# Rate, Composition and Efficiency of Growth in Mice Selected for Large and Small Body Weight\*

B. J. LANG and J. E. LEGATES

North Carolina State University, Raleigh

Summary. Mice selected for high  $(H_6)$  and low  $(L_6)$  6-week body weight and a randombred control population  $(C_1)$  were characterized for rate, composition and efficiency of growth. Individual body weights were obtained from birth to 8 weeks of age on 682 mice representative of the three lines. Individual whole carcass determinations of water, fat, ash and protein (residual) were obtained for 180 mice sampled weekly from 3-8 weeks of age. Efficiency of feed utilization was estimated from individual body weight and feed consumption data obtained on 189 mice from 3-8 weeks of age. Growth curves for body weight and gain in body weight, constructed by line and sex, showed a temporary retardation of maximum growth rate in the  $L_6$  line, which was attributed in part to an extended depression in growth following weaning. The composition relative to the other carcass components. A decrease in fat percent at 7 weeks of age in the  $H_6$  and  $C_1$  lines was not evident in the  $L_6$  line until 8 weeks of age. Females had a higher percentage carcass fat than did males during the 4-7 weeks growth period, but this difference was essentially reduced to zero by 8 weeks of age. Percentage water was highly correlated negatively with percentage fat. Percentages protein and ash were essentially constant across lines and ages. A positive relation between rate and efficiency of growth was observed between lines. Consistent sex differences, males more efficient than females, were observed prior to 6 weeks of age, but were not evident in the later (6-8 week) data.

#### Introduction

Genetic variation in the body weight of mice has been observed to be in a large measure additive, and response to selection has been in reasonable agreement with expectations (MACARTHUR, 1949; FALCONER 1960; ROBERTS, 1966). However, the associated dynamics and physiology of weight changes are neither well defined nor predictable. The complexity of physiological events leading to the expression of body weight changes suggests that there are various metabolic alternatives, such as fat versus protein deposition. FALCONER and KING (1953) have described MacArthur's large strain to be fat but not particularly large in linear dimensions; whereas, Goodale's mice were noted to be large-bodied but not very fat. Likewise, FOWLER (1958) found that the carcass composition of Falconer's N and C strains (FAL-CONER, 1953; FALCONER, 1960) was differentially influenced by selection for body weight.

While experimental selection is most often directed toward effecting a response in a single primary trait, abundant evidence suggests that correlated changes in other traits may be expected. Investigation of growth dynamics and the physiology of correlated responses should provide both a firmer basis for interpreting the effects of selection and insights into the physiological complexities related to the primary selection response. The purpose of this investigation was to characterize correlated changes in rate, composition and efficiency of weight gain in mice selected for large and small 6-week weight.

#### Materials and Methods

Three lines of mice, one selected for large body weight at 6 weeks of age  $(H_6)$ , one selected for small body weight at 6 weeks of age  $(L_6)$  and a randomly selected control line  $(C_1)$  were characterized in terms of rate, composition and efficiency of growth. The reproductive performance and a detailed analysis of the growth curves for these lines already have been reported (Elliott, Legates and Ulberg, 1968; EISEN, LANG and LEGATES, 1969). All three lines were originally derived by reciprocally crossing two  $F_1$  stocks (CAF<sub>1</sub>, AKD2  $F_1$ ) from the Jackson Laboratory, Bar Harbor, Maine. Selection was on a withinfamily basis, and all mice had resulted from 30 or more generations of such selection. Temperature in the colony was regulated by window air conditioning units which permitted fluctuations from 22°-24 °C.

#### 1. Rate of growth

Within each of four mating seasons (summer, fall, winter and spring), individual body weights were collected at 3-day intervals from birth to 30 days of age and at 6-day intervals from 30 to 54 days of age. Data were collected simultaneously for each of the three lines from first litter progenies. The numbers of mice for the four mating seasons, as given in Table 1, represent selection generations 34, 31, 36 and 33 in the  $H_6$  and  $C_1$  lines and selection generations

<sup>\*</sup> Paper number 2640 of the Journal Series of the North Carolina State University Agricultural Experiment Station, Raleigh, North Carolina. Supported by Public Health Service Grant GM 11546-05. Computation was supported by NIH Grant No. FR-00011. The senior author was supported by NIH Training Grant No. 2-Tl-GM-296.

|        | H <sub>6</sub> |         | C <sub>1</sub> |         | L <sub>6</sub> |         |  |
|--------|----------------|---------|----------------|---------|----------------|---------|--|
|        | Males          | Females | Males          | Females | Males          | Females |  |
| Summer | 19             | 30      | 37             | 50      | 25             | 16      |  |
| Fall   | 30             | 22      | 54             | 53      | 26             | 31      |  |
| Winter | 9              | 7       | 37             | 44      | 8              | 5       |  |
| Spring | 31             | 33      | 34             | 39      | 16             | 26      |  |
| Total  | 89             | 92      | 162            | 186     | 75             | 78      |  |

 
 Table 1. Numbers of mice contributing to each line-sexseason subclass mean for growth rate

33, 30, 35 and 32 in the  $L_6$  line. Mean body weights were computed for each of the 15 chronological points within each line-sex subclass. Data for average daily gain were similarly summarized for each of the 14 time intervals.

