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Selection for Efficiency of Feed Utilization in Growing Mice

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Summary. Selection was practised for improved feed efficiency (gain/feed intake) of mice on two alternative feeding regimes. In one set of lines animals were fed ad libitum, in the other set they were individually fed a fixed amount of feed (about 10% below the control ad libitum intake) which was not changed over generations. For each treatment, a pair of replicate lines (E) were selected on efficiency from 3-5 weeks of age for 8 generations and another pair (L) from 5-7 weeks for 7 generations. A control line was maintained for both E and L lines. In terminal generations mice from each line were tested on each feeding regime, and carcasses of ad libitum fed mice were analysed.

The realized heritability (within families) for efficiency averaged 13%, without much variation over treatments. In the E lines efficiency increased by about 18% of the control mean and in the L lines by about 60%, although absolute changes were small, and responses were similar on the two feeding regimes. Weights at the start of test decreased in the E lines and increased in the L lines; weights at the end of test increased in both.

When tested on the alternative regimes, no interactions were detected for live weights, weight gains or efficiency; selection under fixed intake led to the same increase in appetite as did that under ad libitum.

There were no interactions for carcass composition. Selection for efficiency led to an increase in fatness on both selection regimes and both weight ranges.

Key words: Selection – Mice – Feeding Efficiency – Correlation

Introduction

Efficiency of feed utilization of growing animals depends on the interrelationships among food intake, growth and composition of the gain. These are not simply linear: increased appetite leads to increased growth and a spreading of maintenance costs, but if animals become much fatter, this extra gain may be energetically more demanding and at the same time less desired by the consumer. The associations among the characters also depend on the feeding regime: thus under a scheme whereby all animals are fed the same amount of food, gain and efficiency are completely correlated, but not when appetite is given free expression.

Yüksel (1979) has recently reviewed the genetic inter-relationships among the characters in farm and laboratory animals and we merely summarise his findings. Much of the information comes from selection experiments or breeding programmes for single traits. In all species, growth rate and efficiency are highly correlated, and selection for increased growth rate improves efficiency as a correlated response. While selection for increased growth rate increases both food consumption and efficiency, direct selection for efficiency has uncertain consequences on food consumption, except in the pig, where the two are negatively correlated. In other species, changes in food consumption are usually small and, where they occur, uncertain. Changes in carcass composition also fail to yield a regular pattern. Selection for weight gain may increase fatness, not necessarily at the age of selection but at later ages, because of the increased appetite (Hayes and McCarthy 1976). But where selection has been for increased efficiency, the changes in efficiency were generally greater than where selection was for growth rate alone, both in mice (Sutherland et al. 1970, 1974) and in broilers (Pym and Nicholls 1979; Pym and Solvyns, 1979), with the broiler lines selected for efficiency being leaner. In pigs, commercial selection for increased efficiency and leanness has produced little change in daily live weight gain but increased lean gain and reduced food intake (Smith and Fowler 1978); but since intake can be limited managementally, it has been argued that selection for reduced appetite is pointless (Fowler et al. 1976). In laboratory experiments for increased efficiency of lean gain, there were direct responses but little change in food consumption or gross efficiency (Notter et al. 1976; Gosey 1976). There do not appear to have been experiments comparing the genetic changes in efficiency under the alternatives where appetite was given free expression and where it was not.

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In the study reported here, direct and correlated responses to selection for gross efficiency of feed conversion in the growing mouse are examined in relation to two experimental variables: feeding regime and the age range over which efficiency is measured. The feeding regimes were either ad libitum or a fixed amount of food fed to each mouse of each generation, at a level intended to correspond to the mean intake of the base population but actually about 10% lower. These two regimes were used since they might lead to qualitatively different efficiencies: on a fixed amount of food, greater growth, and thus greater efficiency, could arise from a reduction in maintenance requirements, including heat loss, or by achieving a nutritionally less costly body composition. When selected on ad libitum, appetite might also change, not obviously in one direction or the other. The two growth periods were either immediate post-weaning gains, from 3 to 5 weeks of age, or between 5 and 7 weeks, as the mice approached maturity. These two age periods were chosen because sexual maturity occurs around 5 weeks and corresponds with the point of inflexion of the growth curve (Monteiro and Falconer 1966). Growth rates are slower after 5 weeks and if associated with different compositions of the gain, efficiency might reflect different processes.

