

# Selection for weight gain in mice at two ages and under ad libitum and restricted feeding

## 2. Efficiency, consumption and body composition

M. S. Urrutia and J. F. Hayes

Department of Animal Science, Macdonald College of McGill University, 21,111 Lakeshore Road, Ste Anne de Bellevue, Québec H9X 1CO, Canada

Received April 18, 1986; Accepted March 31, 1987

Communicated by E. J. Eisen

**Summary.** Correlated responses in feed efficiency, feed consumption and body composition were investigated after nine generations of selection for weight gain in two age intervals, 28 to 38 or 48 to 58 days old, and under ad libitum feed consumption or intake restricted to 80% of the control lines. Correlated responses in feed efficiency and feed consumption in the ad libitum lines were positive in the early period and negative in the late period. Restricted lines had a positive response in feed efficiency and a negative response in consumption in both periods of selection. Changes in body composition in the early period were the same in all selected lines: a lower crude protein percentage at the start of the period and a lower ash percentage at the end of the period. Body composition at the start of the late period was not altered by selection, while at the end of the period ad libitum lines had higher dry matter percentages and restricted lines had lower fat and higher ash percentages. Body composition at 100 days old was not affected by selection except for dry matter percent, which was lower in the restricted lines.

**Key words:** Mice – Selection – Body composition – Gain

### Introduction

Selection for increased growth in mice has usually been accompanied by correlated changes in feed efficiency, feed consumption and body composition. Feed efficiency and feed consumption have been reported to increase as a result of selection (Fowler 1962; Lang and Legates 1969; Sutherland et al. 1970; Timon and Eisen 1970; Brown and Frahm 1975; Kownacki et al. 1977;

McPhee et al. 1980; Roberts 1981; Stanier and Mount 1972).

Increased fatness, particularly in adulthood, has been an outcome of selection for increased growth (Fowler 1958; Clarke as reviewed by Roberts 1979; Timon and Eisen 1970; Hayes and McCarthy 1976; Eisen et al. 1977; Allen and McCarthy 1980; McPhee et al. 1980; McPhee and Neill 1976; Hull 1960; Bakker et al. 1978; Baker et al. 1979). On the other hand, Lang and Legates (1969), Brown et al. (1977) and McKay et al. (1985) did not observe significant differences in fat percent in their selected lines. Biondini et al. (1968) and Eisen et al. (1977) reported lines that increased in fat and lines that showed no change.

Clarke (as reviewed by Roberts 1979) indicated that selection did not increase fatness up to the age of selection, but that after selection animals became progressively fatter. Hayes and McCarthy (1976) proposed that the differences in fatness due to selection at different ages could be due to the type of genetic variance being utilized. Selection at early ages would favor mainly animals with increased appetites while selection at later ages, when animals are laying down fat at a higher rate, would favor animals that also have a differential ratio of tissue deposition towards lean tissue. This implied that selection under feed restriction, as proposed by Falconer (1960), would lead to leaner and more efficient animals when practiced at later ages. Direct evidence regarding these predictions is very limited. Baker et al. (1979) selected at three ages but only under ad libitum feeding and found the animals selected at later ages to be the leanest and to remain the leanest. Thus, they supported the presence of genetic variation in tissue deposition at later ages. McPhee et al. (1980) selected for weight gain at between 5 and 9 weeks old under feed restriction and

found selected mice to be more efficient but fatter than controls. However, they did not have lines selected under ad libitum feeding, and because of the age period involved selection may have implicated several genetic mechanisms.

A study in which selection is practiced at two ages and under ad libitum and restricted feeding is needed in order to better understand the type of genetic variance being utilized and be able to predict the nature of correlated responses. Such a study has been reported (Urrutia and Hayes 1987), and the present study evaluates the correlated responses in feed efficiency, feed consumption and body composition.

## Materials and methods

### Laboratory procedures

This study was carried out in generation nine of lines selected for weight gain at two ages and under two feeding regimes. The ten line-replicates were: EPR1 and EPR2, early period restricted replicates 1 and 2, selected for increased gain between 28 and 38 days old under a restricted feeding regime; EPA1 and EPA2, early period ad libitum replicates 1 and 2, selected for increased gain between 28 and 38 days of age under an ad libitum feeding regime; LPR1 and LPR2, late period restricted replicates 1 and 2, selected for increased gain between 48 and 58 days of age under a restricted feeding regime; LPA1 and LPA2, late period ad libitum replicates 1 and 2, selected for increased gain between 48 and 58 days of age under an ad libitum feeding regime; and C1 and C2 control line replicates 1 and 2, maintained by random selection. The foundation population and the regular laboratory procedures have been described in an earlier report on direct and correlated responses to selection (Urrutia and Hayes 1987).

