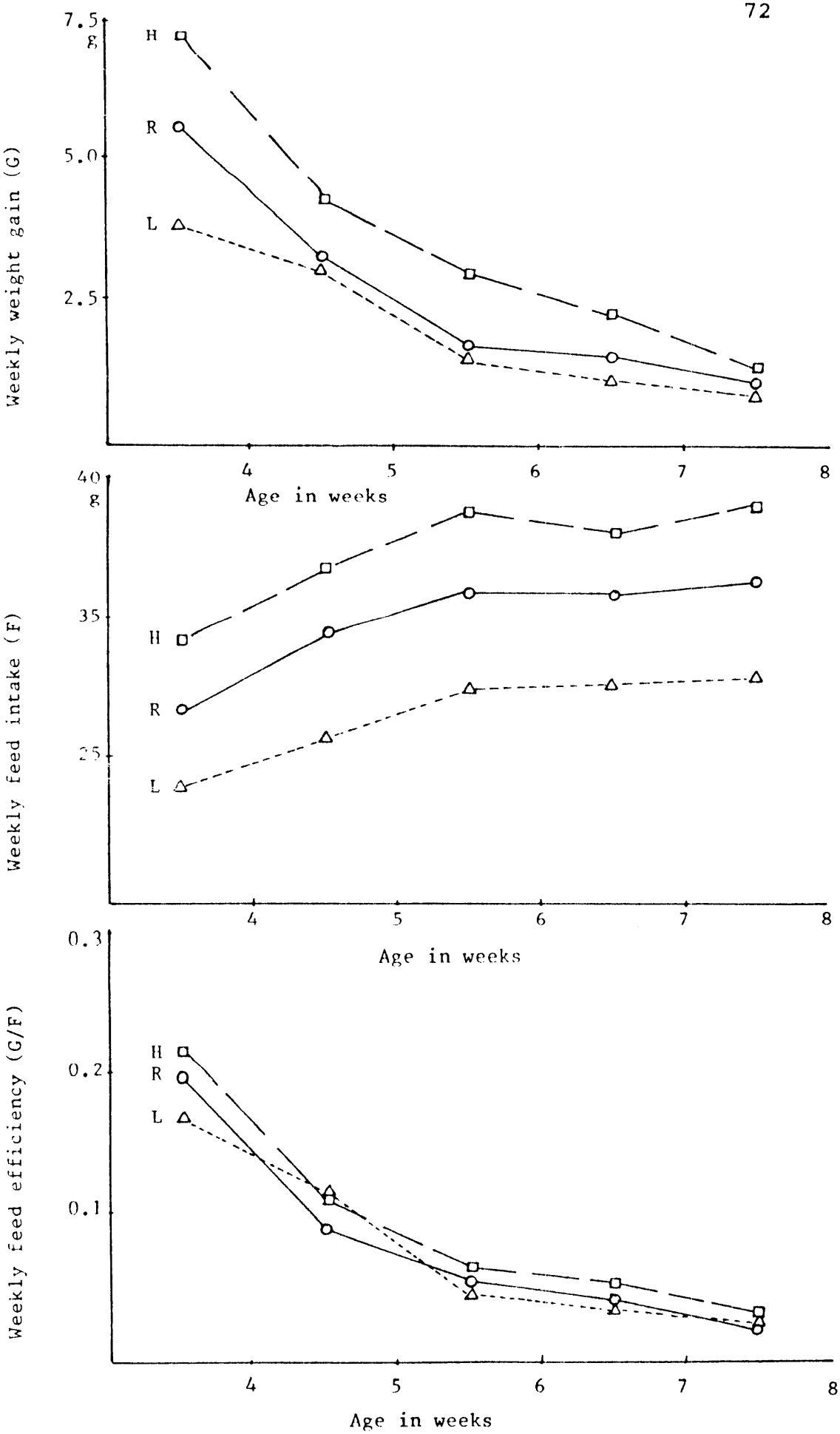

Figure 3.1 Averages of weight gain, feed intake and feed efficiency per week between the ages of 3 and 8 weeks. Lines: H and L are high and low body weight selection lines and R is the unselected line

Table 3.3 Least-squares means ± s.e. for weight gain, feed intake and feed efficiency

	Age (weeks)					
	3-4	4-5	5-6	6-7	7-8	3-8
Weight Gain						
L	3.80 ± 0.096a*	3.03 ± 0.105a	1.46 ± 0.121a	1.13 ± 0.142a	0.97 ± 0.177a	10.39 ± 0.22a
H	7.19 ± 0.098b	4.23 ± 0.107b	2.93 ± 0.120b	2.27 ± 0.144b	1.34 ± 0.201a	17.95 ± 0.42b
R	5.56 ± 0.093c	3.11 ± 0.101a	1.68 ± 0.121a	1.54 ± 0.132c	1.05 ± 0.172a	12.93 ± 0.24c
Feed Intake						
L	22.69 ± 0.336a	26.39 ± 0.369a	30.04 ± 0.424a	30.11 ± 0.50a	30.71 ± 0.62a	139.93 ± 0.84a
H	33.08 ± 0.343b	38.21 ± 0.376b	42.46 ± 0.421b	40.96 ± 0.50b	42.83 ± 0.707b	197.51 ± 1.34b
R	28.13 ± 0.327c	33.78 ± 0.353c	36.68 ± 0.426c	36.41 ± 0.463c	37.80 ± 0.603c	172.77 ± 0.93c
Feed Efficiency						
L	0.168 ± 0.003a	0.115 ± 0.003a	0.049 ± 0.004a	0.037 ± 0.005a	0.031 ± 0.006a	0.080 ± 0.002a
H	0.216 ± 0.003b	0.111 ± 0.004a	0.067 ± 0.004b	0.055 ± 0.005b	0.032 ± 0.007a	0.096 ± 0.002b
R	0.198 ± 0.003c	0.093 ± 0.003b	0.057 ± 0.004a	0.042 ± 0.004a	0.028 ± 0.006a	0.083 ± 0.002a

* Averages bearing similar lower-case letters within each age interval do not differ significantly

Table 3.4 Analyses of variance showing degrees of freedom, mean squares and tests of significance for weight gain, feed intake and feed efficiency between 3 and 8 weeks of age.

Source of Variation	d.f.	Mean Squares		
		3-8 Week Weight Gain	3-8 Week Feed Intake	3-8 Week Feed Efficiency
Line	2	175.01**	10014.54**	0.022**
Sex	1	105.54**	686.18**	0.079**
Age	4	761.96**	3652.30**	1.118**
Line x Sex	2	5.80**	83.44**	0.001
Line x Age	8	28.62**	23.66	0.013**
Sex x Age	4	22.26**	65.68**	0.028**
Experimental Error	1133	1.09	13.44	0.001

** $P < 0.01$

than the R and L lines respectively. The R line mice consumed 23 percent more food to give an increase of 14 percent in body weight compared with the L mice. Figure 3.2 shows average feed intake and weight gain of L, H and R lines from 3 to 8 weeks. Although the R line had a higher weight gain than the L line it grew more slowly and consumed more food than the average of the H and L lines. Males ate more than the females at equal ages because of their bigger size. Line x sex and sex x age interactions were significant because (i) the sex effects were more pronounced in the H line and (ii) the sex effects were larger up to 6 weeks of age in the three lines and smaller from 6 to 8 weeks of age.

Both line and sex had a significant effect on feed efficiency at different ages. The H line was more efficient in feed utilization than both R and L lines. The overall differences between the R and L lines were small and not significant. Feed efficiency of the male mice was higher than the females. Sex x age interactions were significant mainly because of significant sex differences at some ages and none at other ages. Most of the contribution to line x age interaction came from differences in feed efficiency between lines in the earlier portion of the growth period studied.

Means and standard errors for ΔBE, DEI and energetic efficiency (ΔBE/DEI) of the lines and sexes for 3-5, 5-8 and 3-8 weeks are given in Tables 3.5 and 3.6. Analyses of variance for these traits are presented in Table 3.7.

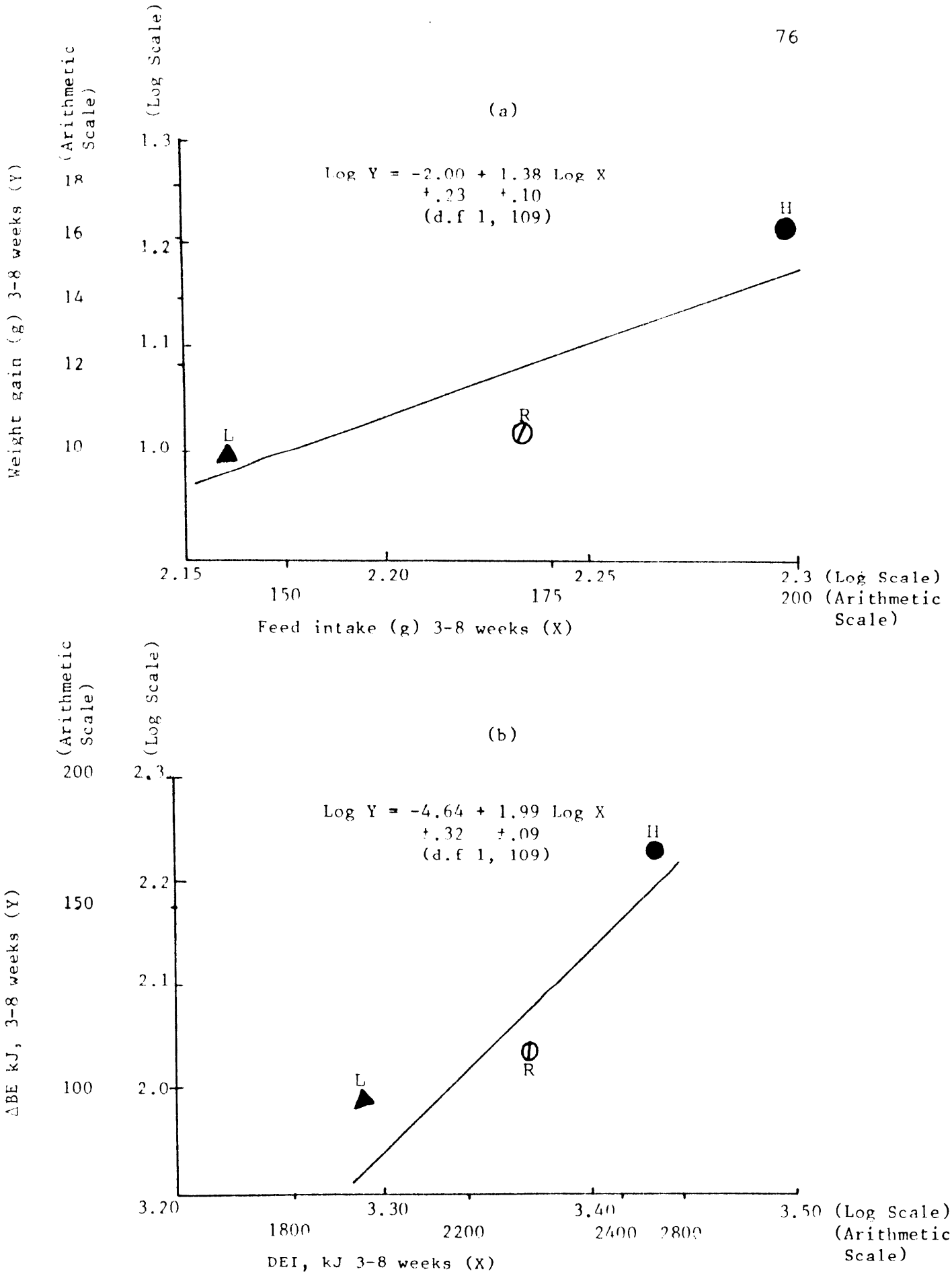

Figure 3.2 Least-squares regressions of (a) log weight gain on log feed intake (b) log increase in body energy (log ΔBE) on log digestible energy intake (log DEI) for the data pooled over the three lines showing lower feed and energetic efficiency of the R line relative to the L and H lines.

Lines: L and H = Low and high body weight selection lines
R = Randombred control line

Table 3.5 Estimates of means ± s.e. for change in body energy (ΔBE), digestible energy intake (DEI) and efficiency of energy utilization (EEF) during 3-5 and 3-8 weeks of age.

