COMPARISONS OF *AD LIBITUM* AND RESTRICTED FEEDING OF MICE SELECTED AND UNSELECTED FOR POSTWEANING GAIN. I. GROWTH, FEED CONSUMPTION AND FEED EFFICIENCY¹

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STUDIES by FALCONER (1959), FOWLER (1962), RAHNEFELD *et al.* (1965), LANG and LEGATES (1969) and SUTHERLAND *et al.* (1970) have shown that feed efficiency in mice increases as a result of selection for increased body size. FOWLER (1962) showed that line differences (high *vs.* control *vs.* low) in energetic efficiency were dependent on the period of the growth cycle in which comparisons were made. None of these studies attempted to describe the nature of the correlated response in feed efficiency or its dependence on level of feeding. In addition, the changes in feed efficiency were not considered in relation to changes in body composition.

In each of these studies comparisons were made on *ad libitum* feeding over fixed age intervals. No attempt was made to measure the possible effects of appetite on the expression of line differences in feed efficiency. Controlled feeding experiments in poultry by LEPORE (1965) and SIEGEL and WISMAN (1966) suggest that correlated changes in appetite may lead to biased measures of efficiency differences in line comparisons made on *ad libitum* feeding. The interpretation of results in any comparison among genetically different lines also will depend on the particular definition of feed efficiency; FOWLER (1962) used the form gain/feed, whereas SUTHERLAND *et al.* (1970) used the reciprocal definition, feed/gain.

The present study was undertaken to measure the efficiency of selected (High) and unselected (Control) lines in *ad libitum* and controlled feeding regimes, and to compare the various measures of efficiency over fixed age and fixed weight intervals. Carcass composition, energetic efficiency and growth curve comparisons between lines and sexes will be reported elsewhere (TIMON *et al.* 1970; TIMON and EISEN 1969).

MATERIALS AND METHODS

The mice used in this study were obtained from 9th generation selection and random control populations developed from a foundation I.C.R. strain obtained from the Institute of Cancer Research, Philadelphia, Pa. The selected line subsequently designated High (H) was selected for

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increased postweaning gain from 21–42 days, while the Control (c) line was randomly selected. In each of the nine generations both populations were propagated by 16 single-pair matings. Random mating of the selected individuals was used, except that full-sib matings were avoided. In sampling these populations, one male and one female mouse were randomly drawn from each of the 16 families in each population. The progenies of random matings among these mice constitute the sample used in this study. To minimize the effects of correlated changes in postnatal maternal performance on postweaning growth, the progenies of all litters in both the High and Control lines were fostered five days after birth on Control line dams of equivalent postpartum age (± 12 hr). Only whole litters standardized to eight mice (4♂♂, 4♀♀) were fostered, and litters were weaned at 21 days. Weights taken over this period (five-day litter weight, individual 12-day and 21-day weights) were recorded to the nearest 0.1 g.

Controlled Feeding: At weaning. High and Control litters of the same age were paired on the basis of similarity in weight to form 27 blocks, each containing eight mice: two Control *ad libitum*, two Control restricted, two High *ad libitum* and two High restricted (one male and one female in each case). Within each block a random male and female mouse from a High line litter were paired on a weight basis with their Control contemporaries. The High restricted male and female mice (HR) were kept on a restricted feed intake in that they were offered the same quantity of feed (adjusted for differences in body weight) as that consumed by the paired Control male and female mice maintained on the *ad libitum* feeding regime (CA). In the formula used for calculating the amount of feed offered to HR individuals,

$$\text{FEED}_{(\text{HR})} = \text{FEED}_{(\text{CA})} \times (\text{BODY WT})^{.75}_{(\text{HR})} / (\text{BODY WT})^{.75}_{(\text{CA})},$$

the correction for body weight is based on the assumption that the maintenance feed requirement is a function of metabolic body size (Brody 1945). In completing the factorial arrangement within each block, the Control mice were restricted to the same percentage reduction in feed offered per gram body weight as that obtained in the High *ad libitum* and High restricted pair. Body weight and feed consumption were recorded to the nearest 0.1 g over two-day intervals. Consequently, the restricted feed aliquots were calculated every two days and were based on the feed intakes of contemporaries over the previous two-day interval. Feed consumption was measured on all mice from 21 to 57 days and restricted feeding began on day 33. A standard feed (Purina Laboratory Chow) was used throughout the postweaning period. It was finely ground ($\frac{1}{2}$ cm plate) and offered in special glass jar feeders.