Materials and Methods

Feeding Regimes

Animals on test were maintained in individual cages. Food intake on the ad libitum regime was measured by using feeding baskets; wastage was treated as if eaten, but little waste was observed. Lines on fixed intake were fed individually every two days on an increasing scale. The amount fed was that consumed by 16 mice (8 of each sex) on ad libitum intake, in a preliminary trial on the unselected base population. In the event, this proved to be about 10% less than the amount consumed by the control lines on ad libitum over the period of the experiment. The amount fed on the fixed intake was adjusted every two days to what was appropriate according to age and sex, except during the first (exploratory) generation of selection, when they were fed the equivalent of one standard deviation of food consumption more. During the selection programme no allowance was made for uneaten food by the animals on fixed intake.

Origin and Designation of Lines

Ten lines of mice were developed and designated as follows. Those selected for efficiency between 3 and 5 weeks of age (early growth) were designated E, while those selected for efficiency between 5 and 7 weeks (late growth) were designated L. A second letter denotes the feeding regime during the selection programme, A for ad libitum and F for a fixed amount of feed. Each of the experimental treatments were replicated. Thus, EA1 and EA2 were the two replicates selected between 3 and 5 weeks on ad libitum feed. Two unselected control lines, EC and LC, were also maintained, with efficiencies measured at ages corresponding to those of the selected lines.

The mice came from roughly equal representations of the six unselected control Q lines (Falconer 1973). From generation 31 of these lines, 2-line and then 4-line crosses were made. From among the 4-line crosses, 28 litters were chosen at random from litters containing at least 4 males and 4 females at weaning (21 days) and with their dams visibly pregnant for a second litter. A male and a female from each litter were assigned at random to each of the 4 E lines (generation 0) and mated to avoid inbreeding. A further 8 pairs (one mouse of either sex from each of 16 different litters) formed the EC (control) line. A similar procedure was applied to the second litters to form the 4 L lines and the LC control, subject to adjustment only when four mice of each sex were not available from some litters.

Selection Programme

Each of the ten lines was subsequently maintained on 8 pair matings, with random mating except for avoidance of close relatives, and within-family selection (at random, for the controls) was practised. Each litter ideally provided 7 young for testing, 3 of one sex and 4 of the other, any numerical deficiencies being made up by extra mice from larger litters. From each litter, one mouse of each sex was selected on its deviation from the family (litter) mean. The weight gain (and the food consumption of those fed ad libitum) was measured for each mouse, the criterion of selection being efficiency (weight gain/food consumed). On the fixed intake, in which uneaten food was also charged to the mouse's account, efficiency ranks identically with weight gain.

Because facilities for individual feeding were limited, the control lines measured only when spare capacity was available at the right time: at generations 4, 8 and 9 in the E lines, and 4, 7 and 8 in the F lines. In retrospect, it would have been desirable to secure a more adequate monitoring of the progress of the selection, rather than concentrate on the final outcome. The presentation of the results will be governed by this limitation.

Selection continued for 8 generations in the E lines, and for 7 in the L lines. In the following generation, but without further selection, samples of mice were taken from the lines selected on each feeding regime and tested on the other, all lines being measured over the appropriate age interval.

Body Composition

After another randomly-mated generation (generation 10 for the E lines and 9 for L), body composition was assessed by chemical analysis on animals, all of which had been fed ad libitum. Each litter from each line supplied 1 female and 1 male chosen at random for dissection and analysis at the starting age (3 weeks for E and 5 weeks for L); this group of 16 mice per line, except for minor losses, were analysed as a bulk sample. At the terminal age, two weeks later, the same litters provided three further mice, two of one sex and one of the other, which were chosen to represent a range of terminal body weights. Three samples per line, one of heavy, one of medium and one of small mice, each comprising 8 animals, were analysed in bulk.