# 2. Composition of growth

Whole body composition analyses were performed on contemporary first litter progeny derived from one generation of random mating within the  $L_6$  and  $C_1$ lines following a regular selection-reproduction interval in the mouse colony. Low reproduction and extensive early postnatal mortality necessitated an additional generation of random mating in the  $H_6$ line to obtain mice for collection of similar data. These mice, so obtained, reflect the genetic constitution of the  $H_6$ ,  $L_6$  and  $C_1$  lines following 33, 32 and 33 generations of selection, respectively.

Body composition was obtained from mice sacrificed at weekly intervals from 3 weeks (weaning) to 8 weeks of age. Litters and mice within litters were sampled randomly at each age to provide 5 mice per line-sex-age subgroup.

Mice chosen for body composition analyses were deprived of food for 6 hours (3 and 4 weeks of age) or 16 hours (5, 6, 7 and 8 weeks of age), killed by over exposure to ether and stored at -24 °C until the time of analysis. The difference between the weights of the chopped whole carcass before and following 26 hours freeze drying was taken as an estimate of carcass water. Values for carcass fat were obtained by direct weighing of the ether extract following 16 hours of continuous extraction of the pulverized, dried carcass with diethyl ether. Direct weights of the ash content of the carcass were obtained following subjection of the fat-free dried carcass to slowly increasing temperatures (50 °C increase each hour from 150-400 °C) and subsequent maintenance of the sample at 400 °C for 16 hours and at 600 °C for an additional 7 hours. Protein was not estimated directly, but it was approximated by the residual weight after water, ether extract and ash had been determined (carbohydrate content assumed to be small and the bias to individual variation in protein content negligible).

## 3. Efficiency of growth

First litter progeny from contemporary matings of the  $H_6$ ,  $C_1$  and  $L_6$  lines were randomly sampled, 2 males and/or 2 females per litter, toward a goal of 16 progeny per line-sex subgroup. Two replications of this basic design were conducted. Numbers of mice included in each line-sex subclass for each replicate are given in Table 2. Progeny sampled were representative of the genetic constitution following 32, 32, 31 and 33, 33, 32 generations of selection in the  $H_6$ ,  $C_1$  and  $L_6$  lines in replications 1 and 2 respectively.

 
 Table 2.
 Numbers of mice contributing to each linereplication-sex subclass mean for efficiency of growth

| Repli-<br>cation | H <sub>6</sub> |         | C <sub>1</sub> |         | L <sub>6</sub> |         |  |
|------------------|----------------|---------|----------------|---------|----------------|---------|--|
|                  | Males          | Females | Males          | Females | Males          | Females |  |
| 1                | 12             | 9       | 18             | 17      | 18             | 21      |  |
| 2                | 14             | 17      | 16             | 16      | 16             | 15      |  |
| Total            | 26             | 26      | 34             | 33      | 34             | 36      |  |

All mice were fed the standard laboratory Purina Chow pellets used in the colony, but in a ground form. Daily individual feed consumption was obtained from 3 to 8 weeks of age, and individual body weights were obtained every third day during the same growth interval.

Efficiency of growth was expressed in terms of grams of body weight gain per gram of feed consumed. The data were summarized into time intervals of 3-6, 4-6, 6-8 and 3-8 weeks of age to represent efficiency of early postweaning gain (prior to sexual maturity), early postweaning gain following weaning depression, late postweaning gain and total postweaning gain to 8 weeks of age, respectively. Least squares analysis of variance procedures were used with the following model, since the preliminary analyses did not indicate that the other interactions were statistically significant:

$$Y_{ijkl} = \mu + g_i + r_j + s_k + (gr)_{ij} + e_{ijkl}$$

where:  $Y_{ijkl} = l^{th}$  observation in the  $i^{th}$  line,  $j^{th}$  replication and  $k^{th}$  sex,

- $\mu$  = the population mean,
- $g_i$  = the effect of the  $i^{th}$  genetic line,
- $r_i$  = the effect of the  $j^{th}$  replication,
- $s_k$  = the effect of the  $k^{th}$  sex,
- $(gr)_{ij}$  = the specific effect of the  $ij^{th}$ , line-replication subclass,
- $e_{ijkl}$  = random effect (assumed to be normally distributed with a mean of 0 and variance  $\sigma_{\ell}^2$ ).