In generation nine, no selection was practiced and mice were weighed when 21, 28, 38, 48, 58, and 100 days old. When 28 days old, ten males and ten females from each of lines EPR1, EPR2, EPA1, EPA2, C1, and C2 were killed and body composition determined. Another ten males and ten females from each of these lines were individually caged and ad libitum feed consumption was measured up to day 38. At day 38, these mice were killed and body composition determined. The same procedure was followed for lines LPR1, LPR2, LPA1, LPA2, C1, and C2 between 48 and 58 days old. Ten males of each line were kept until 100 days old and then weighed, killed and body composition determined.

All mice were fed standard Laboratory Chow from Purina, as in all previous generations. Water was available ad libitum at all times. Lights were kept in a standard regime of 12 h light and 12 h darkness. The temperature in the mouse laboratory varied between 18 °C and 23 °C.

### Body composition analysis

All mice were killed with CO<sub>2</sub>. The gut was excised, its contents removed, and replaced in the abdominal cavity after rinsing with distilled water. Empty body weight was then recorded. Whole mice were placed in individual containers, cut into several pieces and frozen at -18 °C. The frozen carcass was dried in a freeze dryer for approximately 24 to 48 h depending on the size of the mouse. Percentage dry matter of

the carcass was calculated from the empty body weight and the dry carcass weight. For fat content, the whole mouse was placed in cellulose thimbles, dried in a vacuum oven at 100 °C overnight, and fat was extracted using anhydrous ethyl ether in a Soxhlet extractor. Samples were then redried in a vacuum oven at 110 °C for 4 h and fat content calculated. After fat determination the samples were ground and homogenized. Crude protein was determined in duplicate from homogenized samples of 0.3 g by the Kjeldahl procedure (AOAC 1980), using a semiautomatic Kjelfoss instrument. Ash was determined from two homogeneous samples of 1 to 2 g per mouse using a furnace at 600 °C. The arithmetic mean of the duplicates was taken to be the true value of the determination. Where the difference between duplicates was larger than 5% a third determination was made and included in the arithmetic mean.

### Statistical analysis

Efficiency, as the ratio of gain to total consumption, consumption corrected for body weight at the start of the selection period and body composition were analyzed using the General Linear Model procedure of the Statistical Analysis System (1982).

The model was:

$$Y_{ijkl} = \mu + L_i + R_{ij} + S_k + SL_{ik} + SRL_{ijk} + bWt_{ijkl} + e_{ijkl}$$

where:

$Y_{ijkl}$  = observation for the  $l^{\text{th}}$  mouse of the  $ijkl^{\text{th}}$  subclass,

$\mu$  = mean of the population,

$L_i$  = fixed effect of the  $i^{\text{th}}$  line,

$R_{ij}$  = random effect of the  $j^{\text{th}}$  replicate nested within the  $i^{\text{th}}$  line,

$S_k$  = fixed effect of the  $k^{\text{th}}$  sex,

$(SL)_{ik}$  = interaction of the  $k^{\text{th}}$  sex with the  $i^{\text{th}}$  line,

$(SRL)_{ijk}$  = interaction of the  $k^{\text{th}}$  sex with the  $j^{\text{th}}$  replicate of the  $i^{\text{th}}$  line,

$b$  = (where used) regression coefficient of  $Y$  on empty body weight,

$Wt_{ijkl}$  = empty body weight of the  $ijkl^{\text{th}}$  mouse (used only in the analysis of feed consumption),

$e_{ijkl}$  = random error, assumed  $N(0, \sigma^2)$ .

The error term used to test the effect of line and the interaction of line and sex was the mean square for replicates nested within line. All other effects were tested against the residual mean square. Differences between the lines were tested using linear contrasts. The error term used to test the level of significance of contrasts was constructed using the mean square for replicates nested within line. The standard errors of the contrasts, therefore, take into account genetic drift.

The body composition data were analyzed separately for each age. The ages of 28 and 38 days correspond to the start and end of the early selection period. The ages of 48 and 58 days correspond to the start and end of the late selection period. The analysis for 100 days old included all lines in order to detect the effect on body weight and body composition at adulthood of the different selection criteria. The effect of sex and the interactions including sex were not included in the model for this age since only males were present.