After slaughter, the stomach and intestines were removed, leaving the mesenteric fat, and the carcass was weighed and stored at −20°C. Before analysis the carcass was minced three times, using a mincer plate with 3mm holes. A sample of the mince was freeze-dried for 48 hours to obtain the weight of carcass water. Carcass fat was obtained by ether extraction for 16 hours. Total nitrogen was determined by the Kjeldahl procedure, and protein estimated as N X 6.25. Ash content was obtained by raising the temperature from 150 to 400°C at the rate of 50°C per hour, followed by holding at 400°C for 16 hours and finally at 600° for a further 7 hours.

Results

1 Responses to Selection

There was a high degree of consistency between males and females in all traits over all generations, so all the results are presented as unweighted means of the two sexes. There was, however, much unexplained variation between generations, as shown for feed efficiency in Figure 1. Therefore all results for the selection lines will be shown as deviations from such contemporaneous control values as were available.

Live weights, weight gains, feed intakes and efficiency are

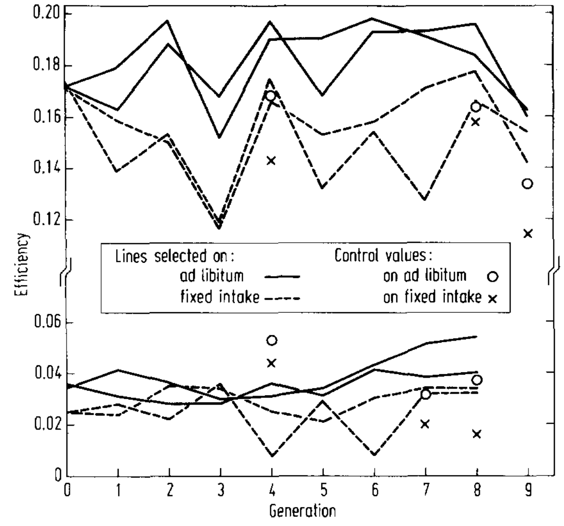

Fig. 1. Mean efficiency of selected lines shown against generation number, E lines above, L lines below, with contemporaneous control values where available.

Table 1. Mean values of live weight, weight gain, feed intake and efficiency of the controls and deviations from controls of lines selected for efficiency between 3 and 5 weeks of age. Efficiency, measured on individuals, is weight gain/feed consumption

Line	Generation	3 wk wt (g)	5 wk wt (g)	Gain (g) 3–5 weeks	Feed Intake (g)	Efficiency
		Selection and measurements on ad libitum feed				
		Control line				
EC (A)	4	10.83	20.59	9.76	57.8	0.168
	8	8.91	17.44	8.53	51.5	0.164
	9	8.06	15.40	7.34	54.3	0.134
		Deviation of selected from control line				
EA1	4	–1.19	–0.77	0.42	–6.0	0.029
	8	–1.40	–0.33	1.09	–2.4	0.032
	9	–0.05	1.11	1.16	–1.1	0.026
EA2	4	–0.73	0.14	0.87	–1.2	0.022
	8	–0.66	–0.17	0.51	–2.4	0.020
	9	0.07	1.51	1.43	–0.6	0.028
		Selection and measurements on fixed feed intake				
		Control line				
EC(F)	4	11.27	18.59	7.32	51.2	0.143
	8	9.57	17.68	8.11	51.2	0.158
	9	8.09	13.98	5.89	51.2	0.115
		Deviation of selected from control line				
EF1	4	–1.11	0.58	1.69	–	0.032
	8	–0.27	0.11	0.38	–	0.008
	9	0.75	2.79	2.05	–	0.039
EF2	4	–1.04	0.15	1.19	–	0.023
	8	–0.50	0.51	1.00	–	0.020
	9	0.23	1.59	1.37	–	0.027
		Average standard errors of deviations from controls (from within line variance)				
	4	0.99	0.74	0.69	2.2	0.014
	8	0.85	0.99	0.54	3.1	0.008
	9	0.66	0.86	0.45	1.6	0.008