STATISTICAL ANALYSIS

The distribution by line-treatment-sex subclasses of the 199 mice that completed the experiment is shown in Table 1. Because of lack of orthogonality in the data due to preweaning or postweaning mortality, all analyses were computed by a generalized least-squares procedure (HARVEY 1960). Two classes of statistical analyses were conducted.

1. *Regression of traits on age and weight:* Only the 110 mice fed *ad libitum* were used in these analyses. The regressions of feed consumption, feed efficiency and weight gain on age (21 to 57 days) were fitted to a third degree orthogonal polynomial equation. The regressions on weight also were fitted to a cubic polynomial, but in these analyses the independent variables

TABLE 1
Classification of mice by line-treatment-sex subclasses

	Ad libitum			Restricted		
	Males	Females	Total	Males	Females	Total
High	27	26	53	20	25	45
Control	29	28	57	20	24	44
Total	56	54	110	40	49	89

were not orthogonal. Linear and quadratic models were also fitted, and the particular equations used are those for which all terms (linear, quadratic or cubic) were significant in at least one line-sex subclass.

A total of 1980 data points (18 age points $\times$ 110 mice) were available for these analyses. In the regressions on age, tests of "lack of fit" to the equation were made by partitioning the residual sums of squares into sums of squares due to "lack of fit" and true error (DRAPER and SMITH 1966). Tests of heterogeneity of regression sums of squares were computed by fitting multiple linear regression models for all combinations of line-sex subclasses, lines and sexes.

2. *Line, sex and feed level comparisons over fixed age and fixed weight intervals:* Changes in the pattern of feed intake and weight gain over the experimental period, evident in the regression analyses, indicated the necessity to analyze the data within particular age periods and over a fixed weight interval. Consequently, the data were classified into three separate age intervals: Period I, 21–33 days; Period II, 33–45 days; and Period III, 45–57 days. Feed efficiency, average daily feed consumption and average daily gain were based on total feed consumed and total weight gained in each particular age interval.

Analysis of these traits over a constant weight interval was only possible in the *ad libitum* mice since some individual weight gains in the restricted mice were negative. A 10 g weight interval, 15–25 g, was chosen in the *ad libitum* mice as this represented the largest constant weight range common to all mice in that group.

A number of different analyses were carried out on the total set of data, the *ad libitum* data only, within the separate age and weight intervals and with and without the inclusion of a covariate. These analyses will be described in reference to the most complete linear model:

$$Y_{ijklm} = \mu + B_i + L_j + S_k + T_l + (BL)_{ij} + (BS)_{ik} + (BT)_{il} + (LS)_{jk} \\ + (LT)_{jl} + (ST)_{kl} + \beta X_{ijklm} + e_{ijklm}$$

where

Y_{ijklm} = observation on the m th mouse in the $ijkl$ th subclass,

μ = population mean,

B_i = fixed effect of the i th block; $i = 1, \dots, 27$,

L_j = fixed effect of the j th line; $j = 1, 2$,

S_k = fixed effect of the k th sex; $k = 1, 2$,

T_l = fixed effect of the l th feeding regime; $l = 1, 2$,

$(BL)_{ij}$, $(BS)_{ik}$, $(BT)_{il}$, $(LS)_{jk}$, $(LT)_{jl}$, and $(ST)_{kl}$ = respective interaction effects,

β = regression of Y_{ijklm} on X_{ijklm} (average body weight in the case of a fixed age interval or number of days required to gain 10 g in the case of the fixed weight interval, 15–25 g),

e_{ijklm} = random effect assumed $N(0, \sigma_e)$.

RESULTS

Comparison of High and Control mice on ad libitum feeding: The results of this section are presented to characterize the differences between lines and sexes in feed consumption, growth rate and feed efficiency under *ad libitum* feeding.

The mean body weights plotted in Figure 1 illustrate the increased growth rate of the High line relative to the Control and the greater growth rate of males compared to females. The lack of any difference in body weight at weaning suggests that the fostering technique was probably successful in minimizing preweaning maternal effects.