Line	Sex	Increase in body energy (ΔBE), kJ		Digestible energy intake (DEI), kJ		Energetic Efficiency (EEF) %	
		3-5 Week	3-8 Week	3-5 Week	3-8 Week	3-5 Week	3-8 Week
L	M	48.92 ± 3.25a	98.15 ± 5.99a	676.50 ± 16.72a	1998.15 ± 63.31a	7.26 ± 0.35a	4.89 ± 0.14a
	F	33.85 ± 3.64b	71.93 ± 6.70b	651.74 ± 18.69a	1870.75 ± 83.98a	5.16 ± 0.40b	3.84 ± 0.16b
	Both	42.22 ± 2.42A	86.50 ± 4.47A	665.49 ± 12.46A	1941.52 ± 47.19A	6.33 ± 0.26A	4.43 ± 0.11A
H	M	98.89 ± 3.64a	180.51 ± 6.70a	1012.77 ± 18.69a	2785.17 ± 83.98a	9.72 ± 0.40a	6.41 ± 0.16a
	F	71.51 ± 3.89b	157.66 ± 7.16b	938.67 ± 19.98b	2550.70 ± 75.67b	7.59 ± 0.42b	6.13 ± 0.17a
	Both	86.11 ± 2.66B	169.85 ± 4.89B	978.19 ± 13.65B	2675.75 ± 51.70B	8.73 ± 0.29B	6.28 ± 0.12B
R	M	75.79 ± 3.34a	129.94 ± 6.15a	870.67 ± 17.15a	2386.53 ± 64.96a	8.71 ± 0.36a	5.42 ± 0.15a
	F	53.01 ± 2.85b	94.37 ± 5.26b	805.63 ± 14.66b	2274.23 ± 55.53a	6.60 ± 0.31b	4.08 ± 0.12b
	Both	62.63 ± 2.17C	109.39 ± 4.00C	833.09 ± 11.15C	2321.65 ± 42.21C	7.49 ± 0.24C	4.65 ± 0.09A

Dissimilar lower case letters for each trait within a line represent significant differences between sexes. Dissimilar upper case letters for each trait represent differences between lines. All differences were tested at 5 percent level of significance.

Table 3.6 Estimates of means ± s.e. for change in body energy (ΔBE), digestible energy intake (DEI) and efficiency of energy utilization (EEF) during 5-8 weeks of age.

Line	Sex	Increase in Body Energy (ΔBE) kJ	Digestible Energy Intake (DEI) kJ	Energetic Efficiency (EEF) %
L	M	49.23 ± 5.54a	1321.65 ± 61.10a	3.71 ± 0.27a
	F	38.08 ± 6.19a	1219.01 ± 68.31a	3.13 ± 0.31a
	Both	44.27 ± 3.69A	1276.03 ± 45.54A	3.45 ± 0.20A
H	M	81.63 ± 6.19a	1772.41 ± 68.31a	4.42 ± 0.31a
	F	86.15 ± 6.62a	1612.03 ± 73.02b	5.25 ± 0.33a
	Both	83.74 ± 4.52B	1697.56 ± 49.88B	4.81 ± 0.22B
R	M	54.15 ± 5.68a	1515.86 ± 62.68a	3.46 ± 0.28a
	F	41.36 ± 4.86b	1468.60 ± 53.58a	2.63 ± 0.24b
	Both	46.76 ± 3.69A	1488.56 ± 40.73C	2.98 ± 0.18A

Dissimilar lower case letters for each trait within a line represent significant differences between sexes. Dissimilar upper case letters for each trait represent differences between lines. All differences were tested at 5 percent level of significance.

Table 3.7 Analyses of variance showing degrees of freedom, mean squares and tests of significance for digestible energy intake (DEI), change in body energy (ΔBE) and energetic efficiency (ΔBE/DEI).

Source of Variation	d.f.	MEAN SQUARES								
		DEI (kJ)			ΔBE (kJ)			ENERGETIC EFFICIENCY (ΔBE/DEI)		
		3-5 Weeks	5-8 Weeks	3-8 Weeks	3-5 Weeks	5-8 Weeks	3-8 Weeks	3-5 Weeks	5-8 Weeks	3-8 Weeks
Line	2	808675.8**	1459678.6**	4439511.9**	15760.8**	15936.3**	59846.3**	0.0047**	0.00309**	0.00333*
Sex	1	80947.7**	252776.4	619812.9**	12669.3**	1548.5	23076.2**	0.0122**	0.00024	0.00252**
Line x Sex	2	5975.0	28709.5	36706.0	321.3	752.2	412.1	0.0000	0.00066*	0.00025**
Error	105	5589.9	74655.0	80172.8	211.5	613.9	718.4	0.0003	0.00015	0.00004

** $P<0.01$; * $P<0.05$

The R line mice accumulated 32.6, 5.3 and 20.9 percent more BE at the expense of 20.1, 14.3 and 16.4 percent more DEI than the L line during 3-5, 5-8 and 3-8 weeks. The differences in ΔBE and DEI between H and R lines were respectively 37.5, 79.1, 55.3 percent and 17.4, 14.0 and 15.3 percent for the two traits in the 3-5, 5-8 and 3-8 week periods. The gain in body energy was lower and digestible energy intake was higher for the R line than the average of the H and L lines (Figure 3.2b). Energetic efficiency of the H line was higher than the R and L lines in the three periods. The R line showed significantly higher energetic efficiency in the 3-5 week period. This difference was markedly reduced in the 5-8 week period and as a consequence the difference between the R and L lines was not significant over the whole period of 3-8 weeks studied.

Males, because of their faster growth and larger body size had a higher DEI than the females and showed greater increases in BE in the 3-5, 5-8 and 3-8 week periods for the L and H lines. Sex differences in DEI were significant (M>F) for 3-5, 5-8 and 3-8 week periods in the H and for the 3-5 week period in the R line. Finally, R line males were energetically more efficient than the females during 3-5, 5-8 and 3-8 weeks, L line males were more efficient during 3-5 and 3-8 weeks whereas sex effect was significant only during 3-5 weeks for this trait in the H line. Line X sex interaction effects were significant only for energetic efficiency during 5-8 and 3-8 weeks. For the other traits the sex differences observed were independent of line effects. At no age had females significantly higher averages than the males for any of the energy traits of the three lines studied.

The regression equations relating ΔBE and DEI in the normally growing mice of the L, H and R lines and sexes within lines are presented in Table 3.8. Line and sex averages for maintenance requirements per gram of body weight per week are given in Table 3.9.

Table 3.8 The relationship between the change in body energy (ΔBE) and digestible energy intake (DEI) of the L, H and R lines and sexes within lines

Line	Sex	N	Regression of ΔBE on DEI	r	Tests of differences between slopes: Between sexes	Tests of differences between slopes: Between mouse lines
L	M	20	ΔBE = 0.127 ± 0.031 DEI - 156.2 ± 61.9	0.70	$F_{1,32} = 1.42$ N.S.	L vs H: $F_{1,62} = 2.64$ N.S.
	F	16	ΔBE = 0.067 ± 0.041 DEI - 54.10 ± 76.1	0.41		
	Both Sexes	36	ΔBE = 0.139 ± 0.021 DEI - 182.9 ± 41.8	0.74		
H	M	16	ΔBE = 0.113 ± 0.012 DEI - 138.0 ± 33.1	0.93	$F_{1,26} = 0.31$ N.S.	L vs R: $F_{1,77} = 9.13^{**}$
	F	14	ΔBE = 0.123 ± 0.012 DEI - 156.7 ± 31.6	0.94		
	Both Sexes	30	ΔBE = 0.103 ± 0.006 DEI - 106.1 ± 17.5	0.95		
R	M	19	ΔBE = 0.080 ± 0.008 DEI - 59.8 ± 19.4	0.92	$F_{1,41} = 1.38$ N.S.	H vs R: $F_{1,71} = 6.69^{*}$
	F	26	ΔBE = 0.070 ± 0.004 DEI - 64.0 ± 9.1	0.96		
	Both Sexes	45	ΔBE = 0.078 ± 0.007 DEI - 72.5 ± 16.4	0.86		

N.S. = Not significant: * $P < 0.05$; ** $P < 0.01$

The efficiency of utilization of energy for growth was significantly higher for the H and L lines than the R line. The differences between the H and L lines were not significant. Also, there were no significant differences between males and females.

Large and significant differences in the maintenance requirements were observed between lines and between sexes (Table 3.9). The H mice were heavier and spent less energy for maintenance on a body weight basis, than the R and L mice, the R mice were intermediate in body weight and they spent less energy on maintenance than the L mice which were also lighter in body weight. However, least-squares regression of maintenance energy requirements per gram body weight per week on body weight for the data pooled over the three lines showed a higher maintenance cost of the R line relative to the L and H lines (Figure 3.3).

Table 3.9 Estimates of averages + s.e. for maintenance energy requirements per gram body weight per week for the 3 to 8 week growth period

Line	Sex	N	Mean s.e. (kJ)
	M	20	22.42 ± 0.44a
L	F	16	24.53 ± 0.49b
	Both sexes	36	23.36 ± 0.33A
	M	16	18.85 + 0.49a
H	F	14	20.29 + 0.52b
	Both sexes	30	19.52 + 0.36B
	M	19	20.17 + 0.45a
R	F	26	23.06 + 0.38b
	Both sexes	45	21.84 + 0.29C

Dissimilar lower case letters within each line represent sex differences. Dissimilar upper case letters represent line differences. Sex differences in the H line were significant at 5% level, all other comparisons were significant at 1% level.

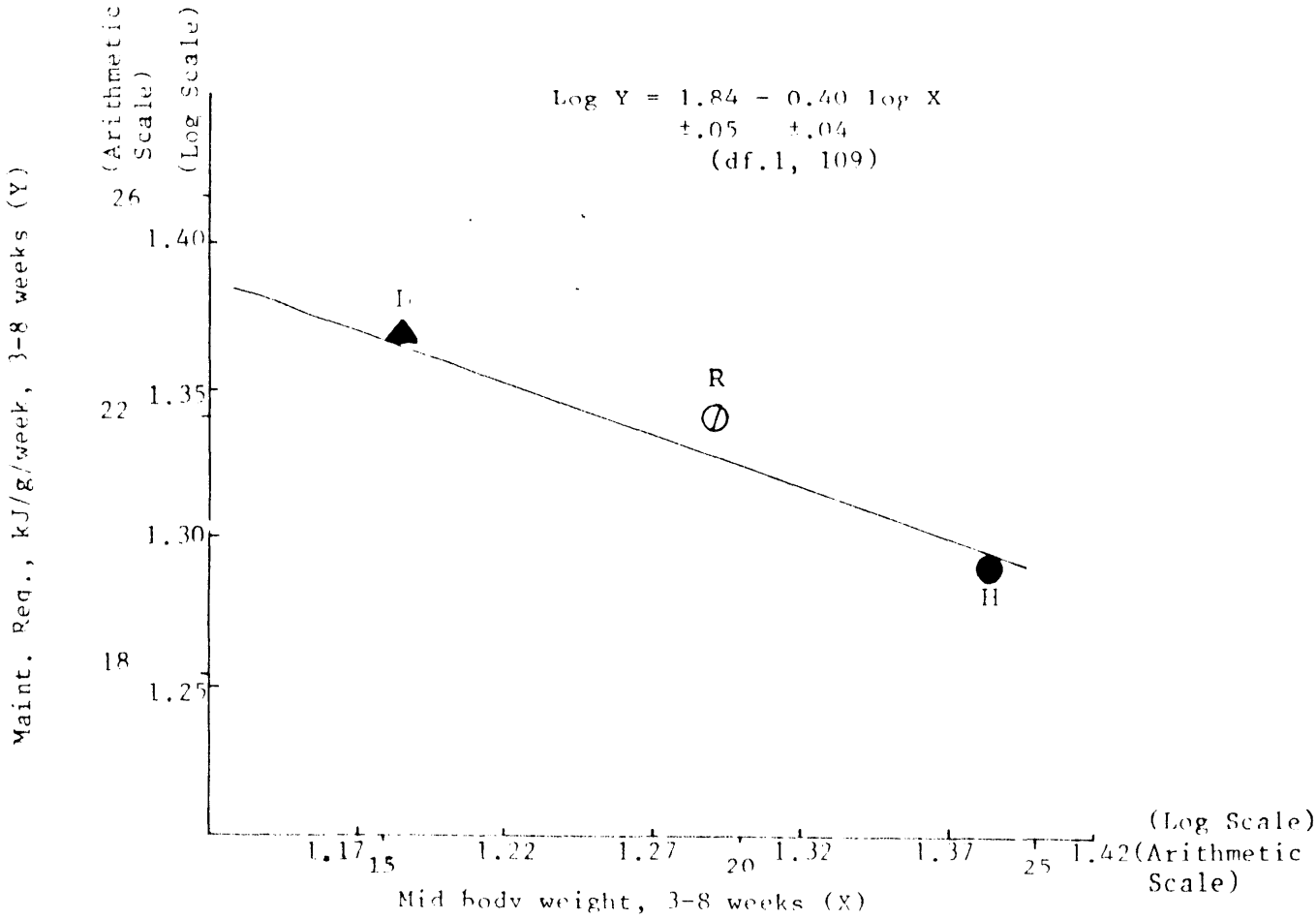

Figure 3.3 Least-squares regression of maintenance energy requirements on body weight for the data pooled over the three lines showing a higher maintenance cost of the R line relative to the L and H lines on a body weight basis.