Table 2. Mean values of live weight, weight gain, feed intake and efficiency of the controls and deviations from controls and deviations from controls of lines selected for efficiency between 5 and 7 weeks of age. Efficiency, measured on individuals, is weight gain/feed consumption

Line	Generation	5 wk wt (g)	7 wk wt (g)	Gain (g) 5–7 wks	Feed Intake (g)	Efficiency
		Selection and measurements on ad libitum feed				
		Control line				
LC(A)	4	18.32	21.92	3.60	67.6	0.053
	7	19.30	21.27	1.97	63.5	0.031
	8	16.47	19.32	2.85	78.0	0.037
		Deviation of selected from control line				
LA1	4	3.13	1.99	–1.16	10.1	–0.022
	7	0.15	1.96	1.81	9.9	0.020
	8	1.33	2.86	1.53	2.7	0.018
LA2	4	4.19	3.27	–0.92	7.0	–0.017
	7	0.68	1.25	0.56	4.5	0.007
	8	2.78	3.22	0.43	3.6	0.004
		Selection and measurements on fixed feed intake				
LC(F)	4	18.42	21.31	2.89	65.7	0.044
	7	18.91	20.25	1.34	65.7	0.020
	8	16.96	18.01	1.05	65.7	0.016
		Deviation of selected from control line				
LF1	4	2.37	1.13	–1.24	–	–0.019
	7	–0.18	0.75	0.93	–	0.014
	8	1.52	2.68	1.16	–	0.018
LF2	4	2.33	–0.02	–2.35	–	–0.036
	7	–0.56	0.18	0.75	–	0.012
	8	–0.45	0.63	1.08	–	0.016
		Average standard errors of deviations from controls (from within line variance)				
	4	1.03	0.80	0.74	2.1	0.011
	7	1.14	0.79	0.59	2.2	0.008
	8	1.23	0.92	0.61	1.7	0.009

given for the E lines (3-5 weeks) in Table 1 and for the L lines (5-7 weeks) in Table 2. In both, weight gains and efficiencies of the unselected controls were generally higher when the mice were fed ad libitum, while voluntary food intake was also somewhat higher than the fixed amount fed. As a summary, differences between the selected lines and the controls are expressed as a percentage of the control line means in Table 3, with pooling of replicates and the two terminal generations (between which no selection was practised).

In the E lines efficiency improved in all lines in each of the three generations measured, though little progress seems to have been made after the fourth generation (Tables 1 and 3). The improvement in efficiency was very similar on ad libitum and on the fixed food intake, the average improvement being about 18% over the level of the control in the last two generations. Though the selected lines on ad libitum consistently ate less food than the control, the reduction in proportionate terms was very small (except for EA1 in generation 4), so that weight gains over the 3-5 week period of measurement were similar under the two regimes. This greater weight gain tended to be achieved by both a reduction in initial weight and an increase in terminal weight.

Efficiency and weight gains were poorer in the selected L lines than in their control at the fourth generation, when the selected lines also showed much higher initial (5 week) weights (Tables 2, 3). There are not sufficient data to examine a time trend in the LC control line, but it seems more likely that some accident of sampling happened to it rather than simultaneously to the four selected lines. By the final two generations all four L lines had improved efficiencies, LA1 showing the greatest deviation from the control and LA2 the least. Though the improvements in efficiency were small in absolute terms, in proportionate terms the mean increase was 61% over the controls at the end, and much larger than in the E lines. Unlike the E lines, the L lines selected under ad libitum

Table 3. Deviations of selected lines from controls expressed as a percentage of the control mean. Replicates and last two generations pooled

Lines	Generation	Start wt.	End wt.	Gain	Feed intake	Efficiency
		Early lines (3–5 weeks)				
EA	4	−9	−2	7	−6	15
	8 and 9	−6	4	15	−3	18
EF	4	−10	2	20	–	19
	8 and 9	1	9	19	–	19
		Late lines (5–7 weeks)				
LA	4	20	12	−29	13	−37
	7 and 8	7	12	47	8	37
LF	4	13	3	−62	–	−62
	7 and 8	1	6	85	–	86