#### **Results and Discussion**

#### 1. Rate of growth

Average body weights plotted for each line-sex subclass are graphically presented in Figure 1. Means

|         | H <sub>6</sub> |      |                |      | C1    |      |         | L <sub>6</sub> |                |      |                |      |
|---------|----------------|------|----------------|------|-------|------|---------|----------------|----------------|------|----------------|------|
|         | Males          |      | Females        |      | Males |      | Females |                | Males          |      | Females        |      |
|         | x              | s    | $\overline{x}$ | s    | x     | \$   | x       | s              | $\overline{x}$ | s    | $\overline{x}$ | s    |
| Birth   | 1.57           | 0.14 | 1.48           | 0.15 | 1.49  | 0.14 | 1.45    | 0.12           | 1.27           | 0.10 | 1.24           | 0.11 |
| 12-days | 6.24           | 0.83 | 6.01           | 0.89 | 6.28  | 0.81 | 6.09    | 0.94           | 5.03           | 0.96 | 5.18           | 0.93 |
| 21-days | 8.95           | 1.37 | 8.48           | 1.35 | 8.64  | 1.30 | 8.19    | 1.21           | 6.81           | 1.18 | 6.81           | 1.19 |
| 42-days | 22.39          | 2.39 | 19.10          | 2.33 | 19.58 | 2.33 | 16.78   | 2.25           | 14.06          | 2.02 | 12.77          | 1.62 |
| 54-days | 25.43          | 2.12 | 21.43          | 2,26 | 22.41 | 2.41 | 18.47   | 2.20           | 16.47          | 2.03 | 14.62          | 1.61 |

Table 3. Means  $(\bar{x})$  and standard deviations (s) for weights at key ages for lines and sexes pooled over seasons\*

\* The numbers of individuals represented are given in Table 1.



Fig. 1. Growth curves for each line-sex subclass

and standard deviations for weights at certain key ages pooled over seasons are given in Table 3.

The curves in Figure 1 reflect both the line differences in 6-week body weight and the asymmetry of selection response from the control population, as reported by LEGATES and FARTHING (1962). It is of interest to note in both sexes that the C<sub>2</sub> mice are larger than the H<sub>6</sub> mice at 12 and 15 days. Investigation of the maternal performance of the H<sub>6</sub>, L<sub>6</sub>, and C<sub>2</sub> (a control line from the same foundation as C<sub>1</sub>) lines by reciprocal cross-fostering revealed that this situation resulted from the poorer postnatal maternal ability of the H<sub>6</sub> line (WHITE, LEGATES and EISEN, 1968). LEGATES and FARTHING (1962) did not find that direct response to selection for large 6-week body weight in the H<sub>6</sub> line continued after 15 generations. Nevertheless, postweaning gain increased slightly in the  $H_6$  line during an additional 10 generations of selection, compensating for the decline in the response of weaning weight.

The average daily weight gains (Figure 2) further reveal the differences in preweaning growth among the  $H_6$  and  $C_1$  lines. Comparisons of the  $L_6$  and  $C_1$ lines show that preweaning growth rate in the  $L_6$ line had been reduced by the selection for small 6-week body weight. The biphasis nature of the curves for the average daily weight gain in Figures 2, identify the first point of inflection for the curves in Figure 1 to be prior to 12 days of age and the second point was usually during the fourth week.

Line comparison of early postweaning gain (3-6 weeks of age) generally show that the H<sub>6</sub> line gained more rapidly and the L<sub>6</sub> more slowly than the C<sub>2</sub> line. The poor maternal ability of the L<sub>6</sub>, possibly due to



Fig. 3. Average percentage composition of water and fat for the whole carcass from three to eight weeks of age

a limited milk supply after 15 days, delayed the start of the postweaning growth phase. The small  $L_6$  mice were slow to accommodate the change to a solid diet after weaning.