## Results

### Efficiency and consumption

Least-square means for gross efficiency (gain/feed consumption) and consumption corrected for body weight

**Table 1.** Efficiency of feed utilization (gain/consumption) and consumption in g corrected for body weight at the start of the selection period. Early period of selection. *NS*: not significant

a Least-squares means $\pm$ SE		
Line	Efficiency	Consumption
EPR1	0.076 $\pm$ 0.006	40.8 $\pm$ 1.02
EPR2	0.092 $\pm$ 0.006	41.6 $\pm$ 1.08
EPA1	0.078 $\pm$ 0.006	46.0 $\pm$ 0.98
EPA2	0.095 $\pm$ 0.006	44.4 $\pm$ 1.01
C1	0.074 $\pm$ 0.006	43.3 $\pm$ 1.06
C2	0.068 $\pm$ 0.006	44.4 $\pm$ 0.99
b Linear contrasts		
C-EPR	-0.013 <i>NS</i>	2.6 ( $P=0.059$ )
C-EPA	-0.016 <i>NS</i>	-1.4 <i>NS</i>
EPA-EPR	0.003 <i>NS</i>	4.0*

\*  $P < 0.05$ **Table 2.** Efficiency of feed utilization (gain/consumption) and consumption in g corrected for body weight at the start of the selection period. Late period of selection. *NS*: not significant

a Least-squares means $\pm$ SE		
Line	Efficiency	Consumption
LPR1	0.022 $\pm$ 0.006	40.4 $\pm$ 1.14
LPR2	0.019 $\pm$ 0.006	40.8 $\pm$ 1.10
LPA1	0.000 $\pm$ 0.006	46.1 $\pm$ 1.13
LPA2	0.001 $\pm$ 0.006	43.5 $\pm$ 1.12
C1	0.004 $\pm$ 0.006	45.7 $\pm$ 1.11
C2	0.007 $\pm$ 0.006	49.4 $\pm$ 1.10
b Linear contrasts		
C-LPR	-0.015**	7.0*
C-LPA	0.005*	2.7 <i>NS</i>
LPA-LPR	-0.020**	4.3 <i>NS</i>

\*  $P < 0.05$ \*\*  $P < 0.01$ **Table 3.** Carcass composition at the start of the selection period. Dry matter as % of empty body weight, fat as % of dry matter, and ash and crude protein as % of the fat free body (FFB). Early period of selection. *NS*: not significant

a Least-squares means $\pm$ SE					
Line	Empty body weight (g)	Dry matter	Fat	Ash	Crude protein
EPR1	18.5 $\pm$ 0.32	30.7 $\pm$ 0.42	28.8 $\pm$ 0.96	14.2 $\pm$ 0.20	81.1 $\pm$ 0.43
EPR2	17.4 $\pm$ 0.32	29.2 $\pm$ 0.42	27.1 $\pm$ 0.96	14.1 $\pm$ 0.20	81.0 $\pm$ 0.43
EPA1	18.9 $\pm$ 0.32	29.6 $\pm$ 0.42	27.6 $\pm$ 0.96	13.8 $\pm$ 0.20	81.0 $\pm$ 0.43
EPA2	18.9 $\pm$ 0.32	30.3 $\pm$ 0.42	28.0 $\pm$ 0.96	14.0 $\pm$ 0.20	81.8 $\pm$ 0.43
C1	20.7 $\pm$ 0.32	30.2 $\pm$ 0.43	29.9 $\pm$ 0.98	14.0 $\pm$ 0.20	83.0 $\pm$ 0.44
C2	19.6 $\pm$ 0.33	29.9 $\pm$ 0.42	27.3 $\pm$ 0.96	14.5 $\pm$ 0.20	83.5 $\pm$ 0.43
b Linear contrasts					
C-EPR	2.18*	0.12 <i>NS</i>	0.62 <i>NS</i>	0.09 <i>NS</i>	2.3**
C-EPA	1.26 <i>NS</i>	0.13 <i>NS</i>	0.80 <i>NS</i>	0.37 <i>NS</i>	1.9*
EPA-EPR	0.92 <i>NS</i>	-0.01 <i>NS</i>	-0.18 <i>NS</i>	-0.28 <i>NS</i>	0.4 <i>NS</i>

\*  $P < 0.05$ \*\*  $P < 0.01$ 

at the start of the selection period are presented in Table 1a for the early period and Table 2a for the late period. Linear contrasts among the lines are presented in part 'b' of the Tables.

In the early period, gross efficiency was higher in the ad libitum and restricted lines than the control, but the difference was not significant. Ad libitum consumption corrected for initial body weight was highest in the ad libitum line and lowest in the restricted line. The difference between the restricted and ad libitum lines was significant and the the difference between restricted and control lines was very close to significance ( $P=0.059$ ).

In the late period of selection, gross efficiency was significantly higher in the restricted line and the control line had significantly higher gross efficiency than the ad libitum line. Consumption corrected for body weight was lowest in the restricted line and intermediate in the ad libitum line. The difference between restricted and control lines was significant.