Table 4. Realized heritabilities (within family) for feed efficiency: total response, calculated as a deviation from controls averaged over the last two generations, divided by cumulative selection differential

Generations	Ad libitum		Fixed	
	Early			
	EA1	EA2	EF1	EF2
8 and 9	0.19 ± 0.04	0.15 ± 0.04	0.13 ± 0.04	0.13 ± 0.04
	Late			
	LA1	LA2	LF1	LF2
7 and 8	0.15 ± 0.03	0.08 ± 0.02	0.11 ± 0.03	0.11 ± 0.03

showed some increase in food intake and their improved efficiency stemmed from even greater weight gains. The greater gains tended to come more from an increase in final weight than reduction in initial weight, particularly under ad libitum.

Realized heritabilities were calculated for the two generations after selection had been stopped by dividing the total response, expressed as a deviation from controls by the cumulative selection differential. Results are shown in Table 4, with standard errors computed by Hill's (1972) method. The estimates are rather consistent and although somewhat higher in the E lines (0.15) than the L lines (0.10), are not significantly so, since only one control line is involved in each case. The overall estimate of realized heritability (h_w^2) is 0.13, which is for selection within full sib families. The intra-class correlation (t) among full sibs for efficiency, averaged for the separate lines over the whole experiment, was about 0.4, and from this the heritability of individual feed efficiency can be calculated as $2(1-t)h_w^2 \sim 0.16$.

Standard errors calculated from the within line variances are given for deviations of line means from the controls in Tables 1 and 2. These are given only as a guide, but cannot be used for significance testing since drift variance is not included. Only for efficiency, on which an estimate of genetic variance could be obtained from the realized responses, could appropriate (although approximate) standard errors be computed as in Table 4.

2 Tests under the Alternative Feeding Regime

Generation 9 of the E lines and 8 of the L lines were tested on both feeding regimes, and results are given in Table 5. All lines consumed more food and were somewhat more efficient when fed ad libitum than on the fixed amount fed. But on both feeding regimes, the mice selected on that regime were no better than those selected on the other. The only hint to the contrary comes from line LA1. An analysis of variance, even though using error variances which were too small because drift was ignored, confirmed that line × treatment interactions were non-significant for all traits.

3 Carcass Analyses

The results of the analyses of carcasses carried out on animals fed ad libitum at the end of the experiment are summarised in Table 6. The components for the control

Table 5. Comparisons of lines on different diets: control line means and deviations from controls.

	Early lines (3–5 weeks). Generation 9						
	Ad libitum				Fixed intake (51.25 g feed)		
	n	Gain (g)	Feed (g)	Effic.	n	Gain (g)	Effic.
EC	28	7.34	54.3	0.134	29	5.89	0.115
		Deviation from control					
EA1	23	1.16	–1.1	0.026	22	2.03	0.038
EA2	25	1.43	–0.6	0.028	29	1.16	0.026
EF1	19	2.10	3.1	0.030	30	2.05	0.039
EF2	32	1.54	0.9	0.026	31	1.37	0.027
SE[a]		0.46	1.6	0.008		0.44	0.007
	Late lines (5–7 weeks). Generation 8						
	Ad libitum				Fixed intake (65.7 g feed)		
	n	Gain (g)	Feed (g)	Effic.	n	Gain (g)	Effic.
LC	27	2.85	78.0	0.037	28	1.05	0.016
		Deviation from control					
LA1	23	1.53	2.7	0.018	23	1.23	0.019
LA2	23	0.43	3.6	0.004	23	0.54	0.008
LF1	21	0.56	3.5	0.005	23	1.16	0.018
LF2	20	0.31	–0.7	0.005	23	1.08	0.016
SE[a]		0.62	1.7	0.009		0.61	0.009

[a] Average standard error of deviation from controls, calculated from within line variance

lines are shown as percentages of total carcass weight, and values for the selected lines were computed similarly, but are shown as deviations from the controls. Values for the three bulk samples from each line at the terminal weights (5 weeks for E and 7 for L) have been pooled, as there was not a consistent relationship between weight and composition. The standard errors in Table 6 were calculated from an analysis of variance of the sample means, in which the effects of body size and lines of mice within sizes were removed. Strictly, these errors apply only to the samples at the end of the test period, at 5 and 7 weeks respectively for the E and L lines. The errors were applied at the start of the test periods also, as no independent estimates were available.