## 2. Composition of growth

Average percentages of water and fat from the whole carcass determinations are graphically presented

in Figure 3. Comparison of the  $H_6$  and  $C_1$  lines with respect to percentages water and fat at points along the chronological axis shows that the  $C_1$  line is consistently lower in percentage water and higher in percentage fat. It should be recalled that the  $H_6$ and  $C_1$  line mice were not from contemporary matings. A repetition of the analyses for percentage water at 5 weeks of age was conducted utilizing contemporary



Fig. 4. Average percentage composition of protein and ash for the whole carcass from three to eight weeks of age

matings. These later data gave similar line-by-sex comparisons, but the magnitude of line differences were much reduced. While the interpretation of these comparisons must therefore be conditional, there was no indication that the more rapid growth in the  $H_6$  line, within the growth interval examined, resulted from an increase in the relative rate of fat deposition. These results concur with the data obtained from the C strain of Falconer, but are in contrast with the increased fat deposition noted in the large line of Falconer's N strain (FOWLER, 1958).

Chronological differences are evident in the pattern of fat deposition for the  $L_6$  and  $C_1$  lines. Prior to 6 weeks of age the  $L_6$  line is consistently higher in percentage water and lower in percentage fat than the  $C_1$  line. At 7 weeks of age the situation is markedly reversed due to the apparent delay in the peak for rate of fat deposition in the  $L_6$  line. At or just prior to 8 weeks of age the line differences are essentially zero. The trend is evident in both males and females, as is the complementary change in percentage water. It would be of interest to ascertain if this later decrease

 Table 4. Analysis of variance for percentage body composition of water, fat,

 protein and ash

| · · · · · · · · · · · · · · · · · · · |      | Mean Squares |           |         |          |  |  |  |
|---------------------------------------|------|--------------|-----------|---------|----------|--|--|--|
| Source                                | d.f. | Water        | Fat       | Protein | Ash      |  |  |  |
| Total                                 | 179  | 7.235        | 9.446     | 0.569   | 0.057    |  |  |  |
| Lines                                 | 2    | 23.447**     | 13.501*   | 1.417*  | 0.302**  |  |  |  |
| Sex                                   | 1    | 15.283*      | 26.053*   | 3.655** | 0.516**  |  |  |  |
| $Lines \times sex$                    | 2    | 2.330        | 3.809     | 0.398   | 0.037    |  |  |  |
| Ages (5)                              |      |              |           |         |          |  |  |  |
| Linear                                | 1    | 559.005**    | 605.330** | 0.317   | 0.158*   |  |  |  |
| Quadratic                             | 1    | 49.91 3 **   | 31.356**  | 0.755   | 0.356**  |  |  |  |
| Ĉubic                                 | 1    | 118.444**    | 117.259** | 0.273   | 0.220 ** |  |  |  |
| Residual                              | 2    | 8.912*       | 14.679*   | 0.876   | 0.307*   |  |  |  |
| $Lines \times ages$                   | 10   | 4.916*       | 12.700**  | 2.146** | 0.184**  |  |  |  |
| $Sex \times ages$                     | 5    | 4.257        | 7.959     | 0.583   | 0.082    |  |  |  |
| $Lines \times sex \times ages$        | 10   | 1.771        | 2.107     | 0.631   | 0.049    |  |  |  |
| Residual                              | 144  | 2.742        | 4.576     | 0.429   | 0.037    |  |  |  |
|                                       |      |              |           |         |          |  |  |  |

\* and \*\* indicate statistical significances of mean squares at the 0.05 and 0.01 probability levels, respectively.

in fat deposition in the  $L_6$  line (noted between 6 and 7 weeks of age in both the  $H_6$  and  $C_1$  lines and between 7 and 8 weeks of age in the  $L_6$  line) is the result of a delay in the processes of physiological maturation for the  $L_6$  mice.

In all three lines females evidenced a larger relative amount of fat deposition between 4 and 7 weeks of age, when compared to males. This difference is markedly reduced or reversed by 8 weeks of age.

Percentages of protein and ash are presented in Figure 4. Line differences are not as evident in these two variables with the possible exception of a slightly higher protein and ash content in the  $L_6$  line at the time of, and immediately following, weaning. Such a difference would concur with the earlier suggestion of more weaning stress in the  $L_6$  line.

 Table 5. Phenotypic correlations\* between percentage composition for various body composition components

|                       | Water                | Fat          | Protein |
|-----------------------|----------------------|--------------|---------|
| Fat<br>Protein<br>Ash | 0.95<br>0.48<br>0.29 | 0.73<br>0.49 | 0.59    |

\* Based on 144 degrees of freedom within line, sex and age, all correlations significant at the 0.01 level of probability.

The analysis of variance for percentage body composition is given in Table 4 to provide a further assessment of the statistical significance of the plotted values. Line and sex differences were statistically significant for water, fat, protein and ash. Age effects were important for both fat and water. Most of the variance in both of these variables is accounted for by the decreasing linear trend with age for water and a corresponding increasing linear trend for fat. Only the lines x ages interactions are significant. As evident from the preceding figures, most of the contribution to these interactions comes from differences in percentage body composition in the early and late portions of growth interval studied. A striking negative relationship exists between water and fat content. This is further revealed by the simple correlations in Table 5, which have been computed within line, sex and age. It is interesting to note that there is a negative relation between fat percentage and each of the other body composition components.