Age trends: The regressions of feed consumption, feed efficiency (gain/feed) and weight gain on age shown in Tables 2 and 3 and Figures 2a, 2b and 2c were all highly significant ($P < .001$). On the average, the regressions on age accounted for 48, 24 and 22% of the variation in feed consumption, feed efficiency and

FIGURE 1.—Plotted growth curves by line-sex subclasses under *ad libitum* feeding.

weight gain, respectively. Although considerable variation in these traits was unexplained by the equations, in general the tests of “lack of fit” to the equations (Table 2) were nonsignificant ($P > .05$), indicating their unbiased nature.

FIGURE 2a.—The regressions of feed consumption (g) on age (days) under *ad libitum* feeding.

FIGURE 2b.—The regressions of feed efficiency (gain/feed) on age (days) under *ad libitum* feeding.

The regression curves in Figure 2a indicate that average daily feed consumption increased in both lines and in both sexes up to about 40 days of age, after which there was a slight though consistent decrease in all groups except Control males. The curves indicate that average feed consumption was larger in High than in Control mice and larger in males than in females. Both line and sex differences in feed consumption increased up to six weeks of age. Thereafter,

FIGURE 2c.—The regressions of weight gain (g) on age (days) under *ad libitum* feeding.

TABLE 2

Analyses of variance in the regressions of feed consumption, feed efficiency and weight gain on age

Source	df	Mean squares		
		Feed consumption	Feed efficiency	Weight gain
High Males				
Regression	3	551.89***	1.497***	103.06***
Residual	482†	3.84	0.016	1.49
Lack of fit	14	3.36 ^{NS}	0.038**	5.84***
Error	468	3.85	0.016	1.35
Control Males				
Regression	3	573.74***	1.691***	84.59***
Residual	518	4.13	0.018	1.17
Lack of fit	14	3.45 ^{NS}	0.020 ^{NS}	1.99 ^{NS}
Error	504	4.15	0.018	1.15
High Females				
Regression	3	486.13***	1.201***	79.63***
Residual	464	2.79	0.018	1.28
Lack of fit	14	2.49 ^{NS}	0.033*	6.04***
Error	450	2.80	0.018	1.12
Control Females				
Regression	3	554.15***	1.287***	55.57***
Residual	500	3.13	0.022	0.85
Lack of fit	14	3.79 ^{NS}	0.033 ^{NS}	2.66***
Error	486	3.11	0.022	0.79

^{NS} Not significant

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

† Residual degrees of freedom equal 483, 519, 465 and 501 for feed efficiency and weight gain of High males, Control males, High females and Control females, respectively.

the sex differences remained relatively constant, but a switch in levels of feed intake between Control males and High females caused a slight reduction in the average line difference between six and eight weeks. The analyses of variance in Table 3 show that these regression curves differ principally in the level of feed consumption (elevations, $P < .001$), though the rate of change in feed intake over time (slopes) was also significantly different ($P < .05$).

Age trends in feed efficiency (gain/feed) were characteristically negative (Figure 2b). A marked initial difference between the sexes persisted throughout the entire period. In contrast, differences in efficiency between High and Control mice gradually increased, reaching a maximum by day 33.

The regressions of weight gain on age (Figure 2c) show that rate of gain decreased almost linearly over the 21–57 day period. These regressions are nearly parallel, indicating that the Control and High lines differ mainly in rate of growth. Comparing Figures 2a, 2b and 2c, it is clear that the significant decrease in feed efficiency (gain/feed) in the age interval 21 to 57 days was caused jointly by increased feed consumption and decreased weight gains. These trends are

TABLE 3

Heterogeneity of regression sums of squares among line-sex subclasses. Regression of feed consumption, feed efficiency and weight gain on age

Source	df	Mean squares		
		Feed consumption	Feed efficiency	Weight gain
Residuals				
Line (L)	1	307.57***	0.135***	28.39***
Sex (S)	1	239.65***	0.220**	41.38***
L × S	1	10.42 ^{NS}	0.002 ^{NS}	0.23 ^{NS}
Error	1964	3.49	0.019	1.19
Slopes				
Line (L)	1	21.57*	0.069 ^{NS}	7.16*
Sex (S)	1	13.74*	0.031 ^{NS}	3.49 ^{NS}
L × S	1	9.63 ^{NS}	0.001 ^{NS}	0.13 ^{NS}
Error	1964	3.49	0.019	1.19
Elevations				
Line (L)	1	286.00***	0.066 ^{NS}	21.23**
Sex (S)	1	225.91***	0.188**	37.89***
L × S	1	0.74 ^{NS}	0.001 ^{NS}	0.11 ^{NS}
Error	1964	3.49	0.019	1.19

^{NS} Not significant

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

typical of mammalian growth (HANKINS and TITUS 1939; BRODY 1945; KLEIBER 1961).