Lines: L and H = Low and high body weight selection lines
R = Randombred control line

3.3 EXPERIMENT 2: (a) Maintenance requirements of growing mice on restricted intake

3.3.1 MATERIALS AND METHODS

An experiment using growing mice was conducted for calculating maintenance requirements during the period of their active growth. The number of mice available were 17, 22 and 22 for the L, H and R lines respectively. The mice were 3 weeks old initially but were acclimatized over a period of one week before the start of the feeding trial by feeding *ad libitum* the same food, using the same feeding device as described in Section 3.2.1. At 4 weeks of age, individual mice were offered maintenance food at the rate of 1.29, 1.26 and 1.32 g per g of body weight per week for the L, H and R lines respectively, calculated by extrapolating the regression of weight gain between 3-5 weeks on *ad libitum* feed intake during this period, using data from Experiment 1. The maintenance requirements of the L, H and R mice calculated by extrapolation were not significantly different from each other; nevertheless these values were useful approximations as a starting point in this experiment.

The sudden reduction in feed intake from *ad libitum* to the extrapolated maintenance diet resulted in a drop in body weight of all mice. Therefore, the quantity of food offered had to be increased slowly until the average body weights of 4-week old mice of each line were almost recovered. The quantity of food offered was then reduced slowly to a level where the body weights showed neither significant gains nor losses and the mice were then maintained on that diet for a period of 3 weeks. The quantity of food consumed on per g body weight basis per day during the 3 week constant body weight period was the estimated maintenance food requirement for each line. All mice were offered 2 day's feed allowance every alternate day, when they were also weighed. It was observed that the mice finished the offered food in about 36 hours and starved for about 12 hours between feeding intervals. One mouse from the H line and two mice from the R line died during the trial. One mouse each from the H and R lines had to be

removed from the experiment due to sickness. The number of mice from each line at the end of the experiment were L 17 (7M, 10 F), H 20 (11 M, 9 F) and R 19 (11 M, 8 F).

3.3.2 RESULTS

Maintenance feed requirements per gram of body weight per week obtained from feeding growing mice of the L, H and R lines on a constant diet to keep their body weight in equilibrium over a period of 3 weeks are presented in Table 3.10 and in Figure 3.4. The maintenance feed requirements calculated from the regression of weight gain from 3 to 5 weeks on feed intake during this period from the data in Experiment 1 are also shown for comparison. Sex differences were not significant.

Table 3.10 Maintenance feed requirements (g) per week per g of body weight of the growing mice of the L, H and R lines.

	Growing mice	
	Maintenance feed requirements estimated from	
	Experiment 1	Experiment 2
Line	Extrapolation of regression of 3-5 week gain on feed intake	Fixed rates
L	1.29 ± 0.201	1.50
H	1.26 ± 0.106	1.25
R	1.32 ± 0.140	1.35

The energy content of food estimated by burning samples of dried food in a bomb calorimeter was 16.8 kJ/g. By converting feed intakes of the restricted feed mice to energy units the maintenance energy requirements per gram of body weight per week are calculated as 25.2 kJ, 21.0 kJ and 22.7 kJ for the L, H and R lines respectively. These values are in close agreement with the values of 23.36 kJ, 19.52 kJ and 21.84 kJ estimated from the body composition and feed energy data in Experiment 1. Weighted averages for maintenance requirements over the two experiments were 23.95 kJ, 20.11 kJ and 22.09 kJ for L, H and R mice respectively. Because the mice in the present study were fed on fixed restricted diets, the mean maintenance intakes have no standard errors.

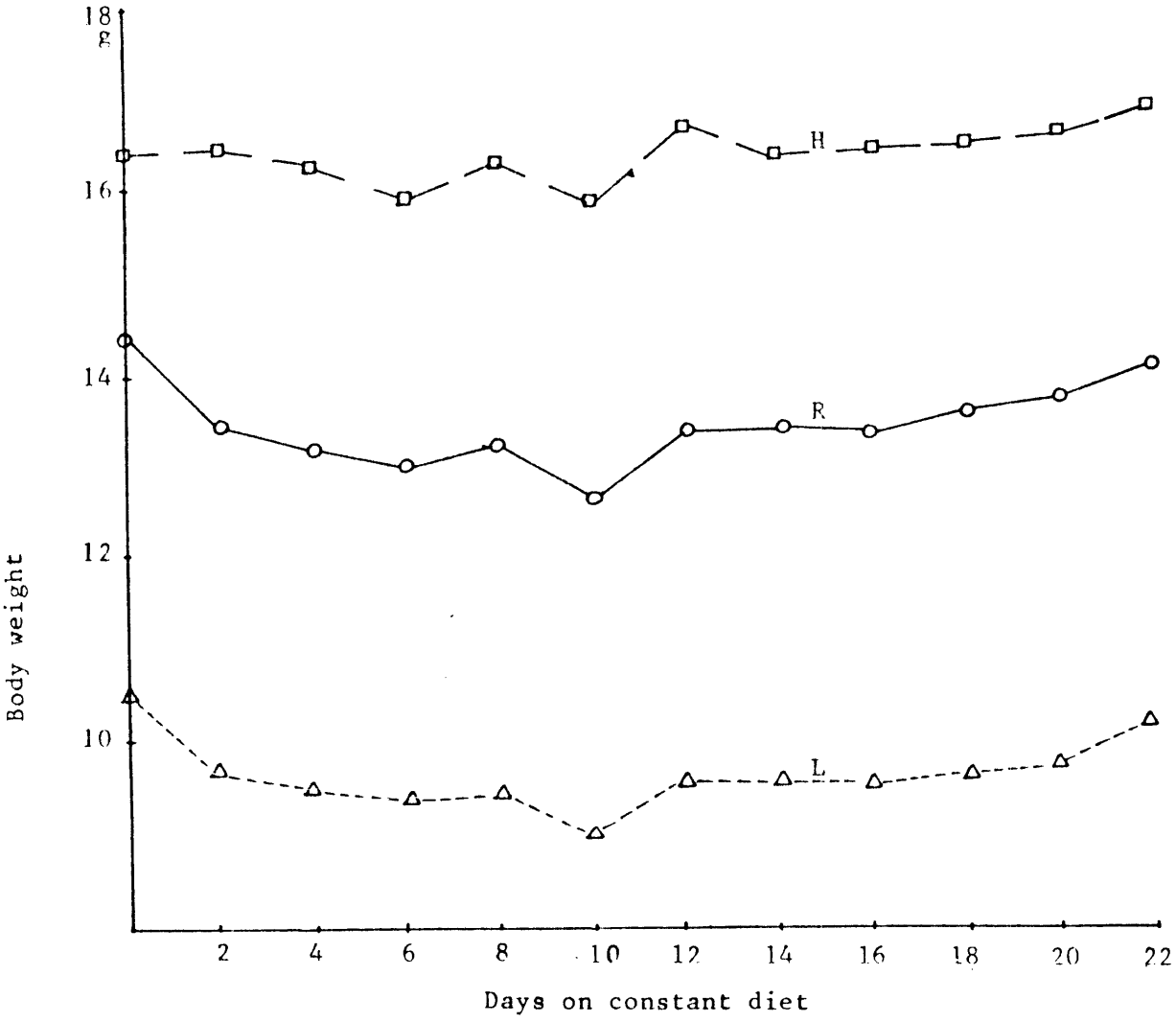

Figure 3.4 Body weights of mice offered a maintenance diet at the rate of 1.25, 1.35 and 1.5g per g of body weight per week for H, R and L lines, respectively.

3.4 EXPERIMENT 2: (b) Maintenance requirements of adult mice

3.4.1. MATERIALS AND METHODS

The mice used in the preceding experiment were allowed *ad libitum* feeding for 13 weeks during which time they had fully recovered from the effect of restricted feeding. By then the mice were 23 weeks of age and had stopped growing. At this age 17 L (7 M, 10 F), 20 H (11 M, 9 F) and 14 R (8 M, 6 F) were available for the present study.

Body weight and feed intake of these mice were recorded on alternate days over a period of 14 days. Neither body weight nor feed intake changed significantly during this period. As the feed intake of adult mice is used only for maintenance, their feed intake reflects the cost of maintaining the adult body weight. The feed intake per g of body weight of the adult mice was compared with the maintenance requirements of the growing mice measured in Experiments 1 and 2.

3.4.2 RESULTS

Feed intake and body weights of the adult mice of the selected and unselected lines are shown in Table 3.11.

Table 3.11 Least-squares averages ± s.e. of body weight and weekly feed consumption of adult mice

Line	Body Weight (g)			Feed Intake (g)		Feed intake/g body weight/ week
	Intial	First Week	Second Week	First Week	Second Week	
L	21.2±0.9	21.1±0.9	21.3±1.0	27.6±1.0	26.3±1.1	1.27±0.050a
H	39.5±0.8	39.2±0.8	39.4±0.9	41.3±1.0	41.8±1.0	1.05±0.024b
R	32.4±1.0	32.3±1.0	33.4±1.1	39.1±1.1	40.2±1.2	1.21±0.035a

Dissimilar lower case letters represent significance between lines ($P<0.05$).

On per gram body weight basis, the feed and energy requirements of the adult mice were 10-16% less compared with the growing mice on *ad libitum* and restricted feed intakes in Experiments 1 and 2 respectively, and the differences were significant. However, ranking of the lines for maintenance requirements was consistent over the three feeding trials involving growing or adult mice.

3.5 EXPERIMENT 3: Digestibility determination

3.5.1 MATERIALS AND METHODS

The adult mice used in Experiment 2 were used for the digestibility trial carried out at the same time. The digestibility of the food was measured by collecting faeces from each mouse twice daily over a 3-day period, weighing the dried material, and burning a sample of dried faeces, and also dried food, in a bomb calorimeter. Separation of urine and faeces was not attempted but excreta were separated from feed residues, if there was any spillage.

3.5.2 RESULTS

Table 3.12 presents least-squares averages for gross energy intake (GEI), faecal energy (FE), digestible energy intake (DEI) and percent digestibility in adult mice. Mean energy content per gram of faeces of the three lines was 6.53 kJ; there were no significant differences between lines. The energy content per gram of food was 16.8 kJ.

Table 3.12 Least-squares means ± s.e. of percent digestibility and related traits (kJ) measured over a three day period

Line	Gross Energy Intake (GEI)	Faecal Energy (FE)	Digestible Energy Intake (DEI)	DEI as a percent of GEI (digestibility)
L	212.5 ± 7.9a	40.3 ± 1.8a	172.2 ± 6.4a	81.1 ± 0.4a
H	300.7 ± 7.3b	59.2 ± 1.6b	241.5 ± 5.9b	80.3 ± 0.3a
R	308.3 ± 8.7b	60.1 ± 1.9b	248.2 ± 7.1b	80.5 ± 0.4a

Dissimilar lower case letters in the Table 3.12 represent significance between lines. All differences were significant at $P<0.01$.

The digestible energy intake (DEI) was calculated as a product of gross energy of food consumed and digestibility in the following manner:

DEI = Food consumption (g) x energy content of food (16.8 kJ/g) x digestibility (0.806).

Where 0.806 refers to 80.6 percent average digestibility weighted over the L, H and R lines.

There were no significant line differences for percent digestibility although large differences in GEI, FE and DEI were observed between L and H, and L and R lines.

3.6 DISCUSSION

The mice of the H line consumed more food, showed rapid gains and an improved feed efficiency as compared to the mice of the R and L lines. The L mice in comparison to the R mice ate less but the changes in weight gain or feed efficiency were not consistent over the 5 week period from 3 to 8 weeks. The R line was more efficient during 3 to 4 weeks of age than the L line. This situation was reversed during the next week and thereafter the two lines showed little difference in feed efficiency. Because feed efficiency is expressed as a ratio of the gain to food, it must therefore improve if either gain is increased or feed intake is decreased. The increased feed intake of the H mice was due to their bigger size and not because of an increase in appetite per unit of body weight. Feed intake per gram of body weight per week averaged over the whole range of ages from 3 to 8 weeks was 1.64 ± 0.011 for the H line, 1.77 ± 0.010 for the R line and 1.92 ± 0.012 for the L line and the differences were significant ($P<0.01$). The feed intake and feed efficiency patterns of the present study do not follow those of Timon and Eisen (1970) and Roberts (1981). In their lines selected for large size, food consumption per gram of body weight increased and the associated greater increases

in weight gain produced an improvement in feed efficiency. Recently Lynch and Roberts (1984) however, reported that on a per gram basis, small mice ate more than large mice which is consistent with the present findings.