## 3. Efficiency of growth

Mean efficiencies of food utilization for each linereplication-sex subclass are given in Table 6.

Among line comparisons of the 3-6 week efficiency values indicate a positive genetic relationship between rate and efficiency of growth as shown by FALCONER,

1960; FOWLER, 1962; RAHNEFELD et al., 1965. Line comparisons within all four age intervals show that the  $\mathrm{H}_6$  line consistently exceeded the  $\mathrm{C}_1$  line in efficiency of feed utilization. Differences between the  $C_1$ and  $L_6$  lines failed to demonstrate this consistency. The superiority in efficiency of the  $C_1$  line in the 3-6 week age interval was reduced essentially to zero upon omission of the data for 3-4 weeks. In the 4-6 week interval, there is no evidence for differences in efficiency between  $L_6$  and  $C_2$  line females; however,  $L_6$  males had a higher efficiency of feed utilization than did the  $C_1$  line males. With this exception, line comparisons were similar between sexes. The H<sub>6</sub> line was more efficient in the second replication than in the first; whereas, an opposite relationship between replications was demonstrated by the  $C_1$  and  $L_6$  lines.

Comparison of the 3-6 and 4-6 week data (Table 6) suggests that the early gain (3-4 weeks)was proportionately less efficient in the  $L_6$  line. This observation is in agreement with the report of FowLER (1962). The extended weaning depression in the  $L_6$  line, suggested earlier, was undoubtedly a contributing factor in the lower efficiency of early postweaning growth.

A more critical examination of these observations is provided through the analysis of variance. The results of these analyses, performed in accordance with the linear model presented earlier, are given in Table 7. Line differences in efficiency of feed utilization were highly significant for each of the age intervals examined.

Highly significant line differences in efficiency were observed for the 6-8 week growth interval. An interpretation of these line differences, however, cannot be readily given. The highly significant line differences appear to be attributable to inefficiency in the  $C_1$  line (Table 6). More specifically it appears to be due to a low rate of growth in the  $C_1$  line males, as is evident from the gains in body weight given in Table 8. The generality of this relationship is not borne out by the body weight and growth rate data previously presented for the  $C_1$  line (Figures 1 and 2 and Table 3). The 3 to 6 week weight gains of the

Table 6. Average efficiency of feed utilization (gms. gain in body wgt./gms. feed consumed) and standard errorsfor each line-replication-sex subclass

| Age    | Repli- | $\mathbf{H}_{6}$                   |                                    | C <sub>1</sub>                   |                                    | L <sub>6</sub>                     |                                    |  |
|--------|--------|------------------------------------|------------------------------------|----------------------------------|------------------------------------|------------------------------------|------------------------------------|--|
| (wks.) | cation | Males                              | Females                            | Males                            | Females                            | Males                              | Females                            |  |
| 3-6    | 1<br>2 | $.159 \pm .006$<br>$.171 \pm .004$ | $.138 \pm .006$<br>$.143 \pm .005$ | $.158 \pm .006 \\ .156 \pm .004$ | $.133 \pm .004$<br>$.127 \pm .004$ | $.146 \pm .005$<br>$.132 \pm .004$ | $.117 \pm .005$<br>$.105 \pm .006$ |  |
| 4-6    | 1      | $.136 \pm .007$                    | $.120 \pm .008$                    | $.132 \pm .008$                  | $.113 \pm .005$                    | $.136 \pm .005$                    | $.106 \pm .005$                    |  |
|        | 2      | $.155 \pm .006$                    | $.129 \pm .007$                    | $.129 \pm .006$                  | $.106 \pm .006$                    | $.122 \pm .005$                    | $.097 \pm .007$                    |  |
| 5-8    | 1      | $.048 \pm .004$                    | .041 ± .006                        | $.037 \pm .004$                  | $.038 \pm .006$                    | $.051 \pm .005$                    | $.042 \pm .004$                    |  |
|        | 2      | $.052 \pm .003$                    | .055 ± .007                        | $.034 \pm .004$                  | $.037 \pm .004$                    | $.047 \pm .005$                    | $.038 \pm .005$                    |  |
| 3-8    | 1      | $.110 \pm .004$                    | $.096 \pm .004$                    | $.106 \pm .003$                  | $.092 \pm .003$                    | $.102 \pm .003$                    | $.084 \pm .002$                    |  |
|        | 2      | $.117 \pm .003$                    | $.104 \pm .003$                    | $.102 \pm .003$                  | $.087 \pm .002$                    | $.093 \pm .002$                    | $.075 \pm .002$                    |  |