Weight trends: The regressions of feed consumption and feed efficiency on body weight are presented in Figures 3a and 3b. The regressions were highly significant and, on the average, accounted for 61 and 21% of the variation in feed consumption and feed efficiency, respectively. It is apparent from Figure 3a that at any point between 10 and 30 g body weight, female mice in both lines consumed more feed than males of the same weight. The analysis of variance in Table 4 shows that this sex difference in feed intake over the weight interval studied was due primarily to significantly ($P < .05$) different slopes.

The significance of the sex $\times$ line interaction in the slopes suggests further that the feed intake-body weight association is peculiar to each sex-line subgroup. The line difference in the slopes was also highly significant ($P < .001$) and though not consistent within sexes, it indicates that feed intake per gram body weight was larger in the selected mice at all body weights.

The regressions of feed efficiency on body weight (Figure 3b) also showed a marked difference ($P < .001$) between the High and Control lines. Although the association between feed efficiency and body weight is expected to be linear and negative (HANKINS and TITUS 1939), the regressions in the High males and High females do not follow a linear pattern. Table 4 also shows that there was a significant ($P < .05$) interaction between line and sex. However, despite this heterogeneity, it is evident from Figure 3b that the High mice were more efficient than

FIGURE 3a.—The regressions of feed consumption (g) on body weight (g) under *ad libitum* feeding.

FIGURE 3b.—The regressions of feed efficiency (gain/feed) on body weight (g) under *ad libitum* feeding.

TABLE 4

Heterogeneity of regression sums of squares among line-sex subclasses. Regression of feed consumption and feed efficiency on body weight

Source	df	Mean squares	
		Feed consumption	Feed efficiency
Residuals			
Line (L)	1	57.14***	0.901***
Sex (S)	1	26.48**	1.019***
L × S	1	40.28***	0.036 ^{NS}
Error	1964	2.64	0.019
Slopes			
Line (L)	1	50.51***	0.736***
Sex (S)	1	14.93*	1.019***
L × S	1	53.97***	0.078*
Error	1964	2.64	0.019
Elevations			
Line (L)	1	42.49***	0.464***
Sex (S)	1	2.66 ^{NS}	0.937***
L × S	1	17.04*	0.181**
Error	1964	2.64	0.019

^{NS} Not significant

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Controls at any point in the body weight range from 15–30 g, while over the entire range of weights, males were more efficient than females.

Comparisons over fixed age and fixed weight intervals: The results reported thus far indicate that growth rate, feed consumption and feed efficiency are non-linear functions of age and weight. Consequently, these traits were analyzed within three consecutive age intervals and over a constant weight interval. Although the relationships studied were approximately linear within the three age intervals (21–33, 33–45, and 45–57 days), there was considerable heterogeneity in the regressions of the three traits on body weight. Therefore, the validity of covariance analysis based on body weight is questionable.

The least-squares mean differences in feed efficiency, feed consumption and weight gain given in Table 5 confirm the observations that the differences between lines and sexes change markedly over the 21–57 day period and are dependent on body weight. High mice had a higher feed efficiency than Controls in Periods I and II (21–45 days) but did not differ significantly ($P > .05$) in Period III. High mice consumed significantly ($P < .01$) more feed than Controls over all three age periods, though the magnitude relative to the increasing average feed consumption decreased. In contrast, sex differences in feed consumption increased both in magnitude and significance from Period I to Period III.

The results of the analysis of the traits in the fixed-weight interval may be compared with the fixed-age analysis of Period I since the average ranges in age overlapped considerably (24–37 *vs.* 21–33 days). It is evident from the unadjusted

TABLE 5
Least-squares estimates of the overall means, and differences between lines (H — C) and sexes (M — F) in feed efficiency, average daily feed consumption (ADFC) and average daily gain (ADG) under ad libitum feeding