#### Body composition

Least-squares estimates of means for empty body weight and body components at the start of the early period of selection are presented in Table 3a and linear contrasts among the lines are presented in Table 3b. Empty body weight is expressed in g, dry matter is expressed as a percentage of empty body weight, fat is expressed as a percentage of dry matter, and ash and protein are expressed as a percentage of the fat-free body (FFB).

The control line had the highest empty body weight and the line selected under restriction the lowest. The difference between these two lines was significant, and the differences between ad libitum and control lines and among selected lines were not. All lines had very

**Table 4.** Carcass composition at the end of the selection period. Dry matter as % of empty body weight, fat as % of dry matter, ash and crude protein as % of the fat free body (FFB). Early period of selection. *NS*: not significant

a Least-squares means $\pm$ SE					
Line	Empty body weight (g)	Dry matter	Fat	Ash	Crude protein
EPR1	22.4 $\pm$ 0.46	31.9 $\pm$ 0.49	26.1 $\pm$ 1.32	14.6 $\pm$ 0.25	81.3 $\pm$ 0.45
EPR2	20.5 $\pm$ 0.44	31.6 $\pm$ 0.47	26.4 $\pm$ 1.27	14.2 $\pm$ 0.24	81.8 $\pm$ 0.44
EPA1	23.0 $\pm$ 0.43	31.2 $\pm$ 0.46	23.9 $\pm$ 1.24	14.5 $\pm$ 0.24	81.9 $\pm$ 0.43
EPA2	22.8 $\pm$ 0.44	31.7 $\pm$ 0.47	25.8 $\pm$ 1.27	14.3 $\pm$ 0.24	81.4 $\pm$ 0.44
C1	22.6 $\pm$ 0.46	30.9 $\pm$ 0.48	24.6 $\pm$ 1.30	15.2 $\pm$ 0.25	81.4 $\pm$ 0.45
C2	21.6 $\pm$ 0.44	29.7 $\pm$ 0.47	21.5 $\pm$ 1.27	15.3 $\pm$ 0.24	81.3 $\pm$ 0.44
b Linear contrasts					
C-EPR	0.68 NS	- 1.45 ( $P=0.077$ )	- 3.18 NS	0.84*	- 0.24 NS
C-EPA	0.80 NS	1.16 NS	- 1.78 NS	0.80*	- 0.30 NS
EPA-EPR	1.48 NS	- 0.29 NS	- 1.40 NS	0.04 NS	0.06 NS

\*  $P < 0.05$ **Table 5.** Carcass composition at the start of the selection period. Dry matter as % of empty body weight, fat as % of dry matter, ash and crude protein as % of the fat free body (FFB). Late period of selection. *NS*: not significant

a Least-squares means $\pm$ SE					
Line	Empty body weight (g)	Dry matter	Fat	Ash	Crude protein
LPR1	24.7 $\pm$ 0.45	33.3 $\pm$ 0.54	28.3 $\pm$ 1.49	14.7 $\pm$ 0.19	79.1 $\pm$ 0.38
LPR2	25.4 $\pm$ 0.45	32.8 $\pm$ 0.54	26.0 $\pm$ 1.49	15.2 $\pm$ 0.19	78.5 $\pm$ 0.37
LPA1	25.6 $\pm$ 0.45	33.4 $\pm$ 0.54	29.5 $\pm$ 1.49	14.8 $\pm$ 0.19	80.1 $\pm$ 0.37
LPA2	26.7 $\pm$ 0.47	34.0 $\pm$ 0.54	29.9 $\pm$ 1.49	15.0 $\pm$ 0.19	80.1 $\pm$ 0.38
C1	26.3 $\pm$ 0.47	33.5 $\pm$ 0.56	20.5 $\pm$ 1.53	15.0 $\pm$ 0.20	79.2 $\pm$ 0.38
C2	26.0 $\pm$ 0.45	33.6 $\pm$ 0.54	29.2 $\pm$ 1.49	15.5 $\pm$ 0.19	80.9 $\pm$ 0.37
b Linear contrasts					
C-LPR	1.06 NS	0.58 NS	2.69 ( $P=0.091$ )	0.31 NS	1.08 NS
C-LPA	0.00 NS	- 0.13 NS	0.11 NS	0.36 NS	0.07 NS
LPA-LPR	1.06 NS	0.71 NS	2.58 ( $P=0.098$ )	- 0.05 NS	1.15 NS

similar mean dry matter percentages; none of the differences among lines was significant. The fat and ash percentages were highest in the control line, followed by the line selected under restriction; however, differences among lines were not significant. The differences between lines for crude protein were significant, with the control line having a significantly higher protein percentage than restricted and ad libitum lines. The ad libitum line had a higher protein percentage than the lines selected under restriction, but this difference was not significant.