Table 7. Analyses of variance for the efficiency of feed utilization for the 3-6, 4-6, 6-8, and 3-8 week intervals

|                    |      | Mean Squares |            |            |           |  |  |  |
|--------------------|------|--------------|------------|------------|-----------|--|--|--|
| Source             | d.f. | 3-6 wks.     | 4-6 wks.   | 6-8 wks.   | 3-8 wks.  |  |  |  |
| Line               | 2    | 0.01210**    | 0.00571 ** | 0.00271 ** | 0.00483** |  |  |  |
| Replication        | 1    | 0.00029      | 0.00001    | 0.00002    | 0.00016   |  |  |  |
| Sex                | 1    | 0.03427**    | 0.02683**  | 0.00027    | 0.01112** |  |  |  |
| Line × replication | 2    | 0.00157*     | 0.00245*   |            | 0.00102** |  |  |  |
| Individuals        | 182  | 0.00038      | 0.00061    | 0.00036†   | 0.00013   |  |  |  |

\* and \*\* indicate statistical significance of mean squares at the 0.05 and 0.01 probability levels, respectively. † based on 184 degrees of freedom, since line  $\times$  replication effects not significant.

individually fed mice for the three lines compare favorably with the gains that can be computed from Table 3, where the mice were group fed.

The more efficient growth of males as compared with females (Table 6) is responsible for the highly significant sex effects in the 3-6, 4-6 and 3-8 week age intervals. There is an absence of significant sex differences in efficiency of growth following 6 weeks efficiency of growth were altered by selection for large or small body size.

## 4. General Discussion

Response to selection for 6week weight and the concomitant changes in growth rate and body composition of the mice studied here parallel the N strain of Falconer as reported by Fow-LER (1958). Protein composition remained essentially constant

over the 3 to 8 week interval, with a small, yet significant, superiority of the males over females. With the constancy of protein percentage, increased protein anabolism in these mice represented a uniform proportion of the total body weight increase for the age interval studied. Ash percentage also did not change perceptibly with age nor due to selection. A small, but significant, sex difference for ash was evident,

Table 8. Average gain in body weight (gms.) and standard errors for individually fed mice by line-replication-sex subclass

| Age<br>Interval<br>(wks.) | Repli- | H <sub>6</sub>            |                                    | C1                             |                                | L <sub>6</sub>                 |                                  |
|---------------------------|--------|---------------------------|------------------------------------|--------------------------------|--------------------------------|--------------------------------|----------------------------------|
|                           | cation | Males                     | Females                            | Males                          | Females                        | Males                          | Females                          |
| 3-6                       | 1      | $14.02 \pm .71$           | $12.50 \pm .24$                    | $13.37 \pm .40$                | $10.71 \pm .32$                | 8.42 ± .28                     | $7.03 \pm .40$                   |
|                           | 2      | 15.97 ± .64               | 12.38 ± .69                        | $13.55 \pm .32$                | $10.62 \pm .41$                | 9.26 ± .40                     | $6.99 \pm .51$                   |
| 4-6                       | 1<br>2 | 9.48 ± .46<br>11.77 ± .60 | ${}^{8.63 \pm .38}_{8.83 \pm .48}$ | $8.75 \pm .36 \\ 8.86 \pm .35$ | $7.10 \pm .24 \\ 6.90 \pm .37$ | $6.46 \pm .25 \\ 6.82 \pm .37$ | $5.08 \pm .32$<br>$5.06 \pm .40$ |
| 6-8                       | 1      | $3.28 \pm .29$            | $2.89 \pm .44$                     | $2.33 \pm .20$                 | $2.26 \pm .31$                 | $2.50 \pm .24$                 | $2.02 \pm .19$                   |
|                           | 2      | $4.01 \pm .32$            | 3.96 ± .47                         | $2.38 \pm .28$                 | 2.47 ± .24                     | $2.81 \pm .26$                 | $2.02 \pm .24$                   |
| 3-8                       | 1      | 17.30 ± .87               | $15.39 \pm .50$                    | 15.70 ± .38                    | $12.97 \pm .44$                | $10.92 \pm .24$                | 9.05 ± .38                       |
|                           | 2      | 19.98 ± .76               | $16.34 \pm .54$                    | 15.93 ± .36                    | 13.09 $\pm$ .26                | 12.07 $\pm .28$                | 9.01 ± .35                       |

of age. Some residual sex variation may remain, however, as based on expressions of the  $L_6$  line. While this observation is in itself quite superficial, an examination of Figure 2 of FowLER (1962) shows the last point of distinctive sex difference in gross efficiency to be 7-8, 7-8 and 9-40 weeks of age in large, control and small lines respectively. These observations may further support the suggestion made earlier, with regard to fat deposition, that a temporal delay of physiological events associated with sexual maturity may have occurred in the  $L_6$ line. ELLIOTT, LEGATES and ULBERG (1968) found evidence of delayed sexual maturity in the  $L_6$  line.