Feed		Period I†		Period II‡		Period III‡		Weight constant†	
		Unadjusted	Adjusted	Unadjusted	Adjusted	Unadjusted	Adjusted	Unadjusted	Adjusted
Efficiency	Mean	.204	...	.075	...	.033	...	.185	...
	H — C	.019*	.015	.017*	.048***	.000	.024	.062***	.010
	M — F	.028**	.020	.014	.041**	.014*	.031*	.069***	.029**
ADFC	Mean	4.432	...	6.133	...	5.936	...	5.207	...
	H — C	.401***	.155	.465***	-.088	.285**	-.458*	.141	-.118
	M — F	.253*	-.162	.266**	-.261*	.430***	-.379	-.128	-.325**
ADG	Mean	.906	...	.464	...	.198	...	.967	...
	H — C	.162***	.095**	.138***	.260***	.013	-.106	.356***	.049
	M — F	.188***	.073	.107***	.221***	.097***	-.034	.343***	.111*

† Unadjusted and adjusted indicate that model included and excluded covariance on average body weight, respectively.

‡ Unadjusted and adjusted indicate that model included and excluded covariance on number of days required to gain 10 g in the weight range of 15–25 g, respectively.

* $P < 0.05$, ** $P < 0.01$, *** $P < .001$.

analyses in Table 5 that both sex and line differences in feed efficiency and gain were more completely expressed (200–300% greater) when comparisons were made over a fixed-weight interval.

This result is meaningful because comparisons made at the same age among genetically differentiated lines with respect to growth rate do not account for differences in stage of growth (maintenance requirements) or the composition of weight gains which can exist at any given time interval. Since growth processes in general are functionally associated with body weight (BRODY 1945), comparisons over a weight-constant interval may reflect more closely the differences in net efficiency which exist among the lines. However, such comparisons will be influenced by maintenance costs if differences in efficiency of tissue growth exist. Since slower-growing individuals will take longer to gain the prescribed 10 g, they will have an increased maintenance cost which will be proportional to the number of days required to gain the 10 g. Assuming that growth rate was linear in all subgroups between 15 and 25 g (see Figure 3b), and that maintenance costs as a function of body weight did not vary over lines and sexes, the adjusted weight constant comparisons among lines and sexes (Table 5) may be interpreted as a measure of differences in the net efficiency of growth. Again, there was a contrast between the sex and line responses in feed efficiency since adjusting for maintenance completely removed the line difference (unadjusted, 0.062 *vs.* adjusted, 0.010) but not the sex difference (0.069 *vs.* 0.029). A similar pattern was observed for average daily gain in the weight-constant analysis. If the stated assumptions are valid, this result suggests that selection for postweaning gain has caused a change in gross efficiency but not in net efficiency of tissue growth. However, differences in net efficiency appear to exist between male and female mice.

The differences in feed consumption at constant body weight (covariance analyses) show a variable pattern in the lines and sexes. No significant difference existed between High and Control mice except in Period III ($P < .05$), whereas the only significant sex difference was found in Period II. In agreement with the regressions in Figure 3a, these estimates show that at similar body weights, females consumed more feed than males. It is worth noting that in these covariance analyses significant line $\times$ sex interactions were found in average daily feed consumption in Period II and Period III. This same interaction was also significant in the analysis of food consumption over the constant weight interval 15–25 g and it suggests that comparisons of High and Control mice cannot be generalized over both sexes. An earlier study of this same stock (I.C.R.) by EISEN and LEGATES (1966) reported significant sex $\times$ genotype interactions for postweaning gain and 56-day weight, traits which are clearly dependent on food consumption. However, LANG and LEGATES (1969) did not find any evidence of this interaction in other stocks in this laboratory.

A summary of the analyses over the three separate periods is presented in Table 6. The changes in all three traits over time were reflected in the highly significant ($P < .001$) period differences, with the greatest changes occurring between Periods I and II. It also was evident from the analyses of variance that there were no significant interactions of lines or sexes with periods except in

TABLE 6

Least-squares estimates of the overall means and differences between lines (H — C), sexes (M — F) and periods ($P_I - P_{II}$, $P_I - P_{III}$, $P_{II} - P_{III}$) in feed efficiency, average daily feed consumption (ADFC) and average daily gain (ADG) under ad libitum feeding

	Feed efficiency	ADFC	ADG
Mean	.104	5.501	.523
H — C	.012**	.384***	.104***
M — F	.019***	.317***	.131***
$P_I - P_{II}$	.127***	—1.675***	.441***
$P_I - P_{III}$	.170***	—1.487***	.706***
$P_{II} - P_{III}$	.042***	.188***	.265***