The level of feed intake has a significant effect on feed efficiency and a decrease in feed intake per unit of body weight would be expected, at least over some range of intake, to lead to higher efficiency. However, in an analysis of feed efficiency between lines, besides appetite other factors such as maintenance requirement and utilization of the energy available for growth should also be taken into account. Lines of mice selected for body weight or growth rate and the related unselected lines have been shown to differ in thermoregulatory aspects (McCarthy, 1980), in overall maintenance energy needs (Stephenson and Malik, 1984) and in efficiency of utilization of energy for growth (Canolty and Koong, 1977; Stephenson and Malik, 1984).

Energetic efficiency is the ratio of energy stored in the tissue synthesized over the five week period (ΔBE) to metabolizable energy intake or DEI as was used in this study. Because only one diet was used, the DEI was directly proportional to the feed intake and the differences in ΔBE between lines were due to different amounts of fat and protein tissue in the three lines. Line differences in the mean energetic efficiency were significant between H and L and H and R lines with the H line having a higher efficiency in each instance. Differences between selected and unselected lines of mice have been reported elsewhere (Eisen *et al.*, 1977) with increased efficiency of lines selected for increased body weight or weight gain. Digestibility was not responsible for the observed line differences in energetic efficiency in the present study.

The DEI, energy requirements for maintenance and energy requirements for growth are important components of energetic efficiency. Because only a small portion of the total DEI is used for growth, therefore, small changes in energy partitioning can have large effects on growth. There were no differences between the H and L lines in the efficiency of energy utilization

for growth which is given by the slope of the line in regression of ΔBE on DEI. However on a per unit body weight basis, the maintenance requirement of the H line was substantially lower. Therefore, more energy was available for growth and because of a higher DEI, the H line mice were able to direct greater amounts of digestible energy into tissue synthesis. A lower DEI and higher maintenance requirement of the L line mice means that lower amounts of digestible energy were available for growth with an overall effect of low growth rate. The DEI of the R line compared with the L line was higher, maintenance requirement lower, and energy available for growth higher. However, these advantages over the L line were lost by a comparatively less efficient use of the energy available for growth by the R line with a net result that there was no difference in overall efficiency between the two lines. After taking account of the relationship between maintenance energy costs and body weight, the R line was found to have a relatively higher maintenance requirement. The R line was less efficient than the H line partly because of a higher maintenance requirement and partly because of a lower efficiency of energy utilization. It appears that although the R line had a DEI considerably in excess of maintenance requirements, all the excess energy was not used for growth and perhaps a part of it was lost through an inefficient conversion to waste heat. This problem has been investigated in more detail by Stephenson and Malik (1984) who reported such a loss to the extent of 18 percent in the R line. In comparison, the H and L lines appeared to direct most or all of the DEI above maintenance requirements into growth.

Maintenance requirement undoubtedly has a major effect on efficiency. Therefore, accuracy of its measurement is critical in an analysis of feed and energetic efficiency differences between lines. If reliable body composition data are available, estimation of maintenance requirements pose no particular problems. The maintenance requirements of the mice of the three lines used in this study were estimated by three different methods in an attempt to obtain a reasonable accurate measure so that there would be some consistency in the observations between experiments, reduced possibility of chance associations and a greater reliability of the results. The

maintenance energy requirements were estimated from DEI and body composition data (Experiment 1), from feed requirements per unit of body weight measured by keeping the body weight of growing mice constant over a period of three weeks (Experiment 2a) and from feed requirements per unit of body weight of the adult mice (Experiment 2b). The estimated mean value of maintenance requirements from the three experiments agreed in that the H line had the lowest maintenance energy requirement (kJ/g body weight) followed by the R and L lines respectively. The weighted averages from Experiments 1 and 2 were 23.95 kJ, 20.11 kJ and 22.09 kJ per gram body weight per week for the L, H and R mice respectively. The maintenance requirements for adult mice were lower.

Taylor (1969) suggested three models relating the metabolic heat production to body weight. The three situations considered were metabolic heat production in relation to body weight in (i) mature animals of different species ($Q_I = 70\ M^{0.73}$; Brody, 1945), (ii) normally growing animals of different species ($Q_{II} = 94\ \alpha^{0.27}\ W\ (e^{-\alpha W} + \frac{1}{2})$ and (iii) animals reaching an immature equilibrium weight on restricted food intake ($Q_{III} =$ kW ; Taylor and Young, 1968). When body weight was expressed as a proportion of mature weight (u), the three equations were rewritten as (i) $q_I max = 70.5u^{0.73}$; $q_{II} max = 70.5\ u^{0.58}$ and $q_{III} max = 70.5\ u(1-0.54\ \ln u)$ respectively together with a general model for normally growing and mature animals as $q_{max} = 117.5u\ (\bar{e}^{\ 2.3u} + \frac{1}{2})$. Where, Q and q refer to the heat production in kilocalories and M is mature weight in kilograms. It was shown that the curve representing proportionality to metabolic weight ($q_{max} = 70.5\ u^{0.73}$) when consistent with Brody's interspecies relationship at maturity, falls below the other three curves and does not fit the observed fact that the estimates of basal metabolism during growth tend to be above the interspecies curve. Park (1982) suggested that although the extrapolation of the interspecies relationship between metabolic rate and metabolic weight was valid for mature animals, the same was not valid for growing animals. Mount (1968) from a thorough discussion of the exponential relating to body weight indicated that in young growing mammals as opposed to adult animals of different body weights the

exponential coefficient may be near unity.

The maintenance costs used for between line comparisons in the present study were obtained by subtracting the energetic cost of lean and adipose tissue from the digestible energy intake and not from any extrapolation of the relationship between energy intake and metabolic body weight. The maintenance requirements per unit of body weight on *ad libitum* diet were calculated by dividing the maintenance requirements of the individual mice by their mean weight for the 3 to 8 week period ($\frac{1}{6}\sum_{i=3}^{8} Wi$) and did not involve a theoretical metabolic body weight. The estimated maintenance requirements, which are closely related to metabolic heat production were calculated firstly from growing mice on *ad libitum* intake and secondly from young mice on restricted intake, which is very similar to Taylor and Young (1968) experiment. These facts and the finding that both methods gave very similar results would justify using $W^{1.0}$ rather than $W^{0.73}$.

An important factor in the determination of the maintenance requirements and the overall efficiency is the environmental temperature. Trayhurn (1980) reported that 50 percent or more of the maintenance energy of mice is used for thermoregulation at a temperature of 22°C. Terroine (cited by Brody (1945, Figure 11.13)) has shown that fasting metabolism of rats is increased at 22°C by 50 percent above that at 30°C, substantially increasing maintenance requirement. A low temperature means that the body heat will be readily lost to the environment. In this situation a large mouse with a comparatively smaller surface area has obvious advantages. In the present study, the mice were housed at 24°C, 9°C below the thermoneutral temperature. As the H mice would have a smaller area per unit of body mass relative to the L mice, the energy cost of thermoregulatory thermogenesis would be expected to be lower in the H line and higher in the L line. It is logical to assume that under low temperature conditions, the feed intake and the energy requirement would increase to meet the extra energy needs for thermoregulation. However, feed intake cannot indefinitely follow increases in energy requirements because feed consumption capacity of an individual animal is limited.

Stephenson (1984) measured body weight, weight gain and feed intake of the L, H and R lines of mice at 32°C, 25°C and 21°C and found that there was no effect of temperature on mean body weight or weight gain in the R and L lines and the increased appetite of these mice at lower temperatures was used solely for thermoregulatory thermogenesis. Contrary to the expectations, the H line mice had greater increases in feed intake when the temperature was below thermoneutrality and they used some of the extra DEI to increase their growth rate. Large and significant changes in feed intake between the three lines indicated genotype x thermoregulatory energy cost interactions.

The results of the present study which demonstrate differences between lines in the efficiency of energy utilization support the findings of Canolty and Koong (1977) that mice selected for rapid growth rate utilized metabolizable energy more efficiently than did the randomly mated control. The selection for rapid gain, however, did not alter the maintenance requirements in their study. The data used in the study of Canolty and Koong were obtained from two groups of mice fed restricted and *ad libitum* diets. Also, different levels of diet were used in their experiment. In comparison, mice in the present study were fed *ad libitum* on standard mouse nuts and they were selected for body weight at 8 weeks rather than for weight gain. Given these differences between studies, it is difficult to make meaningful comparisons. Timon *et al.* (1970) found that selection for high postweaning gain had little effect on the efficiency of energy utilization for gain in terms of fat and protein deposition. The discrepancy between their findings and this investigation may be explained on the basis of the different criterion of selection and crossfostering of the selected mice to the control dams as was done in their study. Whether or not crossfostering had any effect on the growth rates of the selected mice was not reported. However, carryover effects of maternal influences on postweaning growth have been found in other studies with mice (Legates, 1972).

The line comparisons in the present study were made at the same ages. An alternate way of examining relative efficiencies of fast and slow gaining lines is on a weight constant basis. Both methods have the disadvantage that the comparisons cannot be made at the same physiological stage of development. If the comparison between lines of different growth rates is made over a constant age interval, the more rapidly growing lines weigh more and, therefore, have more weight to maintain. On a weight constant basis line comparison will also be influenced by the maintenance cost although now the slower growing lines will have an increased maintenance cost which will be proportional to the number of days required to gain the prescribed weight. This of course is a problem whether measurements are taken at a fixed age or a fixed weight. Fewer studies have been conducted on a weight constant basis. Timon and Eisen (1970) examined their mouse data over an age constant (21-57 days) and a weight constant period of 10g (15-25g) and found that the relative efficiency of the fast gaining line was significantly higher than the control line on both age and weight basis.

An interesting feature of the present study is the relative inefficiency of the R line in the utilization of energy for growth (Figure 3.2). Canolty and Koong (1977) found similar results. The control mice appear to consume dietary energy in excess of their basic maintenance and growth requirements which partly explains their inefficiency.

In summary, the results of this study provide evidence of changes in feed and energetic efficiencies as a consequence of artificial selection for body weight. The higher efficiency of the H line compared with the L line was due to its relatively lower maintenance cost per unit of body weight. The increased efficiency of the H line over the R line was because of a more efficient use of energy available for growth by the H mice and a lower maintenace requirement. The differences between the R and L lines for the gross feed and energetic efficiency were small. The R line had a lower maintenance energy

requirement per unit of body weight and higher energy available for growth than the L line. However, because of a comparatively less efficient use of the energy available for growth by the R line, there was no difference in overall efficiency between the two lines.

SECTION 4

BREEDING SCHEME FOR ESTIMATION OF HETEROSIS AND RECOMBINATION EFFECTS

4.1 INTRODUCTION

Diversity among breeds within each livestock species offers the opportunity to increase production efficiency. Various crossbreeding systems may be used to exploit between-breed genetic variation. However, the predictability and value of this approach are enhanced if information is available about the genetic sources controlling the important characters. Two major components of genetic differences have different expression in offspring and dam. These may be studied as average direct effects of the offspring (g^O), maternal genetic effects (g^M), heterosis in the crossbred progeny (h^O) and dam (h^M), and epistatic recombination losses in the offspring (r^O) and dam (r^M). Recombination losses occur in F_2 and backcross generation due to segregation and recombination of genes brought together from the two purebred parents in the F_1.

Theoretical expectations for the proportion of heterosis and recombination effects in different crosses were given by Dickerson (1969, 1973). The contribution of h^O, h^M, r^O and r^M in a few selected crossbreeding systems are presented in Table 4.1.

Table 4.1 Partitioning of crossbred performance as a deviation from purebred mean into heterosis and recombination effects

Mating System	Crossbreeding parameters			
	h^O	h^M	r^O	r^M
Two-breed cross				
F_1	1	0	0	0
F_2	½	1	½	0
F_3	½	½	½	0
B_1^*	½	1	¼	0
Three-breed cross	1	1	¼	0
Four-breed cross	1	1	½	0
Synthetics (equal percentage of each of N breeds)	(N-1)/N	(N-1)/N	(N-1)/N	(N-1)/N

* B_1 - Parental breed x F_1

In any crossbreeding programme, purebred performance of the parent breeds will usually be known. Breed differences in maternal effects can be obtained from reciprocal F_1 comparisons. There is, however, a lot of confusion in the literature about the estimation of heterosis and epistatic recombination effects expressed in the dam and in the offspring. Frequently reported estimates are confounded combinations of h^O, h^M, r^O and r^M (nitter, 1978).