The absence of significant specific line-sex and specific replication-sex effects in the preliminary analyses suggested that the sex differences observed were generally independent of both line and replication effects. Thus, the current data, with the possible exception of the 6-8 week age interval, offer no suggestion that the difference between sexes in

and in this case the percentage ash for females exceeded that for the males.

In conformity with other reports (FOWLER, 1958; FOWLER, 1962; BIONDINI, SUTHERLAND, and HAVER-LAND, 1968) fat and water percentages changed most with age and due to selection. A novel feature of our results is the identification of an apparent temporal delay in fat deposition for both females and males of the  $L_6$  line. The  $L_6$  mice were in actuality selected for a slow developmental rate, since the criterion for selection was small weight at a given age. The impact of the genetic retardation in development was further compounded by the difficulty experienced by the  $L_6$  in the change to solid food at weaning. Nonetheless, even when the  $L_6$  mice were nursed by  $H_6$  and  $C_2$  mothers their growth was retarded (WHITE, LEGATES and EISEN, 1968).

Since only one strain was examined little information is available to clarify the contrast between the N and the C strains regarding increased fat Vol. 39, No. 7

deposition in relation to selection for body weight (FOWLER, 1958). While the average divergence of the  $H_6$  and  $L_6$  is not large (approximately 8 g at 6 weeks), it was achieved without the accumulation of genes for increased rate of fat deposition. BION-DINI, SUTHERLAND and HAVERLAND (1968) demonstrated an increase in percent fat for two or three selected replicates, but strangely a significant decline in percent fat occurred in the randomly maintained control. Extraction of comparative information from their results is further complicated, since the basis for selection and the age at slaughter differed markedly from those of the other studies cited.

There is evidence that selection for decreased fatness can be effective, particularly in swine (HETZER and HARVEY, 1967). DICKERSON (1947) and DICKER-SON and GOWEN (1947) have supported the contention that the ability to deposit fat late in the growth period provides the most efficient physiological mode to achieve increased weight for age. PALMER et al. (1946) showed that a strain of rats which were selected for increased feed efficiency had a higher fat percentage and a lower water content than the rats selected for low efficiency. However, the present results of selection for increased body weight at six weeks with mice suggest that this physiological pathway is not always followed. HULL (1960) selected among three lines of mice for large body weight at three, four and one-half and 6 weeks of age to examine the effect on the fat content of the carcass. Selection for weight at an early age did not reduce the fat content. Even though the growth regulatory mechanism is not clearly understood, the practice with economic species is to select for an efficient combination of growth and degree of fatness.

#### Zusammenfassung

Bei Mäusen, die auf hohes  $(H_6)$  und geringes  $(L_6)$ 6 Wochen-Körpergewicht selektiert waren, und einer unselektierten Kontrollpopulation  $(C_1)$  wurde die Zuwachsrate, die Veränderung des Wasser-, Fett-, Protein- und Aschegehaltes während des Wachstums sowie die Wuchsleistung untersucht. Das Körpergewicht von der Geburt bis zum Alter von 6 Wochen wurde an 682 einzelnen Mäusen, die repräsentativ für die drei Linien sind, festgestellt. Die Ermittlung des Wasser-, Fett-, Asche- und (Rest-)Proteingehaltes der Tiere erfolgte wöchentlich für 180 Mäuse im Alter von 3-8 Wochen. Die Futterverwertung (Wuchsleistung) wurde für 189 drei bis acht Wochen alte Mäuse auf Grund von Einzelgewichten und Futterverbrauch geschätzt.