** P < 0.01, *** P < 0.001

TABLE 7

Least-squares estimates of the overall means and differences between lines (H — C), sexes (M — F) and feeding regimes (A — R) in feed efficiency, average daily gain (ADG) and average daily feed consumption (ADFC)

	Feed efficiency†		ADFC†		ADG†	
	Unadjusted	Adjusted	Unadjusted	Adjusted	Unadjusted	Adjusted
Mean	.029	...	5.401	...	.175	...
H — C	.012***	.012**	0.574***	0.046	.082***	.057*
M — F	.002	.000	.193**	0.327***	.031	.004
A — R	.053***	.051**	1.265**	0.207	.316***	.267**

† Unadjusted and adjusted indicate that model included and excluded covariance on average body weight, respectively.

* P < 0.05, ** P < 0.01, ***P < 0.001

TABLE 8

Mean values for feed efficiency, average daily feed consumption (ADFC) and average daily gain (ADG) by line-sex-feeding regime subclasses

		Males		Females	
		Ad lib.	Restricted	Ad lib.	Restricted
ADG	Control	.349	.066	.248	.101
	High	.427	.165	.318	.181
	H—C	.078	.099	.070	.038
ADFC	Control	6.01	4.82	5.69	4.84
	High	6.41	5.68	6.02	5.56
	H—C	0.40	0.86	0.33	0.72
Feed efficiency	Control	.058	.014	.044	.021
	High	.067	.029	.053	.033
	H—C	.009	.015	.009	.012

average daily gain, which was just significant ($P < .05$). Therefore, the linear contrasts in Table 6 may be interpreted as a summary of the differences in feed consumption, weight gain and feed efficiency between lines and sexes over an age-constant (21–57 days) interval under *ad libitum* feeding.

Ad libitum and restricted feeding: The results of the comparisons made under *ad libitum* and restricted feeding regimes are summarized in Tables 7 and 8. The feed consumption estimates (Table 7) indicate a large difference (1.26 g) between mice on *ad libitum* and restricted feeding regimes. This difference was largely due to variation in body weight, as the estimate after correction for body weight was only 0.21 g. A significant line $\times$ feeding regime interaction in feed consumption indicated that the experimental procedure failed to achieve the same degree of feed restriction in the Controls as in the High mice. The failure to impose a similar restriction in both lines arose largely in the early stages of the restriction period when body weight changes, and consequently the restricted feed aliquots which were adjusted for body weight, were very erratic. In the early stages of the restriction most mice lost weight. Since this may have temporarily imposed stress on individuals, only the effects of restriction over the total period can be assessed.

The High line had a higher feed efficiency than Controls under both *ad libitum* and restricted feeding. Although the means in Table 8 suggest that this difference in feed efficiency was larger under restricted feeding than in the *ad libitum* regime in both sexes, the line $\times$ feeding regime interaction was not significant in either the adjusted or the unadjusted analysis. To examine the effect of the large variation in the early phase of restriction the data were reanalyzed from day 45–57. The results did not differ from the complete analysis, and again the line $\times$ feeding regime interaction was not significant.

In contrast to the line responses there was no overall significant sex difference in feed efficiency but a highly significant sex $\times$ feeding regime interaction in both the adjusted and unadjusted means. In this case it is in the *ad libitum* environment that the greatest difference in efficiency is expressed. It can be seen from Table 8 that the sex difference averaged for High and Control lines is larger in the *ad libitum* environment than in the restricted regime. This is in complete contrast to the line $\times$ feeding regime interaction which showed that line differences in efficiency were more fully expressed in the restricted environment. There was a highly significant sex $\times$ feeding regime interaction ($P < .001$) in average daily gain also.

DISCUSSION

Definitions of feed efficiency: When considering the trait, feed efficiency, it is important to realize that efficiency *per se* is never really measured. Rather, direct measurements of growth (x_1) and feed consumption (x_2) are made and efficiency is then defined as an index (x_1/x_2 or x_2/x_1) of these two traits. SUTHERLAND (1965) and MAGEE (1962) have considered the automatic aspect of the relationship between feed efficiency and weight gain and have indicated the situations in which this relationship will attain particular values. Whereas SUTHERLAND (1965) chose to use the index, feed/gain, as a "measure of biological efficiency,"

MAGEE (1962) preferred the reciprocal form, gain/feed, which he termed "desirable feed efficiency." TITUS, MEHRING and BRAMBAUGH (1953) also drew attention to the alternate forms and suggested the terms, feed efficiency (gain/feed) and feed conversion (feed/gain).