Table 4 presents the data for the end of the early period of selection. The ad libitum line had the highest empty body weight and the line selected under restriction the lowest, but the difference was not significant. Dry matter and fat percentages were not significantly different among lines; however, the control line had the lowest dry matter and fat percentages and the lines

selected under restriction the highest. The control line had a significantly higher ash percentage than selected lines. All lines were very similar for crude protein percentages. The decrease in certain body components at the end of the period, compared with the start of the selection period, was due to single housing. It is not intended that comparisons be made between the two ages.

Data for body composition at the start of the late period of selection are presented in Table 5 and for the end of the selection period in Table 6. At the beginning of the late period of selection differences between the selected and control lines were not significant for any of the variables considered. Empty body weight was highest in the control line and lowest in the line selected under restriction. Dry matter, fat, and crude protein percentages were lowest in the restricted line, while ash percentages were very similar for all lines.

**Table 6.** Carcass composition at the end of the selection period. Dry matter as % of empty body weight, fat as % of dry matter, ash and crude protein as % of the fat free body (FFB). Late period of selection. *NS*: not significant

a Least-squares means $\pm$ SE					
Line	Empty body weight (g)	Dry matter	Fat	Ash	Crude protein
LPR1	24.6 $\pm$ 0.54	32.2 $\pm$ 0.60	23.0 $\pm$ 1.62	16.0 $\pm$ 0.20	79.5 $\pm$ 0.40
LPR2	25.5 $\pm$ 0.54	32.3 $\pm$ 0.60	24.8 $\pm$ 1.62	15.7 $\pm$ 0.20	79.5 $\pm$ 0.40
LPA1	26.0 $\pm$ 0.54	33.1 $\pm$ 0.60	26.2 $\pm$ 1.62	15.3 $\pm$ 0.20	78.4 $\pm$ 0.40
LPA2	26.4 $\pm$ 0.54	32.6 $\pm$ 0.60	27.3 $\pm$ 1.62	15.5 $\pm$ 0.20	79.4 $\pm$ 0.40
C1	26.3 $\pm$ 0.53	32.1 $\pm$ 0.59	24.9 $\pm$ 1.58	15.2 $\pm$ 0.19	79.7 $\pm$ 0.39
C2	26.2 $\pm$ 0.54	32.0 $\pm$ 0.69	24.5 $\pm$ 1.62	15.3 $\pm$ 0.20	80.1 $\pm$ 0.40
b Linear contrasts					
C-LPR	1.16 ( $P=0.058$ )	0.21 <i>NS</i>	0.79 <i>NS</i>	-0.58*	0.45 <i>NS</i>
C-LPA	0.01 <i>NS</i>	-0.77*	-2.07 <i>NS</i>	-0.16 <i>NS</i>	1.03 <i>NS</i>
LPA-LPR	1.15 ( $P=0.060$ )	0.56 ( $P=0.065$ )	2.86*	-0.42 ( $P=0.060$ )	0.58 <i>NS</i>

\*  $P < 0.05$ **Table 7.** Body weights in g and carcass composition at 100 days old. Dry matter as % of empty body weight, fat as % of dry matter, and ash and crude protein as % of a fat free body (FFB). Early and late period of selection. *NS*: not significant