4.2 MATING SCHEME FOR PARAMETER ESTIMATION

A mating scheme using three lines/breeds and procedures for the estimation of direct genetics, maternal genetic, direct heterosis, maternal heterosis and recombination effects in the offspring (Malik, 1984) are presented in Figure 4.1 and Table 4.2.

The 3-way mating scheme shown in Figure 4.1 is designed to utilize full heterosis in the offspring and maternal performance and to minimize recombination losses in F_2. There is no epistatic recombination loss in maternal heterosis because F_1 dams are used.

4.3 DISCUSSION

The estimation of various genetic effects is made by specific breed and crossbred comparisons using linear contrasts of least-squares means. These are also estimated by mating type comparisons, where the mean of the crossbred type represents the value of reciprocal crosses in that type. This approach has been used previously by other workers (Hayman, 1958; Hayman and Mather, 1955; Jinks and Jones, 1958). If facilities are available, the use of least-squares analysis based on the general linear models procedures (Kinghorn, 1982) is analytically more efficient as it utilizes the maximum information without confounding of the effects.

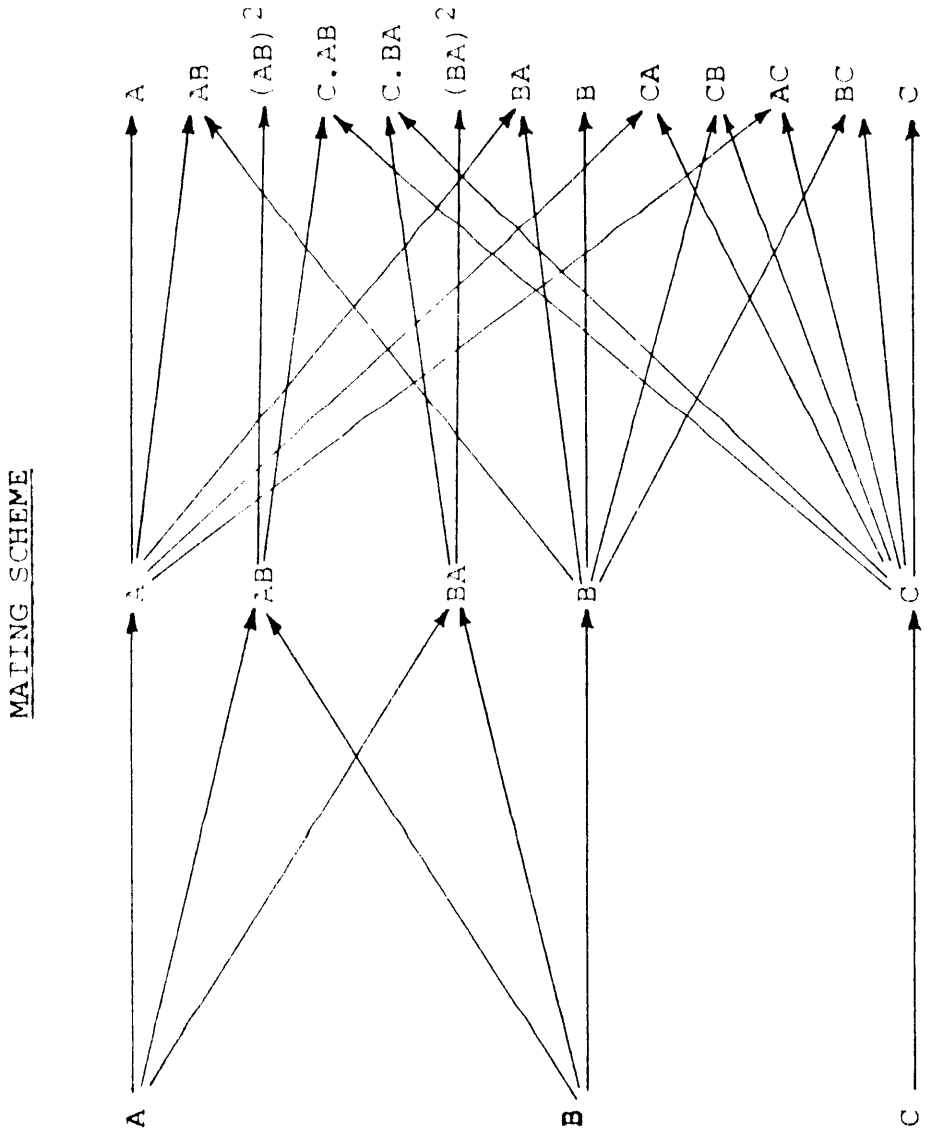

FIGURE 4.1 Breed of sire is indicated by the first sysbol of the cross. Squared symbols represent F_2.

Table 4.2 Estimation of genetic effects

Effects	Estimated from	
	Breed/crossbred comparison	Mating type comparison
* $g_A^O - g_B^O$	$\bar{A} - \bar{B} + \overline{AB} - \overline{BA}$	$\bar{P}_1 - \bar{P}_2 + \bar{F}_{1AB} - \bar{F}_{1BA}$
* $g_A^M - g_B^M$	$\overline{BA} - \overline{AB}$	$\bar{F}_{1BA} - \bar{F}_{1AB}$
* h_{AB}^O	$\frac{1}{2}\left[(\overline{AB} + \overline{BA}) - (\bar{A} + \bar{B})\right]$	$\bar{F}_1 - \bar{P}$
h_{AB}^M	$\{\{\left[\overline{C(AB)} + \overline{C(BA)}\right] - \left[\overline{CA} + \overline{CB}\right]\}$	$\{2\left[\overline{3\text{-way}} - \overline{2\text{-way}}\right]$
	$-\{\frac{1}{2}\left[\overline{(AB)^2} + \overline{(BA)^2}\right] - \frac{1}{4}\left[\bar{A} + \bar{B} + \overline{AB} + \overline{BA}\right]\}\}$	$-\left[\bar{F}_{2AB} - \frac{1}{2}(\bar{F}_{1AB} + \bar{P})\right]\}$
r_{AB}^O	$2\{\left[\overline{(AB)^2} + \overline{(BA)^2}\right] - \frac{1}{2}\left[\bar{A} + \bar{B} + \overline{AB} + \overline{BA}\right]\}$	$2\{\left[2\bar{F}_{2AB} - (\bar{P} + \bar{F}_{1AB})\right]$
	$-\{\left[\overline{C(AB)} + \overline{C(BA)}\right] - \left[\overline{CA} + \overline{CB}\right]\}$	$-\left[2(3\text{-way}) - (\bar{F}_{1CA} + \bar{F}_{1CB})\right]\}$

Bar over designation represents its mean. Symbols used: $P = \frac{A + B}{2}$, $F_1 = \frac{AB + BA}{2}$ etcetera

* Effects $g_A^O - g_C^O$, $g_B^O - g_C^O$, $g_A^M - g_C^M$, $g_B^M - g_C^M$, h_{AC}^O and h_{BC}^O can be estimated in a similar manner.

Heterosis and recombination effects are measured directly but their partitioning into individual and maternal components is realized by indirect comparisons among crosses. The term heterosis used here refers to both intra- and interlocus interactions. On other formulations (Mather and Jinks, 1971; Kinghorn, 1980; Hill, 1982; Jakubek and Hyanek, 1982) the use of terms "dominance" and "epistasis" have specific meanings. The recombination effects are based on 2-locus interactions and will be underestimated if the recombination effects are important. Experimental results to test theoretical predictions in farm animals are required.

If sufficiently accurate estimates of the genetic effects involved are known, predictions of crossbred performance under various crossbreeding schemes can be made. Equations for the expected contribution of genetic effects in purebreds and their crosses are presented in Appendix U.

SECTION 5

THE CROSSING EXPERIMENT -

ESTIMATION OF DIRECT AND MATERNAL ADDITIVE AND NON-ADDITIVE EFFECTS FROM CROSSING THREE LINES OF MICE

5.1 INTRODUCTION

The theory of genetic parameters required for comparing efficiency of various crossbreeding systems has developed considerably in recent years, whereas experimental evidence has lagged behind. There is now a need for appropriate mating schemes and estimation procedures to give unconfounded estimates of various genetic effects, and based on these schemes, the experimental data to check the validity of theoretical expectations. A mating scheme and procedure for obtaining unconfounded estimates of genetic effects of the offspring and dam were given in the previous section. A crossbreeding study for the partitioning of the phenotypic differences between three diverse populations of mice into direct genetic effects of the offspring (g^O), maternal genetic effects (g^M), direct heterosis (h^O), maternal heterosis (h^M) and recombination effects of the offspring (r^O) is presented in this section. The mating Scheme and appropriate procedures for estimation of the genetic effects from this scheme given in Section 4 are used for this work.

5.2 MATERIALS AND METHODS

5.2.1 Design of the Experiment

The three-way crossbreeding scheme shown in Figure 4.1 of Section 4 was used for the estimation of genetic parameters. Symbols A, B and C in the figure correspond respectively to the high body weight (H), low body weight (L) and randombred control (R) lines of mice used in this study. All the 13 genetic groups (Table 5.1) produced by this crossbreeding scheme were contemporaneous in order to reduce environmental differences as far as possible. Matings were random throughout except that full-sib matings were deliberately avoided. Females were bred when 6 to 8 weeks old by pairing them singly with males of similar ages. Litter sizes of more than 8 pups were reduced to 8 pups three days after birth. Those litters which had 8 or less than 8 pups were retained as such. The incidence of litter sizes with less than 8 pups was

approximately 10% and evenly spread over all genetic groups so there was no bias arising from litter size.

5.2.2 Feeding and Management of the Mice and Collection of Data

All mice were housed in a mouse colony with the temperature maintained at approximately 24°C and a light to darkness ratio of 14:10 hours. The young mice were weaned at 21 days of age. The food offered to all mice was a commercially prepared pelletted ration (Fielder's mill, Tamworth, N.S.W.) with gross energy content of 16.8 kJ per g of food. After weaning the weaned mice were placed individually in cages where they had *ad libitum* access to water and food. The weaned mice were fed the same batch of food as offered to mothers, though not as pellets but in mill ground form. The food was offered in the specially designed containers described earlier in Section 3.2.1. Each mouse was offered about 25 g food three times a week. At every feeding time, the left over food was weighed and feed consumption measured from the difference between the food offered and food left over. No bedding was provided so that any food spillage could be detected. Any spilled food was carefully isolated from the excreta and replaced in the feeding jars before weighing. Cages were cleaned thrice a week to maintain cleanliness and eliminate contamination.

The number of mice available from each of the 13 genetic groups for 3 and 8 week body weights, carcass composition (fat and protein) and 3 to 8 week feed intake, weight gain and feed efficiency are presented in Table 5.1. Whole carcass fat and protein weights were measured as described in Section 2.2.1 at 3 and 8 weeks of ages. All data were recorded on the exact day assigned for measurement. The statistical analyses were carried out for body weights and weights of fat and protein at 3 and 8 weeks as well as weight gain, feed intake and percent feed efficiency $\left(\frac{\text{Gain} \times 100}{\text{Feed}}\right)$ during 3-8 weeks.

Table 5.1 Number of mice sampled at 3 and 8 weeks for the analysis of body weight and other traits*

Line/ Line Cross	Age		
	3 Weeks		8 Weeks
	Body Weight	Carcass Composition	Traits Studied at This Age and From 3 to 8 Weeks
L	75	20	17
H	64	17	18
R	81	20	18
LXH (F_1)	72	18	19
HXL (F_1)	70	18	15
LXR (F_1)	63	19	19
RXL (F_1)	69	18	18
HXR (F_1)	46	18	17
RXH (F_1)	101	24	18
LHXLH (F_2)	108	19	19
HLXHL (F_2)	131	20	21
RXLH (3-Way)	69	18	17
RXHL (3-Way)	86	17	16
Total	1035	246	232

* For information on the traits measured see text

5.2.3 Statistical Analyses

The analyses were carried out by least-squares procedures for data with unequal subclass numbers as outlined by Harvey (196)). Genetic groups (lines and line crosses), sex and genetic group x sex interactions were included in the following model to estimate genetic group means:

$$Y_{ijk} = \mu + L_i + S_j + (LS)_{ij} + e_{ijk}$$

where

Y_{ijk} = k^{th} observation of the ij^{th} subclass

μ = Overall mean

L_i = Fixed effect of the i^{th} line (i = 1, ..., 13)

S_j = Fixed effect of the j^{th} sex (j = 1, 2)

$(LS)_{ij}$ = Two way interaction involving line and sex

e_{ijk} = Random error (NID, O, σ^2).