The product-moment correlation (ρ) between these alternate forms (x_1/x_2 , x_2/x_1) will always be negative but will never equal minus one. In this experiment values of this correlation ranged from -0.7 to -0.9 . The extent to which ρ will differ from minus one is a function of the variance of x_1/x_2 .

Since these alternate indices of efficiency are not the same, it is of interest to describe the differences. Using PEARSON's (1897) approximations of the expected value and variance of a ratio, the factors contributing to these differences become evident.

$$E(x_1/x_2) = (\mu_1/\mu_2) + (\mu_1/\mu^3_2)\sigma^2_2 - (1/\mu^2_2)\sigma_{12} \quad (1)$$

may be contrasted with

$$E(x_2/x_1) = (\mu_2/\mu_1) + (\mu_2/\mu^3_1)\sigma^2_1 - (1/\mu^2_1)\sigma_{12}, \quad (2)$$

and

$$\text{Var } (x_1/x_2) = (1/\mu^2_2)\sigma^2_1 - 2(\mu_1/\mu^3_2)\sigma_{12} + (\mu^2_1/\mu^4_2)\sigma^2_2 \quad (1a)$$

may be compared with

$$\text{Var } (x_2/x_1) = (\mu^2_2/\mu^4_1)\sigma^2_1 - 2(\mu_2/\mu^3_1)\sigma_{12} + (1/\mu^2_1)\sigma^2_2, \quad (2a)$$

where μ_1 , μ_2 and σ^2_1 , σ^2_2 are means and variances of weight gain and feed consumption, respectively, and σ_{12} is the covariance between gain and feed consumption.

These formulas clarify some of the consequences of comparing animals on the basis of fixed weight, fixed age or fixed feed intervals. In comparisons over a fixed weight interval, feed consumption provides a direct measure of gross economic efficiency and will be perfectly correlated with feed/gain but nonlinearly ($|\rho| < 1$) related with gain/feed. The latter would be perfectly correlated with gain which is a direct measure of gross economic efficiency when comparisons are made over a constant feed interval.

Since both feed consumption and weight gain will vary when comparisons are made over a constant age interval, a choice of the alternate forms cannot be made based on the previous considerations. However, if we consider the variances of x_1/x_2 vs. x_2/x_1 , it is clear from expressions (1a) and (2a) that both variances are functions of σ^2_1 , σ^2_2 and σ_{12} and differ only in the coefficients of these terms. Comparing these corresponding coefficients. $1/\mu^2_2$ vs. μ^2_2/μ^4_1 , μ_1/μ^3_2 vs. μ_2/μ^3_1 , and μ^2_1/μ^4_2 vs. $1/\mu^2_1$, shows that the coefficients from expression (1a) will always be less than those in (2a) when $\mu_1 < \mu_2$. In mammals average weight gain (μ_1) is always less than average feed consumption (μ_2); i.e., $\mu_1 = K \mu_2$, $0 < K < 1$. It is easily shown that the coefficients of σ^2_1 , σ_{12} and σ^2_2 in formula (2a) will be greater than their corresponding terms in (1a) by an amount $1/K^4$. Consequently the variance of x_2/x_1 will be considerably greater than the variance of x_1/x_2 . The coefficient of variation will also be greater for x_2/x_1 but not to the same extent since the means are different, $\overline{(x_2/x_1)} > \overline{(x_1/x_2)}$. In this study, the coefficients of variation for x_2/x_1 and x_1/x_2 were 79.9% and 23.7%, respectively. On this basis

gain/feed would be preferred to feed/gain when comparisons are made over a constant age interval.

Efficiency in the biological sense is also dependent on the tissue composition of the weight gain as well as on the feed requirement for maintenance. Since tissue fat contains more energy than protein (9.45 *vs.* 5.65 kcal/g), any efficiency index which does not account for this difference will underestimate the efficiency of the animals with a higher amount of fat. That this bias will be greater when the index, feed/gain, is used can be seen by expressing total dry weight gain as $\Delta_b = \Delta_f$ (gain in fat tissue) + Δ_{ff} (gain in fat-free tissue), and substituting this expression for gain into formulas (1) and (2). Clearly, Δ_f will appear in all terms in the $E(x_2/x_1)$, but only in the mean (μ_1) and covariance term (σ_{12}) in $E(x_1/x_2)$.