a Least-squares means $\pm$ SE					
Line	Body weight	Dry matter	Fat	Ash	Crude protein
EPR1	38.1 $\pm$ 1.41	40.0 $\pm$ 1.23	44.6 $\pm$ 2.59	14.3 $\pm$ 0.40	80.3 $\pm$ 0.80
EPR2	33.7 $\pm$ 1.58	39.6 $\pm$ 1.38	42.5 $\pm$ 2.89	14.9 $\pm$ 0.45	79.2 $\pm$ 0.90
EPA1	40.9 $\pm$ 1.49	40.7 $\pm$ 1.30	45.9 $\pm$ 2.73	14.6 $\pm$ 0.42	79.1 $\pm$ 0.85
EPA2	38.2 $\pm$ 1.41	40.2 $\pm$ 1.23	40.1 $\pm$ 2.59	13.3 $\pm$ 0.40	79.9 $\pm$ 0.80
LPR1	36.4 $\pm$ 1.41	40.4 $\pm$ 1.23	43.5 $\pm$ 2.59	14.8 $\pm$ 0.40	78.8 $\pm$ 0.80
LPR2	35.9 $\pm$ 1.49	38.5 $\pm$ 1.30	40.3 $\pm$ 2.73	15.1 $\pm$ 0.42	79.2 $\pm$ 0.85
LPA1	38.1 $\pm$ 1.41	41.1 $\pm$ 1.23	45.6 $\pm$ 2.59	14.1 $\pm$ 0.40	79.5 $\pm$ 0.80
LPA2	40.4 $\pm$ 1.49	42.1 $\pm$ 1.30	46.0 $\pm$ 2.72	13.4 $\pm$ 0.42	76.6 $\pm$ 0.85
C1	41.7 $\pm$ 1.69	41.4 $\pm$ 1.47	46.8 $\pm$ 3.09	14.3 $\pm$ 0.48	79.4 $\pm$ 0.96
C2	40.1 $\pm$ 1.49	41.3 $\pm$ 1.30	46.4 $\pm$ 2.72	13.5 $\pm$ 0.42	78.5 $\pm$ 0.85
b Linear contrasts					
C-EPR	4.94 ( $P=0.051$ )	1.57 ( $P=0.098$ )	3.01 <i>NS</i>	-0.69 <i>NS</i>	0.801 <i>NS</i>
C-EPA	1.33 <i>NS</i>	0.94 <i>NS</i>	3.57 <i>NS</i>	-0.03 <i>NS</i>	-0.56 <i>NS</i>
C-LPR	4.69 ( $P=0.057$ )	1.92 ( $P=0.053$ )	4.63 <i>NS</i>	-1.03 <i>NS</i>	-0.09 <i>NS</i>
C-LPA	1.64 <i>NS</i>	-0.25 <i>NS</i>	1.20 <i>NS</i>	0.141 <i>NS</i>	0.92 <i>NS</i>
EPA-EPR	3.61 <i>NS</i>	0.63 <i>NS</i>	-0.56 <i>NS</i>	-0.66 <i>NS</i>	-0.24 <i>NS</i>
LPA-LPR	3.05 <i>NS</i>	2.17*	3.43 <i>NS</i>	-1.17 ( $P=0.089$ )	-1.01 <i>NS</i>
LPR-EPR	0.25 <i>NS</i>	-0.35 <i>NS</i>	-1.62 <i>NS</i>	0.34 <i>NS</i>	-0.71 <i>NS</i>
LPA-EPA	-0.30 <i>NS</i>	1.19 <i>NS</i>	2.37 <i>NS</i>	0.17 <i>NS</i>	-1.48 <i>NS</i>

\*  $P < 0.05$ 

At the end of the late period of selection there were significant differences in body composition between control and selected lines and among selected lines. Empty body weight was lowest in the restricted line and highest in the control line; this difference was very close to significance ( $P=0.058$ ). The difference between restricted and ad libitum lines was also very close to significance ( $P=0.060$ ). Dry matter was highest in the ad libitum line. The difference between ad libitum and control lines was significant, and the difference between selected lines was close to significance ( $P=0.065$ ). For

fat percentage, the ad libitum line was highest, the restricted line lowest, and the control line intermediate. The difference between ad libitum and restricted lines was significant. The control line had the lowest ash percentage and the restricted line the highest. The difference between control and restricted lines was significant and the difference between ad libitum and restricted lines was close to significance ( $P=0.060$ ). For protein percentages, the ad libitum line was lowest and the control line highest; however, none of these differences between lines was significant.

Empty body weights and body composition data at 100 days of age are reported in Table 7. Empty body weights were highest in the control line and lowest in the lines selected under restriction. Both these differences were very close to significance ( $P=0.051$  and  $P=0.057$ , respectively), whereas other differences between lines were not significant.

With respect to body composition, dry matter was lowest in the line selected under restriction in the late period and highest in the line selected under ad libitum feeding in the same period. The difference between ad libitum and restricted lines was significant and the difference between restricted lines in the late period and control lines was close to significance ( $P=0.057$ ). The control line had the highest fat percentage followed by the line selected ad libitum in the late period. The line selected under restriction in the late period had the lowest fat percentage, although differences among lines were not significant. Restriction at both ages resulted in marginally higher ash contents, though not significantly so. Non-significant line differences for protein percentages were found at this age; however, the protein percentages were highest in lines selected in the early period and lowest in the line selected ad libitum in the late period.

## Discussion

In previous studies feed efficiency and feed intake have been reported to increase as a result of selection for increased weight gain (Hetzl and Nicholas 1982; Rahnefeld et al. 1963; Timon and Eisen 1970). The results obtained in the early period in the ad libitum line are in agreement with these earlier studies; however, the results in the restricted line differ from previous reports. McPhee et al. (1980) reported that lines selected under restriction had the same consumption and higher efficiency than controls; thus, ad libitum intake did not change with selection. Results from this study indicated that gross efficiency was higher in the restricted line compared to the control line, but consumption was lower.