The estimates of genetic effects were obtained from linear contrasts using least-squares averages in the manner shown in Table 4.2. The differences between the L, H and R lines for the direct genetic effects (g^O), maternal genetic effects (g^M) and direct heterotic effects (h^O), as well as maternal heterosis (h^M) and recombination effects of the offspring (r^O) in crosses between H and L lines were estimated. Estimation of average direct and maternal genetic effect differences between lines is not the same as estimating the genetic effects of the lines as a deviation from the population mean. Therefore, the estimates of average direct genetic and maternal genetic effects obtained from linear contrasts shown in Table 4.2 refer to differences between lines for these effects.

The standard error for each linear contrast was estimated as $(\Sigma\Sigma l_i l_j c_{ij} \hat{\sigma}^2_e)^{\frac{1}{2}}$ where $\hat{\sigma}^2$ is the error variance of the trait analysed, l_i and l_j respectively are the coefficients of i^{th} and j^{th} line means in the contrast (see Table 4.2), c_{ij} is the $(ij)^{th}$ inverse element of the sums of squares-crossproduct matrix.

Several assumptions were implied in the model. If environmental influences were properly randomized it could be assumed that each parental population phenotypic mean should be determined completely by the direct genetic and maternal genetic effects. Any additional effect in the F_1 cross should be due to direct heterosis. Additional effects in the F_2 should be due to maternal heterosis and the recombination effects of parental gametes in the offspring. It was also assumed that sex-linked, cytoplasmic, paternal and grand maternal effects were not important.

5.3 RESULTS

Least-squares averages for body weights, weights of fat and protein, feed intake, weight gain and feed efficiency of the different lines and line crosses are presented in Tables 5.2 and 5.3.

Table 5.2 Least-squares means ± s.e. for body weight and carcass traits at 3 and 8 weeks of age

Line/ Line Cross	Body Weight (g)		Carcass Composition (whole carcass)			
			Fat Weight (g)		Protein Weight (g)	
	3 week	8 week	3 week	8 week	3 week	8 week
L	6.37±0.08	16.88±0.50	0.49±0.04	1.55±0.34	1.08±0.06	3.18±0.13
H	10.84±0.20	28.87±0.49	0.93±0.04	3.21±0.33	1.83±0.06	5.29±0.13
R	9.88±0.18	22.21±0.49	0.87±0.04	2.20±0.33	1.66±0.05	4.11±0.13
LXH	10.07±0.18	24.34±0.47	0.89±0.04	2.28±0.32	1.68±0.06	4.55±0.12
HXL	8.25±0.20	23.38±0.53	0.69±0.04	2.15±0.36	1.37±0.06	4.27±0.14
LXR	9.10±0.18	21.10±0.47	0.78±0.04	1.89±0.34	1.54±0.06	3.83±0.13
RXL	8.48±0.19	19.82±0.49	0.50±0.04	1.72±0.35	1.43±0.06	3.70±0.14
HXR	9.96±0.23	25.62±0.50	0.81±0.04	2.42±0.34	1.65±0.06	4.71±0.13
RXH	10.60±0.16	27.84±0.49	0.92±0.04	2.81±0.32	1.75±0.05	5.08±0.12
LHXLH	9.22±0.15	23.10±0.47	0.81±0.04	2.08±0.32	1.57±0.06	4.21±0.12
HLXHL	9.06±0.15	24.22±0.45	0.80±0.04	2.25±0.31	1.47±0.06	4.38±0.12
RXLH	9.80±0.19	23.80±0.04	0.85±0.04	2.12±0.34	1.67±0.06	4.33±0.13
RXHL	9.95±0.18	24.83±0.04	0.84±0.04	2.44±0.35	1.70±0.06	4.56±0.13

Table 5.3 Least-squares means ± s.e. for feed intake, weight gain and feed efficiency between 3-8 weeks

Line/ Line Cross	Feed Intake (g)	Weight Gain (g)	Feed Efficiency (%)
L	146.10±4.66	10.51±0.46	7.25±0.25
H	209.64±4.52	18.03±0.44	8.68±0.24
R	166.15±4.52	12.33±0.44	7.38±0.24
LXH	173.98±4.40	14.27±0.43	8.23±0.24
HXL	189.32±4.96	15.13±0.49	7.97±0.26
LXR	170.94±4.40	12.00±0.43	7.06±0.24
RXL	165.15±4.52	11.34±0.44	6.88±0.24
HXR	198.66±4.66	15.66±0.46	7.86±0.25
RXH	214.78±4.52	17.24±0.44	8.00±0.24
LHXLH	172.62±4.20	13.58±0.43	7.88±0.24
HLXHL	186.62±4.20	15.16±0.41	8.11±0.22
RXLH	185.46±4.66	14.00±0.46	7.56±0.25
RXHL	197.93±4.79	14.88±0.47	7.52±0.25

The body weights of the H and R line mice at 3 weeks and of the L line mice at 3 and 8 weeks in the present experiment were significantly lower than the mice of the same lines in the experiment reported in Section 3. Three generations of relaxed selection employed to develop contemporary crosses required for the present design resulted neither in a significant reduction in body weight of the H line nor in any increase in the L line at 8 weeks of age (age at which selection was carried out). There are no known reasons which would have influenced the performance of the mice in the present experiment and the observed differences in mice weights between the two experiments may have been due to unnoticed environmental influences or errors associated with the sampling of mice or both. The R line was more stable. The difference in 3 week body weight of the R line between experiments was small and possibly was a random effect. At 8 weeks, the body weight of the R line in the previous and the present experiment (23.44 ± 0.29 cf 22.21 ± 0.49) respectively was not significantly different. Similarly gain in body weight (12.93 ± 0.24 cf 12.33 ± 0.44) and feed intake (172.77 ± 0.93 cf 166.15 ± 4.52) were not significantly different.

Figure 5.1 shows the mean values of the body weight gains against feed intake of the 13 genetic groups used in this study. The selection lines and their derived crossbreds showed higher gains in weight relative to feed intake than the purebred R line or crossbreds involving R line.

Percent feed efficiency of the selection lines and their derived crossbreds was significantly higher than the purbred R line and crossbreds involving R line (8.02 ± 0.19 cf 7.47 ± 0.15, $P < 0.05$).

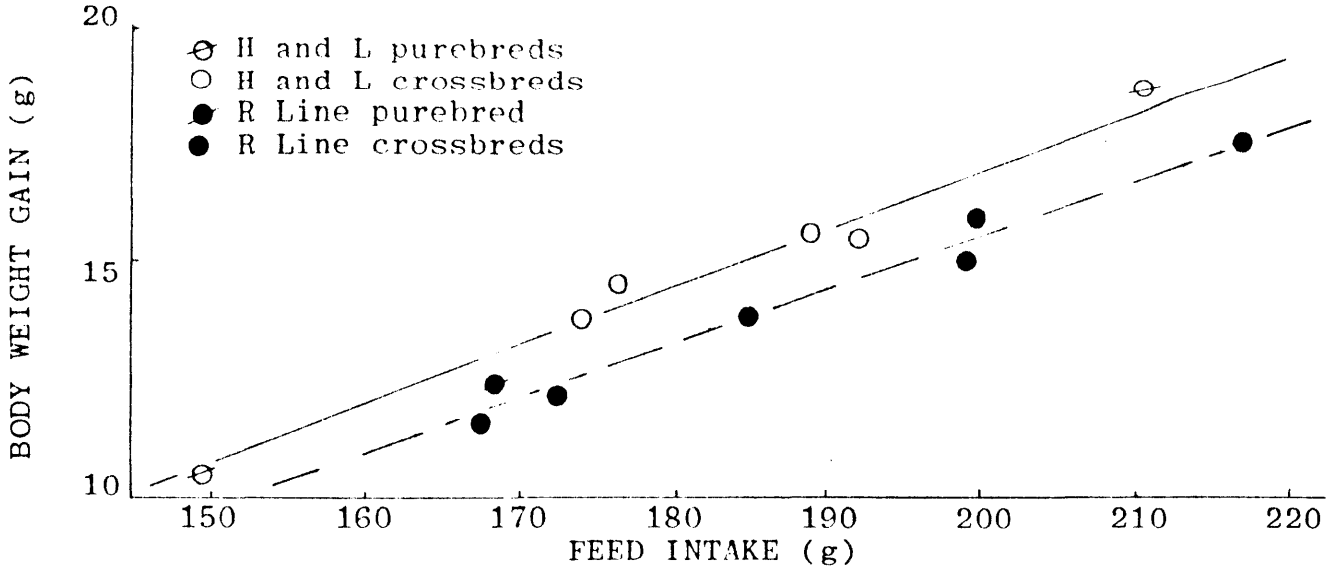

Figure 5.1 Least squares regression of body weight gain on feed intake for the selection lines and their derived crossbreds versus purebred R and crossbreds with an R parent. The difference in adjusted means for weight gain was significant at 1% level ($F_{1,9(\text{elevations})} = 32.94^{**}$).

The analyses of variance for weaning and postweaning traits are presented in Tables 5.4 and 5.5, respectively. Line effects were significant ($P < 0.01$) for all traits. Sex effects were significant ($P < 0.01$) for all the pre- and postweaning traits except fat weight at 3 and 8 weeks, and protein weight at 3 weeks. Males were heavier than the females both at 3 and 8 weeks. They consumed more food but also showed higher weight gain and were more efficient than the females. The line x sex interaction was significant ($P < 0.5$) only for weight of the protein at 8 weeks. In lines and crosses with higher body weights there was a relatively greater sex difference.

Table 5.4 Degrees of freedom, mean squares and tests of significance from the least-squares analyses of variance for weaning traits

		MEAN SQUARES		
Source	d.f.[+]	Body Weight	Fat Weight	Protein Weight
Line	12	119.68**	0.42**	0.94**
Sex	1	10.53**	0.06	0.02
Line x Sex	12	1.21	0.01	0.04
Error		1.73	0.03	0.06
		(1009)	(220)	(220)

[+] Degrees of freedom for error mean squares in parenthesis;
* $P < 0.05$; ** $P < 0.01$

Differences in direct genetic effects (g^O) (Table 5.6) between H and L lines were significant for all the traits, between H and R lines at 8 weeks for all traits except weight of fat, and between R and L lines for body weights, weight of protein at 3 and 8 weeks, and for weight of fat at 3 weeks. The direct genetic effects from H-R comparison for 3 week fat weight and from R-L comparison for feed efficiency were negative. For all other comparisons, direct genetic effects showed the following trend: H>R>L.

Table 5.5 Degrees of freedom, mean squares and tests of significance from the analyses of variance for 8 week body weight, protein and fat weight, and 3-8 week feed intake, weight gain and feed efficiency

Source	df	Body Weight	Fat Weight	Protein Weight	Feed Intake	Weight Gain	Feed Efficiency
Line	12	212.04**	6.61**	5.71**	6171.00**	104.38**	16.51**
Sex	1	629.53**	2.49	33.24**	5371.43**	548.09**	48.32**
Line x Sex	12	6.59	2.90	0.60*	341.89	5.40	1.22
Error	206	4.24	1.95	0.29	367.12	3.55	1.06

* $P < 0.05$, ** $P < 0.01$

Table 5.6 Differences in Direct Genetic Effects (g^0) between H and L, H and R, and R and L lines

Trait	Line Difference		
	$g^0_H - g^0_L$	$g^0_H - g^0_R$	$g^0_R - g^0_L$
Body Weight (g)			
3 week	2.65±0.31**	0.32±0.32	2.89±0.31**
8 week	11.03±0.99**	4.44±0.98**	4.05±0.97**
Fat Weight (g)			
3 week	0.22±0.08**	-0.05±0.08	0.25±0.08**
8 week	1.53±0.67*	0.62±0.66	0.48±0.66
Protein Weight (g)			
3 week	0.44±0.11**	0.07±0.11	0.47±0.11**
8 week	1.83±0.26**	0.81±0.26**	0.80±0.25**
Feed Intake (g)			
3-8 week	78.88±9.24**	27.97±9.10**	14.26±9.03
Weight Gain (g)			
3-8 week	8.38±0.91**	4.12±0.89**	1.16±0.89
Feed Efficiency (%)			
3-8 week	2.08±0.50**	1.16±0.49*	-0.07±0.49

* $P < 0.05$, ** $P < 0.01$

$(g^0_H - g^0_L \neq (g^0_H - g^0_R) + (g^0_R - g^0_L)$ because of the reciprocal effects specific to the crosses involved in the comparison. This problem can be handled more effectively by the use of general linear models.

The large deviation between the $(g^0_H - g^0_L)$ and sum of $(g^0_H - g^0_R)$ and $(g^0_R - g^0_L)$ for feed intake may be due to very large interaction between maternal and direct effects.

Contrasts for reciprocal F_1 crosses (Table 5.7) provided estimates of maternal effect differences between parental populations.