Die Wachstumskurven für Körpergewicht und Gewichtszunahme, nach Linien und Geschlecht zusammengestellt, zeigten bei der  $L_6$ -Linie eine zeitweilige Verzögerung der maximalen Zuwachsrate, was z. T.

einer längeren Wachstumsdepression nach der Entwöhnung zugeschrieben wird. Es ergab sich kein Bcweis dafür, daß die schnellere Wachstumsrate bei der H<sub>s</sub>-Linie auf eine Erhöhung der Fetteinlagerung im Verhältnis zu den anderen Komponenten zurückzuführen ist. Ein Rückgang des Fettgehalts, der bei den H<sub>6</sub>- und C<sub>1</sub>-Linien im Alter von 7 Wochen festzustellen war, wurde bei der Linie L<sub>6</sub> erst nach 8 Wochen sichtbar. Weibliche Tiere hatten im Alter von 4-7Wochen einen höheren Körperfettgehalt als männliche, im Alter von 8 Wochen war dieser Unterschied aber nicht mehr vorhanden. Der Wassergehalt war in hohem Maße negativ mit dem Fettgehalt korreliert. Die Protein- und Ascheanteile waren im wesentlichen für die Linien und untersuchten Wuchsperioden konstant. Zwischen den Linien wurde eine positive Relation hinsichtlich Wuchsrate und Wuchsleistung festgestellt. Deutliche Geschlechtsunterschiede wurden bis zum Alter von 6 Wochen beobachtet, und zwar wuchsen die Männchen schneller als die Weibchen, später (6.-8. Woche) waren keine Unterschiede mehr feststellbar.

#### Bibliography

T. M. SUTHERLAND, and L. H. 1. BIONDINI, P. E., HAVERLAND: Body composition of mice selected for rapid growth rate. J. Animal Sci. 27, 5-12 (1968). – 2. DICKERSON, G. E.: Composition of hog carcasses as influenced by heritable differences in rate and economy of gain. Iowa Agri. Expt. Sta. Res. Bull. 354, 489-524 (1947). - 3. DICKERSON, G. E., and J. W. GOWEN: Hereditary obesity and efficient food utilization in mice. Science 105, 496 (1947). - 4. EISEN, E. J., B. J. LANG, and J. E. LEGATES: Comparison of growth functions within and between lines of mice selected for large and small body weight. Theor. Appl. Genetics 39, 251 to 260 (1969). — 5. ELLIOTT, D. S., J. E. LEGATES, and L. C. ULBERG: Changes in the reproductive processes of mice selected for large and small body size. J. Reprod. Fertil. 17, 9–18 (1968). – 6. FALCONER, D. S.: Selection for large and small size in mice. J. Genet. 51, 470-501 (1953). - 7. FALCONER, D. S.: Selection of mice for growth on high and low planes of nutrition. Genet. Res. 1, 91-113 (1960). - 8. FALCONER, D. S., and J. W. B. KING: A study of selection limits in the mouse. J. Genet. 51, 561 - 581 (1953). – 9. FOWLER, RUTH E.: The growth and carcass composition of strains of mice selected for large and small body size. J. Agri. Sci. 51, 137-148 (1958). - 10. FOWLER, RUTH E.: The efficiency of food utilization, digestibility of foodstuffs and energy expenditure of mice selected for large or small body size. Genet. Res. 3, 51-68 (1962). - 11. HETZER, H. O., and W. R. HARVEY: Selection for high and low fatness in swine. J. Animal Sci. 26, 1244–1251 (1967). – 12. HULL, P.: Genetic relations between carcass fat and body weight in mice. J. Agric. Sci. 55, 317-321 (1960). -13. LEGATES, J. E., and B. R. FARTHING: Selection for growth and maternal performance in mice. J. Animal Sci. 21, 974 (Abstract) (1962). – 14. MACARTHUR, J. W.: Selection for small and large body size in the house mouse. Genetics 34, 194–209 (1949). – 15. PALMER, L. C., C. KENNEDY, C. E. CALVERLEY, C. LOHN, and P. H. WESWIG: Genetic differences in the biochemistry and physiology influencing food utilization for growth in rats. Techn. Bul. Minn. Agr. Expt. Sta. No. 176, 1-54 (1946). - 16. RAHNEFELD, G. W., R. E. COMSTOCK, W. J. BOYLAN, and MADHO SINGH: Genetic correlation between 314 B. J. LANG and J. E. LEGATES: Rate, Composition and Efficiency of Growth in Mice Theoret. Appl. Genetics

growth rate and feed per unit gain in mice. J. Animal Sci. 24, 1061-1066 (1965). - 17. ROBERTS, R. C.: The limits to artificial selection for body weight in the mouse. I. The limits attained in earlier experiments.

Genet. Res. 8, 347-360 (1966). - 18. WHITE, J. M., J. E. LEGATES, and E. J. EISEN: Maternal effects among lines of mice selected for body weight. Genetics 60, 395-408 (1968).

Received July 28, 1969 Communicated by J. E. LEGATES Professor B. J. LANG and Professor J. E. LEGATES Animal Breeding Section Department of Animal Science North Carolina State University P. O. Box 5127 Raleigh, North Carolina 27607 (USA)