The effect of maintenance on the efficiency index will depend on the stage of growth at which animals are evaluated. Since maintenance feed requirements are proportional to "metabolic" size (body weight⁷⁵) it follows that the effect of maintenance on gross efficiency will increase as animals having genetically different growth rates diverge in body weight. It will depend further on the stage of growth to the extent that maintenance requirements relative to the feed energy of growth will be less in the period of maximum growth before puberty. In view of these considerations and the results of this study, it is clear that the particular results of any comparisons between genetic lines or sexes are in part dependent on the method of analysis and the particular definition of the traits studied.

General conclusions: It is apparent from these data that selection for increased growth rate has resulted in a positive correlated response in feed consumption and this increase relative to the mean is much more pronounced in the early postweaning stage (21–33 days). FOWLER (1962) and LANG and LEGATES (1969) have also observed increased feed consumption in their selected lines, although these authors did not examine the increases relative to body weight. There is strong evidence in this study (Figure 3a) that feed consumption per gram body weight also increased as a result of selection for postweaning gain.

If feed consumption per gram body weight is interpreted as a measure of appetite it can be concluded that selection has resulted in an increase in appetite. This influences the comparisons based on gross efficiency (gain/feed) in two ways. First, it is associated with increased weight gains in the High mice which resulted in these mice being more efficient than the Controls on a gross gain basis. However, this effect is dependent on the average difference between the lines. In the early postweaning stages of the experiment there was little difference in body weight between the High and Control mice (Figure 1) and consequently very little difference in maintenance requirements. Indeed during the early stage the Control line was more efficient than the High line (Figure 3b). From approximately 15 g onwards, the difference in average body weight was appreciable and over the remainder of the weight range the High mice were more efficient than Controls on a gross gain basis. Second, increased feed consumption, in that it may lead to less efficient absorption and utilization of the feed energy (SIEGEL and WISMAN 1966; HEADLEY 1946), may influence the gross efficiency of the selected

mice in a negative way. The larger line difference in efficiency in the restricted feeding regime supports this interpretation. However, it appears that the positive effect of increased gains associated with increased appetite outweighs the negative effects of energy wastage when the differences in maintenance (average body weight) are large enough to influence gross efficiency. The analyses of "energetic efficiencies" in these lines are in accord with this interpretation (TIMON, EISEN and LEATHERWOOD 1970).

These results suggest that nine generations of selection for postweaning weight gain in the High line have had little effect on the net efficiency of tissue growth. The apparent advantage of the High line over the Control in gross efficiency was dependent on the increased gains associated with the pronounced increase in appetite. In contrast, there was evidence of a physiological difference in net efficiency of tissue growth between the sexes.

The dependence of these latter conclusions on assumptions concerning estimated maintenance requirement indicates the need to measure the composition of growth at a number of points over the growth period in relation to body size and utilization of the ingested feed. Such a study would also measure energy balance to examine the possibility of increased wastage associated with increased feed intake in the High line. The differences in the genetic line and sex contrasts suggest the need to include sex comparisons in such a study.

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SUMMARY

Growth rate, feed consumption and feed efficiency were compared in mice selected for increased postweaning weight gain (High line) and Control line mice under *ad libitum* and restricted feeding conditions. Data based on 199 mice recorded over the postweaning growth period, 21–57 days, were analyzed to show the pattern of change and total change in these traits as a result of selection for postweaning weight gain.—The results showed that High mice consumed more feed, grew at a more rapid rate and were more efficient than the unselected Controls. The High mice had a larger appetite as measured by feed consumed per gram body weight. The difference in feed efficiency between High and Control mice was greater under restricted feed but this line $\times$ feeding regime interaction was not statistically significant. Males grew faster and were more efficient than females from the same line. Measured at the same weight, however, females consumed more feed than males. The difficulties in assessing the alternate definitions of feed efficiency are discussed and an attempt has been made to assess the effects of appetite and maintenance requirements on the genetic line and sex comparisons. It is concluded that the most important change as a result of nine generations of selection for postweaning gain was an increase in appetite which in turn resulted in increased growth rate and increased gross efficiency.

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