In the late period of selection consumption was lower in the ad libitum and restricted line than in the control line. These results do not agree with Timon and Eisen (1970) who reported that intake per gram of body weight was larger in selected mice at all body weights. They suggested that perhaps the increased consumption leads to a less efficient absorption and utilization of feed energy and this may influence the gross efficiency of the selected mice in a negative manner. In the present study the increased consumption in the ad libitum line was accompanied by an increased efficiency in the early period, and in the late period the

higher consumption of the control line compared with ad libitum lines was also accompanied by a higher efficiency. In the restricted lines the mechanism seems to be the same at both ages of selection. The fact that consumption and growth are reduced and efficiency is increased would suggest that maintenance requirements are reduced.

Results from these experiments indicate that selection under ad libitum feeding for post-weaning gain at different ages is based on different genetic mechanisms. Ad libitum lines in both periods of selection had higher weight gain than controls. In the early period, where the difference in weight gain was significant, consumption and efficiency were increased over the control line while in the later period, where the difference in weight gain was not significant, consumption and efficiency were below the control line. It appears therefore that the systems upon which selection acts in order to obtain the increased growth are different in the two periods.

With respect to body composition, crude protein percentages were significantly lower in both ad libitum and restricted lines at the start of the early period of selection. This lower crude protein percentage is probably part of the general strategy for increased weight gain in the selected lines, which implies lower body weights at the start of the selection period.

At the end of the early period of selection the control line had a significantly higher ash percentage than selected lines. Since at the start of the selection period selected lines had lower crude protein and lower fat percentages than the control line, while at the end of the selection period selected lines had higher crude protein and fat percentages, these higher rates of crude protein and fat deposition in the selected lines were probably the cause of their lower ash percentage. With respect to fat percentage, though the differences were not significant, the lines selected under feed restriction had the highest fat percentage. Two possible reasons for this increased fat percent are: first, the restricted line is truly fatter than the control line at this age. Since they are smaller animals with reduced growth they are at a later phase with respect to fat deposition, and this implies a greater fat percentage at a given age. Second, the restricted lines were always selected on the basis of their performance in isolation. Since it may be speculated that these lines were being selected for reduced maintenance requirements, and thermoregulation is the major cost within maintenance, the increased fatness in these lines could have been the fastest route to decrease thermoregulatory costs.

The late period of selection for weight gain did not significantly alter body composition prior to the start of the selection period, while at the end of the selection period significant differences between control and selected lines and among selected lines were observed.

Reports in the literature on the effect on body composition of selection for weight gain at an age comparable to the late period of the present study are very scarce. Biondini et al. (1968) selected for increased weight gain between 4 and 11 weeks old under ad libitum feeding in three replicate lines. They observed that two of the three replicates became progressively fatter while the third replicate did not change in fat percentage. Under restricted feeding, McPhee et al. (1980) selected mice for increased weight gain between 5 and 9 weeks old and reported that their selected lines were 3% fatter than controls when all were fed ad libitum. It would seem that the level of restriction applied by McPhee et al. (1980) was acting on the growth portion of the intake; therefore, the effects on carcass composition are not comparable. In the present study the ad libitum line had higher fat percentage than control line at the end of the selection period; therefore this could not have contributed to the increased weight gain observed in these lines. Moreover, these lines had lower consumption than controls. It may be speculated then that these lines had reduced the energetic discrepancy (Stephenson and Malik 1984) and the extra energy saved was utilized in laying down fat.

Selection experiments for increased body weight have reported a tendency towards increased fatness that accentuates with age (as reviewed by McCarthy 1982; Malik 1984). However, it appears that selection for weight gain does not have similar effects. Baker et al. (1979) analyzed lines selected for 3–6 weeks gain at 140 days old and observed very little difference between males from selected and control lines, though females were significantly fatter. In this study only males were analyzed at 100 days old and body weights were found to be lower in selected lines, particularly in the lines selected under restriction. Selection under restriction at both periods had a similar effect in decreasing body weight at adulthood.

Wilson (1973) suggested that selecting for gain at an earlier age would decrease body size. Present findings are in partial agreement, since selection did decrease adult body weight with respect to control lines, but had less effect in decreasing body weight than selection at later ages.

In general, restricted lines remained smaller and leaner in adulthood while ad libitum lines remained approximately the same size as controls with a slightly lower fat percentage.