Table 5.7 Differences in Maternal Genetic Effects (g^M) between H and L, H and R, and R and L Lines

Trait	Line Difference $g^M_H - g^M_L$	$g^M_H - g^M_R$	$g^M_R - g^M_L$
Body Weight (g)			
3 week	1.82±0.22**	9.64±0.23**	0.62±0.23**
8 week	0.96±0.71	2.22±0.70**	1.28±0.68
Fat Weight (g)			
3 week	0.20±0.06**	0.11±0.05*	0.13±0.06*
8 week	0.13±0.48	0.39±0.47	0.17±0.46
Protein Weight (g)			
3 week	0.31±0.08**	0.10±0.08	0.11±0.08
8 week	0.28±0.19	0.37±0.18	0.13±0.18
Feed Intake (g)			
3-8 week	-15.34±6.62*	15.52±6.48*	5.79±6.30
Weight Gain (g)			
3-8 week	-0.86±0.65	1.58±0.64*	0.66±0.62
Feed Efficiency (%)			
3-8 week	0.26±0.36	0.15±0.35	0.18±0.34

* $P < 0.05$, ** $P < 0.01$, $(g^M_H - g^M_L) \neq (g^M_H - g^M_R) + (g^M_R - g^M_L)$ because of the reciprocal effects specific to the crosses involved in the comparison. The large difference between $(g^M_H - g^M_L)$ and sum of $(g^M_H - g^M_R)$ and $(g^M_R - g^M_L)$ for feed intake and weight gain may be due to interaction between maternal and direct effects.

The differences in maternal genetic effects (g^M) between H and L lines were significant for body weight, fat weight and protein weight at 3 weeks and for 3-8 week feed intake. The maternal genetic effects were not significant between R and H lines for weight of fat at 8 weeks, weight of protein at 3 and 8 weeks and feed efficiency. For the remaining traits the differences in maternal genetic effects were significant between these two lines. The R and L lines were significantly

different for maternal genetic effects in respect of body weight and fat weight at 3 weeks only. For the comparisons showing significant direct and maternal genetic effects between lines, the direct genetic component of the differences between H-L, H-R and R-L was larger than the maternal genetic component except for body weight and fat weight at 3 weeks between H and R lines.

Heterosis (due to dominance and epistasis) in F_1 crosses (Table 5.8) of the H and L lines was significant for body weight, and weight of fat at 3 weeks and feed efficiency. Significant positive heterosis in the F_1 crosses between H and R lines was observed for 8 week body weight, feed intake and weight gain. F_1 crosses of the R and L lines showed significant heterosis for body weight and weight of protein at 3 weeks, and feed intake.

Table 5.8 Direct heterosis exhibited in F_1 crosses

Trait	Heterosis in F_1 Crosses h^O_{HL}	h^O_{HR}	h^O_{RL}
Body Weight (g)			
3 week	0.56±0.16**	-0.08±0.15	0.67±0.16**
8 week	0.99±0.50	1.19±0.49*	0.92±0.49
Fat Weight (g)			
3 week	0.08±0.04*	-0.04±0.04	0.04± .04
8 week	-0.17±0.34	-0.09±0.33	-0.07±0.33
Protein Weight (g)			
3 week	-0.07±0.06	-0.05±0.06	0.12±0.06*
8 week	0.18±0.13	0.20±0.13	0.12±0.13
Feed Intake (g)			
3-8 week	3.78±4.61	18.83±4.55**	11.92±4.52**
Weight Gain (g)			
3-8 week	0.43±0.45	1.27±0.45**	0.25±0.44
Feed Efficiency (%)			
3-8 week	0.59±0.25*	-0.10±0.24	-0.34±0.24

* $P < 0.95$, ** $P < 0.01$

Estimates of maternal heterosis (h^M) and recombination effects on the offspring performance (r^O) are given in Table 5.9.

Table 5.9 Meternal Heterosis (h^M) and Recombination Effects (r^O) in the crosses between H and L lines

Trait	Maternal Heterosis		Recombination Effects
	h^M_{HL} (Unbiased)+	$h^M_{HL} + \frac{1}{4} r^O$ (Biased)++	r^O_{HL}
Body Weight (g)			
3 week	0.41±0.20*	0.34±0.15*	-0.32±0.40
8 week	0.68±0.69	0.49±0.50	-0.78±1.37
Fat Weight (g)			
3 week	0.06±0.06	0.06±0.04	-0.02±0.11
8 week	-0.11±0.47	0.02±0.34	-0.60±0.93
Protein Weight (g)			
3 week	0.16±0.08*	0.10±0.06	-0.26±0.16
8 week	0.09±0.18	0.06±0.13	-0.39±0.36
Feed Intake (g)			
3-8 week	-2.90±6.44	1.73±4.62	6.52±12.79
Weight Gain (g)			
3-8 week	0.18±0.63	0.15±0.45	-1.06±1.26
Feed Efficiency (%)			
3-8 week	0.17±0.35	0.10±0.25	-0.52±0.69

\+ Estimated from the equation h^M_{AB} in Table 4.2

++ Calculated as $\frac{1}{2}\{[(RXHL) + (RXLH)] - [(RXH) + (RXL)]\}$

* $P < 0.05$.

Unbiased estimates of maternal heterosis were significant for 3 week body weight and 3 week protein weight. Maternal heterosis derived from a comparison between 3-way and 2-way crosses is biased since it contains a one-quarter component of recombination effects ($\frac{1}{4}r^{O}$). Such estimates were generally lower than those unconfounded with the recombination effects.

None of the estimates of recombination effects were significant and in most cases they were negative. Recombination effects in the dam (r^{M}) could not be measured because F_2 dams were not involved in any of the crosses studied.

5.4 DISCUSSION

The present study was undertaken with *a priori* understanding that differences between lines in direct genetic and maternal genetic effects would constitute the main sources of difference between the different genetic populations for weaning and postweaning traits. Direct heterosis, maternal heterosis and recombination effects were estimated by crossbreeding scheme involving H, R and L lines.

The feed efficiency of the H, R and L lines showed a trend similar to that observed in Section 3. In the first experiment the R and L mice had similar feed efficiency but were significantly lower than the H mice. A striking feature of this experiment was a relatively lower efficiency of the R line and crossbreds derived from one R parent than the selection lines and their crossbreds (Figure 5.1). These results are consistent with the more wasteful use of the dietary energy by the R line reported by Stephenson and Malik (1984) using the same lines of mice as in the present study but at a later generation. Fifty percent inheritance of the R line resulted in a lower efficiency of the R line crossbreds. The feed efficiency situation needs to be analysed in terms of energy parameters before it is possible to provide a full interpretation.

5.4.1 Direct Genetic Effects

Ten generations of divergent selection for body weight can be expected to lead to gene frequency changes at a number of loci in the selection lines. Another cause of change in gene frequency of the selected lines may be attributed to directional dominance which is a well documented feature of body weight selection in the mouse (Roberts, 1967). Changes in gene frequency due to the above reasons would have automatically led to differences in the direct genetic effects of the three lines. From the observations in the present study it appears that the selection for increased 8 week body weight resulted in positive increases in the direct genetic effects. Conversely, as expected, selection for decreased 8 week body weight produced changes in the opposite direction. The positive correlated responses in direct genetic effects of the H and L lines ($a_H^O - a_R^O$ and $a_R^O - a_L^O$) in general reflected positive genetic correlations between 8 week body weight and other traits, namely 3 week body weight, fat and protein weight at 3 and 8 weeks together with feed intake, weight gain and feed efficiency during this period (feed efficiency comparison $a_R^O - a_L^O$ was negative and not significant).

The following deductions can be made from the between-line comparisons for direct genetic effects (Table 5.6). Firstly, they showed a consistent increasing trend from 3 to 8 weeks in all the traits studied, indicating a decreasing importance of maternal effects in the postweaning period of growth. Secondly, selection of the lines used in this study was made at a late postweaning weight and this should have given a greater emphasis to direct genetic effects in the selection response than in experiments where selection, made at an early age, should have given greater emphasis to maternal effects. A further discussion of direct genetic effects observed in this study in relation to maternal influences and similar work reported elsewhere is presented in Section 5.4.3.

5.4.2 Maternal Genetic Effects

The average performance of a population or a line is determined by maternal influences as well as direct genetic effects. The maternal effect is an effect contributed to the phenotypic value of an individual by its dam. The dam therefore, contributes an environmental influence to the offspring but this influence is genetic in the sense that the genotypic differences among dams are expressed in the phenotypic measurements of their progeny (Willham, 1963, 1980). Hence, the phenotypic expression of the traits of young individuals is influenced by two genetic components. The contributions of the maternal genetic component may not necessarily be limited to traits at younger ages since carry-over effects of maternal influences on postweaning weights have been reported in mice (Legates, 1972).

Large and significant differences between lines for maternal genetic effects on 3 week body weight in this study agree with a number of reports reviewed by Legates (1972). Extremely large postnatal maternal effects during the preweaning phase have been reported (Cox *et al.*, 1959; Young *et al.*, 1965; El Oksh *et al.*, 1967; Rutledge *et al.*, 1972; Brandsch and Kadry, 1977; Nagai, 1977). Although diminishing in relative importance they are still present even at the age of sexual maturity. Cox *et al.* (1959) and Young *et al.* (1965) showed that postnatal maternal influences in their mice were responsible for 65 percent of the variance in 3 week body weight and 16 percent of the variance in 8 week body weight. In the present study, 41, 67 and 18 percent of the differences in 3 week body weight, and 8, 33 and 24 percent of the differences in 8 week body weight between the H and L, H and R, and R and L respectively, were accounted for by the maternal genetic effects. For 8 week body weight these differences were significant only between H and R lines.

In contrast with the present findings, Eisen (1973) reported no between-line differences in maternal effects for both pre- and postweaning body weights in mice. However, it is noteworthy that after 22 generations of selection for 12-day litter weight, the difference in weight between the selected and the control line in his study was only 0.63 g at 3 weeks and 1.24 g at 8 weeks. In a study by Bakker *et al.* (1976), maternal genetic effects accounted for 82 percent ($P < 0.01$) and 27 percent ($P < 0.05$) respectively, of the body weight differences at 3 and 6 weeks between two unrelated control populations, but contrary to the present results they did not account for any of the differences between the two unrelated selected populations, one of which was selected for 36 generations for 6 week body weight and another for 73 generations for 3 to 6 week postweaning gain. However, after adjusting for differences in maternal genetic effects of the controls, the maternal genetic effects of the weight gain selection line were less compared with the body weight line. Correlated responses in maternal genetic effects were not significant for either of the two selection lines (Nagai *et al.*, 1976).

The line differences in maternal genetic effects for fat weight at 3 weeks found in the present experiment support the findings of Hayes and Eisen (1979b) for among-line differences for the proportion of fat at 12 days. However, Eisen *et al.* (1977) observed no significant differences between lines in maternal effects on fat and protein as percentages of the whole carcass. The higher maternal effects of the H and R lines in this study may possibly have resulted in higher fat deposition in the progeny of LH and LR crosses presumably through a high level of nutrition relative to growth potential of the progeny in the suckling period. It is not known if there were any differences between the genetic groups with respect to the milk fat content. Bandy and Eisen (1984) reported that for ash, fat, moisture and protein at 6 weeks, differences in direct genetic and maternal genetic effects were similar and favoured the line selected for high body weight at 6 weeks as compared with the line selected for large litter size. Similar results were found for feed consumption and weight

gain. The findings of Bandy and Eisen support the results of this study that maternal effects were present in postweaning traits.

In summary, the present results showed that there were significant differences between the H, L and R lines in direct and maternal genetic effects. As expected, the contribution of direct genetic effects increased during the postweaning period, whereas that of maternal genetic effects decreased. The H line mice were larger, consumed more food, accumulated more fat and protein, grew faster and were also more efficient than both the R and L line mice. The L mice were smaller, their feed intake was low and they were leaner than the other lines. In the H-R and R-L comparisons the differences in direct and maternal genetic effects followed a pattern similar to the overall differences between the three populations for body weight. This pattern generally fits with other studies where selection is for postweaning body weight. A reverse maternal effect is expected in lines selected for postweaning growth rate. Selection for preweaning body weight or growth rate should produce a positive relationship between the direct genetic and maternal contributions.