The two control lines (EC and LC) show good agreement in composition when slaughtered at the same age of 5 weeks. The EC lines increased in fat percentage between 3 and 5 weeks, as expected, but rather unexpectedly, the LC line decreased in fat percentage, as estimated by ether extract, between 5 and 7 weeks.

By far the most striking feature of the carcass results for the selected lines is that, although selected for feed efficiency, they became fatter than the controls at both start and end of test and correspondingly showed a reduced water content. Protein and ash contents also tended to be reduced in the L lines, but not in the E lines at 5 weeks. The replicates within a selection treatment do not appear to resemble each other any more than lines selected on the other treatment. Therefore, just as for traits of the live animal, there appears to be no interaction between feeding regime during selection and carcass composition.

There is, however, some suggestion of a difference between the two ages of the effects of selection on the deposition of fat over the test period. Over the test period, all four E lines became less fat (in percentage terms) than their control but all four L lines put on more fat than their control. Since only one control is involved in each case, the controls may themselves be aberrant, and the declining fat percentage of the LC control from 5 to 7 weeks has already been noted. However, disregarding the controls, the mean fat percentage of the selected E lines increased from 8.4% to 9.7% between 3 and 5 weeks, and that of the selected L lines from 9.2% to 10.0% between 5

Table 6. Carcass composition (%) of control lines, and deviations of selected lines from controls

	Early lines (3–5 weeks). Generation 10							
	3 weeks				5 weeks			
	Water	Fat	Protein	Ash	Water	Fat	Protein	Ash
EC	70.2	6.9	19.0	3.8	69.4	8.7	18.3	3.5
	Deviation from control							
EA1	−1.4	1.8	−0.2	−0.2	−0.8	1.1	−0.4	0.0
EA2	0.6	0.4	−0.6	−0.4	−0.2	−0.8	0.7	0.3
EF1	−1.3	1.3	0.1	−0.1	−1.5	1.1	0.2	0.2
EF2	−1.9	2.7	−0.8	0.0	−3.6	2.4	0.8	0.4
SE[a]	1.5	1.0	0.9	0.5	0.9	0.6	0.5	0.3
	Late lines (5–7 weeks). Generation 9							
	5 weeks				7 weeks			
	Water	Fat	Protein	Ash	Water	Fat	Protein	Ash
LC	69.2	8.4	18.7	3.7	67.8	7.9	20.2	4.1
	Deviation from control							
LA1	−1.0	0.9	−0.2	−0.1	−1.4	1.8	−0.2	−0.1
LA2	−1.1	1.6	0.0	−0.5	−2.0	2.6	−0.4	−0.3
LF1	0.4	0.8	−1.0	−0.2	−1.5	2.4	−0.5	−0.4
LF2	−0.2	0.1	0.4	−0.3	−0.3	1.4	−0.8	−0.4
SE[a]	1.5	1.0	0.9	0.5	0.9	0.6	0.5	0.3

[a] Average SE of deviation from controls estimated from variance among bulk samples within lines

and 7 weeks. Since mean live weight gains were much higher between 3 and 5 than between 5 and 7 weeks (Tables 1, a), it is clear that the E selected lines, though younger, accumulated much more fat than the L lines over their corresponding test periods.

4 Analyses Within Lines and Generations

Analyses of variance were conducted within each line and generation to estimate the between and within full-sib family variance and covariance components for weights at start and end of test, gain, feed intake (in A lines) and efficiency. There were no obvious heterogeneities, so results have been pooled over generations and over replicate lines, and are shown in Table 7. This gives the intra-class correlations of each trait, phenotypic correlations between traits and between-family correlations. If maternal effects are ignored, these can be interpreted as one-half the heritability, phenotypic correlations and genetic correlations respectively.