## References

- Allen P, McCarthy JC (1980) The effects of selection of high and low body weight on the proportion and distribution of fat in mice. *Anim Prod* 31: 1–11
- Baker RL, Carter AH, Cox EH (1979) The effects of selection for body weight at different ages on fat deposition in mice. *NZ Soc Anim Prod* 39: 118–128
- Bakker H, Wallinga JH, Politiek RD (1978) Reproduction and body weight of mice after long-term selection for large litter size. *J Anim Sci* 46: 1527–1580
- Biondini PE, Sutherland TM, Haverland LH (1968) Body composition of mice selected for rapid growth rate. *J Anim Sci* 27: 5–12
- Brown MA, Frahm RR (1975) Feed efficiency in mice selected for preweaning and post-weaning growth. *J Anim Sci* 41: 1002–1007
- Brown MA, Frahm RR, Johnson JJ (1977) Body composition of mice selected for pre-weaning and post-weaning growth. *J Anim Sci* 45: 18–23
- Eisen EJ, Bakker H, Nagai J (1977) Body composition and energetic efficiency in two lines of mice selected for rapid growth rate and their  $F_1$  crosses. *Theor Appl Genet* 49: 21–34
- Falconer DS (1960) Selection of mice for growth on high and low planes of nutrition. *Genet Res* 1: 91–113
- Fowler RE (1958) The growth and carcass composition of strains of mice selected for large and small body size. *J Agric Sci* 51: 137–148
- Fowler RE (1962) The efficiency of food utilization, digestibility of foodstuffs and energy expenditures of mice selected for large or small body size. *Genet Res* 3: 51–68
- Hayes JF, McCarthy JC (1976) The effects of selection at different ages for high and low body weight on the pattern of fat deposition in mice. *Genet Res* 27: 389–403
- Hetzel DJS, Nicholas FW (1982) Direct and correlated responses to selection for post-weaning gain on ad libitum or restricted feeding in mice. *Theor Appl Genet* 63: 145–150
- Hull P (1960) Genetic relations between carcass fat and body weight in mice. *J Agric Sci* 55: 317–321
- Kownacki M, Zielinski W, Jezierski T (1977) Feed efficiency and body composition of selected and unselected mice. *Theor Appl Genet* 50: 179–184
- Lang BJ, Legates JE (1969) Rate, composition and efficiency of growth in mice selected for large and small body weight. *Theor Appl Genet* 39: 306–314
- Malik RC (1984) Genetic and physiological aspects of growth, body composition and feed efficiency in mice: review. *J Anim Sci* 58: 577–590
- McCarthy JC (1982) The laboratory mouse as a model for animal breeding: a review of selection for increased body weight and litter size. Second world congress of genetics applied to livestock production, Madrid, vol 5, pp 66–83
- McKay RI, Graham DA, Parker RJ (1985) Carcass composition of mice after doing long-term selection for large six-week body weight and long six-week tail length. *Can J Anim Sci* 65: 239–242
- McPhee CP, Neill AR (1976) Changes in the body composition of mice selected for high and low eight week weight. *Theor Appl Genet* 47: 21–26
- McPhee CP, Trappett PC, Neill AR, Duncafe F (1980) Changes in growth, appetite, food conversion efficiency and body composition in mice selected for high post-weaning weight gain on restricted feeding. *Theor Appl Genet* 57: 49–56
- Rahnefeld GW, Boylan WJ, Comstock RW, Singh M (1963) Mass selection for post-weaning growth in mice. *Genetics* 48: 1567–1583
- Roberts RC (1979) Side effects of selection for growth in laboratory animals. *Livestock Prod Sci* 6: 93–104
- Roberts RC (1981) The growth of mice selected for large and small size in relation to food intake and the efficiency of conversion. *Genet Res* 38: 9–24

- Stanier MW, Mount LE (1972) Growth rate, food intake and body composition before and after weaning in strains of mice selected for mature body weight. *Br J Nut* 28: 307–325
- Statistical Analysis System User's Guide (1985) Statistical Analysis System Institute Inc, Cary, North Carolina
- Stephenson SK, Malik HC (1984) Energy partitioning and growth in mice selected for high and low body weight. *Genet Res* 43:323–337
- Sutherland TM, Biondini, Haverland LH, Pettus D, Owen WB (1970) Selection for rate of gain, appetite and efficiency of feed utilization in mice. *J Anim Sci* 31: 1049–1057
- Timon VM, Eisen EJ (1970) Comparisons of ad libitum and restricted feeding of mice selected and unselected for post-weaning gain: I. Growth, feed consumption and feed efficiency. *Genetics* 64:41–57
- Urrutia MS, Hayes JF (1987) Selection for weight gain in mice at two ages and under ad libitum and restricted feeding. 1. Direct and correlated responses in weight gain and body weight. *Theor Appl Genet* (in press)
- Wilson SP (1973) Selection for a ratio of body weight gains in mice. *J Anim Sci* 37: 1098–1103