5.4.3 The Relationships Between Direct Genetic, Maternal Genetic and Compensatory Growth Effects

The negative maternal genetic effects in the H and L comparison, calculated from the reciprocal crosses involving these lines (LH-HL), for feed intake and weight gain indicate recuperative capacity of the HL mice in the postweaning period. At 3 weeks, the HL mice weighed 1.82 g less than the LH mice as a result of poor maternal ability but gained 0.86 g more in body weight from 3 to 8 weeks (15.13 g vs 14.27) by consuming 15.34 g more food. The HL mice whose early growth may have been depressed by the inferior maternal ability of the L dams exhibited compensatory growth in the postweaning period when they were no longer dependent upon the maternal source of nutrition. Compensatory growth in mice, between 4 and 8 weeks, has been reported by Monteiro and Falconer (1966) although their analytical methods were markedly different to

those of the present study. They observed increased variance, due to maternal effects, in body weights between birth and 4 weeks, followed by a decrease in variance between 4 and 8 weeks, an indication of compensatory growth. Furthermore, a high litter weight at 4 weeks in their study was followed by low subsequent growth up to 8 weeks and vice versa, conclusive evidence that compensatory growth had taken place. Stephenson and Malik (1984) also reported compensatory growth in the lines of mice used in the present work. Such effects are well documented in mammals and birds (Wilson and Osbourn, 1960).

Experimental studies of compensatory growth following periods of under-nutrition have been reviewed by Wilson and Osbourn (1960). They calculated a recovery index to describe the response to re-alimentation as 100 x (A-B)/A where A = initial weight difference between the experimental groups at the end of the period of restriction and B = the weight difference between the same groups after a period of re-alimentation. Using this method, the recovery index for the HL mice relative to their LH counterparts in the present study was calculated as 47.25%. There was no evidence of compensatory growth in the reciprocal crosses involving the H and R, and R and L lines.

The deduction about an increasing trend of direct genetic effects with age is consistent with the findings of other workers (Bakker *et al.*, 1976; Bandy and Eisen, 1976; Nagai *et al.*, 1976) where the direct genetic effects were shown to increase in importance compared with the maternal genetic effects after weaning. This result is expected because maternal effects diminish in the postweaning period. A comparison between the present results and the findings of Bandy and Eisen (1984) suggests that selection for postweaning weight at a late age places greater emphasis on direct genetic effects compared to selection for postweaning weight at an early age. The body weight line of Bandy and Eisen which was selected at 6 weeks showed little direct genetic effect on birth weight, 12 day weight and 3 week weight and maternal genetic effects were the only significant difference between this line and a

line selected for large litter size. However, maternal genetic effects in their study were influenced by the litter size effect. In the present study the selection at a comparatively late age (8 weeks) resulted in differences between lines in both direct genetic and maternal genetic effects. The direct genetic effects were larger than the maternal genetic effects and were significant even at 3 week body weight for comparisons between H-L and R-L but not for H-R. In contrast with the selection for body weight, the selection for weight gain between 3 and 6 weeks has been shown to give non significant negative maternal genetic effects and positive direct genetic effects to the progeny after adjusting for differences in maternal genetic effects of the control lines (Bakker *et al.*, 1976). Selection for low body weight in the present study produced a negative maternal genetic effect and as a consequence the HL line mice showed a compensatory growth after weaning. From the above discussion it appears that selection for postweaning growth rate or low body weight may favour dams with poor maternal ability. If the difference in maternal effects between the two lines is large, the offspring of the line with poorer maternal ability may show accelerated gains due to compensatory growth. Alternatively, selection for body weight should favour genotypes with high potential for growth and good maternal effects and both contribute to the response.

5.4.4 Heterosis

When two genetically different populations are crossed, the offspring are frequently superior to the mean of the parents, the requirement being that the populations crossed must be genetically distinct. Selection for high and low body weight would have had the effect of creating genetic divergence between the L, H and R lines used in this study, in terms of the alleles they possess that influence body weight and correlated traits. However, any heterosis observed in 3 week body weight may have a strong maternal component. Heterosis for 8 week body weight and postweaning traits on the other hand, when the carry-over effects of the maternal environment are likely to have diminished, should mainly be

due to the interactions between genes of the progeny. In this study, direct genetic effects were more important than heterosis for all the traits. Eisen (1973) from a cross between a line selected for increased 12 day litter weight and its control found direct heterosis for pre- and postweaning body weights but direct genetic effects were at least as important as heterosis. Bakker *et al.* (1976) and Nagai (1976) have also reported significant heterosis for body weight or weight gain in crosses between two selected lines and two control lines of mice. Bandy and Eisen (1984) did not observe direct heterosis in pre- and postweaning body weights but observed direct heterosis for moisture, protein and ash weight in a cross between lines selected for increased 6 week body weight and large litter size. They reported that the differences in litter size between lines suppressed heterosis in body weight. In the present study, however, the effect of litter size was reduced by reducing the size of the larger litters to 8 pups.

Heterosis arises from dominance and epistatic deviations. Comparisons of hybrid offspring deviations from the mid-parent values allow us to draw conclusions about heterosis contributions. If the F_1 mean is mid-way between the parental means, both dominance and epistasis should be unimportant or dominance and epistatic effects balance. If the F_1 mean deviates from the mid-parent value then the genes concerned may show complete or partial dominance and epistasis. Because heterosis in 3 week and 8 week body weight and most of the other correlated traits was in the direction of the larger parental line, it supports the findings of Falconer (1953) and Roberts (1967) that directional dominance favours larger body size.

From the results of the present study and those reported by Bakker *et al.* (1976), Nagai *et al.* (1976) and Bandy and Eisen (1984), it would appear that heterosis is not an uncommon although not a regular feature in crosses of selected lines of mice. In the present work, the magnitude

of heterosis in body weight and weight gain ranged from 4.3 to 8.3 percent. For other traits this range was between 7.4 and 11.3 percent. Nagai *et al.* (1976) observed an increase in the percent direct heterosis for body weight from birth to 31 days and then a decrease at later ages, in crosses between two lines one of which was selected for high 6 week body weight and another for 3 to 6 week weight gain. The magnitude of the increase varied from 1 percent at birth to 19 percent at 31 days followed by a decrease to 6 percent at 63 days. Bakker *et al.* (1976) found a 5 percent direct heterosis for 3 and 6 week body weights and 3 to 6 week weight gain in F_1 crosses between selected and control lines. In previous studies involving these lines (Eisen, 1975; Johnson and Eisen, 1975; White *et al.*, 1970), the extent of heterosis in F_1 crosses ranged from 0 to 7 percent. Eisen (1973) using a line selected for 12-day litter weight crossed with the control line found that the magnitude of heterosis at various body weights from 12 to 70 days of age was at the most 6 percent. The findings in the present study, therefore, fit with the large body of the published work although it is difficult to make valid comparisons between the different studies as the crosses are not comparable. However, it appears that the magnitude of heterosis in crosses between selection lines is not large.

Maternal heterosis when calculated by the method given in Table 4.2 gave significant values for 3 week body weight and 3 week protein weight in the crosses between H and L lines. However, when calculated as the deviation of 3-way crosses from 2-way crosses (biased estimate, Table 5.9), the maternal heterosis was significant only for 3 week body weight. The estimates of maternal heterosis calculated by the latter procedure were lower for most of the traits because of the bias included in these estimates by a ½th component of recombination effects of the offspring ($\frac{1}{2}r^O$). Eisen (1973) for body weights at 12 and 21 days and Nagai *et al.* (1976) for a range of weights between 12 and 63 days have reported significant maternal heterosis in mice. A negative maternal heterosis for 6 week weight reported by Bandy and Eisen (1984) was as a result of increased litter size of the F_1 dams which

negatively influenced the body weight of the progeny at this age. Maternal heterosis in their study was not significant for body composition traits, weight gain and feed efficiency but significant for feed consumption between 3 and 8 weeks. In the present study except for 3 week body weight and protein weight, maternal heterosis was not significant for any of the other body composition traits as well as for feed intake, weight gain and feed efficiency.

The influence of maternal heterosis on progeny traits is important because a significant and positive maternal heterosis suggests an advantage from the use of crossbred dams for characters in young animals. The physiological basis of this lies in the prenatal conditions like uterine influences and postnatal conditions especially milk production, which are more favourable in crossbred than in straightbred females. However, maternal effects (g^M and h^M) are one generation out of phase with the non-maternal part of the character. In the F_2, the non-maternal part loses half the heterosis but the maternal effect shows the full effect of its heterosis because the mothers are now in F_1 stage. Hence the loss in F_2 offspring hybrid vigour may not always be noticeable.

5.4.5 Recombination Effects

There is a good deal of confusion regarding the terminology of recombination loss and epistasis used in the literature. Therefore it is important to reconcile the terminology before discussing the results of 'r' parameter in this study.

Dickerson (1973) used the term "recombination effect" to measure the deviation from a linear association between heterosis and degree of heterozygosity. The coefficient 'r' describes the "average fraction of independently segregating pairs of loci in gametes from both parents which are expected to be non-parental combinations". Kinghorn (1980) used the term 'e' to describe breakdown of favourable epistasis. Under his hypothesis 'x', the coefficient of e is "proportional to the probability that two nonallelic genes chosen randomly in the diploid individual are of different breed origin". Kinghorn

(1983) subsequently proposed that his hypothesis 'x' was equivalent to an additive x additive model of gene interaction and that this in turn is mathematically equivalent to using recombination loss to describe epistatic effects. Hill (1981, 1982) criticised the use of the term recombination loss stating it implies that coupling and repulsion heterozygotes are different. Hill preferred the use of two locus interactions in diploids over the recombination loss formulation. Kinghorn (1983) pointed out that the apparent anomaly that recombination loss relates to cis-acting effects of genes is compensated for by simultaneous use of the parameter h which in fact involves both dominance and epistasis. It follows from the above discussion that the model proposed by Dickerson (1969, 1973) and the hypothesis 'x' of Kinghorn (1980) are mathematically equivalent and will result in similar analyses of variance with linear relationships between the resulting parameter estimates. In the present study Dickerson's models provided the basis for the development of the crossbreeding Scheme in Section 4 which was used to calculate recombination effects.

The estimates of recombination effects in this study had large standard errors, and none were statistically significant. Interestingly, however, all estimates except for feed intake were unfavourable (negative). The possible ways to circumvent the problem of large standard errors would be: i) by increasing the sample size above that was used in the current study (although the number of mice used from each line/line cross for 3 week body weight was large) or, ii) by devising more efficient analytical procedures for their estimation. In an experiment reported in mice (Eisen, 1973) in which recombination effects were measured for body weights at a number of ages between 12 and 70 days, none of the estimates approached statistical significance and all were negative. Kinghorn (1983) in a study using inbred lines of mice reported additive x additive epistatic effects for body weight, tail length, litter size and mortality at 7 weeks. This is the only reported study in mice where epistatic effects were found to be significant. Bandy and Eisen (1984) found negligible recombination losses for body weight, body

composition and feed efficiency and suggested that this may possibly have been due to different selection history of the lines used in their study. Rastogi *et al.* (1982) report small but positive recombination effects for weaning weight and preweaning gains favouring three-breed cross lambs but do not give standard errors of the estimates, hence the value of their estimates is questionable.

In summary, direct genetic and maternal genetic effects favouring H, R and L lines in that order were responsible for between-line differences in most of the traits studied. Direct genetic effects were more important than maternal genetic effects for both preweaning and postweaning traits, whereas maternal genetic effects were important mostly for the preweaning traits. Direct heterosis in F_1 crosses was significant for body weight and some other traits. Maternal heterosis was significant for 3 week body weight and protein weight in crosses between H and L lines. Recombination effects were mostly negative and were not significant.

SECTION 6

GENERAL CONCLUSIONS

GENERAL CONCLUSIONS

Selection for postweaning body weight is effective in bringing about marked changes in growth rate and leads to significant alterations in body composition, feed consumption and feed efficiency. Selection for increased body weight has the effect of increasing feed intake and body fat, yet the feed efficiency is improved apparently by reducing dietary or other variable thermogenic effects. Selection for decreased body weight has the opposite effect on feed intake and body fat, although feed efficiency may not change or even increase. Improvement of feed efficiency in the large mice results from their reduced maintenance requirements per unit of metabolic body weight and greater efficiency of utilisation of energy for growth; and not from improvement in digestive efficiency.

Unconfounded estimates of differences between lines for direct genetic, maternal genetic, direct heterosis, maternal heterosis and recombination effects show that the direct genetic effects account for a major proportion of the phenotypic differences in the body weight, weight gain, body composition, feed consumption and feed efficiency. Maternal effects are relatively small and are more important for weaning traits than for postweaning traits. Direct heterosis in F_1 crosses is observed in body weight and some other related traits. It is indicated that inclusion of F_1 dams in a breeding programme will enhance preweaning growth of the crossbred progeny, presumably by providing a better maternal environment.

A further extension of the present study is indicated, viz:

Determination of the mechanisms involved in changing the metabolic efficiency of the selected mice. Attention should be given to physiological and biochemical measurements associated with growth and energy metabolism such as thermoregulatory thermogenesis, rate and cost of protein and fat synthesis and degradation, and growth related hormonal levels.