A noticeable feature of the results are the negative phenotypic correlations between efficiency and start weight under ad libitum feeding, the between-family correlations between efficiency and start weight also being negative. The responses to selection (Table 3) were less negative in the E lines and were positive in the L lines. This suggests a major part of these correlations were associated with maternal environment.

Discussion

The realized heritability for efficiency averaged only 13%, and the improvement in efficiency was small in absolute terms. Nevertheless, the E lines exceeded the control means by 20% and the L lines by 60%, after only 7 or 6 generations, respectively, of selection (the last two generations were from random mating). The improvement came almost entirely from increased gain, for food intake on ad libitum changed very little. We may ask therefore whether we could have increased efficiency more by selecting for gain alone. The heritability of gain is usually found to be 2-3 times greater than the value obtained here for efficiency. Estimates of the genetic correlation, obtained from

Table 7. Estimates of intra-class correlation (diagonals), phenotypic correlations (below diagonals) and between-family correlations (above diagonals) from within-line analysis of full sib families over all generations

		E lines				
		3 wk wt	5 wk wt	Gain	Feed intake	Efficiency
3 wk wt	Ad libitum	0.75	0.85	–0.01	0.81	–0.62
	Fixed	0.81	0.59	–0.64	–	⌿
5 wk wt	Ad libitum	0.67	0.42	0.52	0.84	–0.17
	Fixed	0.47	0.55	0.22	–	⌿
Gain	Ad libitum	0.06	0.78	0.23	0.27	0.67
	Fixed	–0.54	0.46	0.54	–	⌿
Feed intake	Ad libitum	0.08	0.79	0.51	0.43	–0.51
	Fixed	–	–	–	–	–
Efficiency	Ad libitum	–0.39	0.33	0.78	–0.11	0.36
	Fixed	⌿	⌿	⌿	–	⌿
		L lines				
		5 wk wt	7 wk wt	Gain	Feed intake	Efficiency
5 wk wt	Ad libitum	0.50	0.90	–0.66	0.68	–0.75
	Fixed	0.58	0.86	–0.85	–	⌿
7 wk wt	Ad libitum	0.81	0.38	–0.29	0.75	–0.42
	Fixed	0.75	0.42	–0.45	–	⌿
Gain	Ad libitum	–0.47	0.12	0.30	–0.18	0.98
	Fixed	–0.72	0.09	0.46	–	⌿
Feed intake	Ad libitum	0.55	0.65	0.18	0.32	–0.35
	Fixed	–	–	–	–	–
Efficiency	Ad libitum	–0.57	0.00	0.98	0.03	0.26
	Fixed	⌿	⌿	⌿	–	⌿

No result on fixed intake; ⌿ efficiency ≡ gain on fixed intake;
typical SE: intra-class correlation 0.05; phenotypic correlation 0.03, between-family correlation 0.10

full sib families in this study, were 0.67 for the E lines and nearly 1.0 for the L lines (Table 7). Even the lower values suggest that efficiency would have been improved at least as much by selecting for gain alone, while the higher values would predict selection for gain to be much more effective. Broiler breeders have long taken this simple line, avoiding the extra labour of weighing feed as well. Some early pig experiments (Dickerson and Grimes 1947) came to the same conclusion. More recently, however, a broiler experiment (Pym and Nichols 1979) and some pig work (Smith et al. 1962; Vogt et al. 1963; Park 1965) all suggested that direct selection on efficiency is preferable, if that is the trait to be improved. Our conclusion that efficiency would have changed more by selecting for gain should be qualified; we used a short feeding period of two weeks, and some mice may have had difficulty adapting to single cages.

Two features of the data were unexpected. First, mice selected for improved efficiency became fatter, as was also found in similar circumstances, selecting mice for gain on a fixed intake, by McPhee et al. (1980). This does not accord with the simple view that the energetic cost of the accretion of lean tissue is less than that of fat, as a result of the inclusion of so much water in lean. Nor does it accord with pig experience, noted earlier. However, the customary difficulties of translating across species apart, the bioenergetic arguments are complicated. Webster (1977) points out that perhaps some 70% of a growing animal's energetic input is dissipated as heat. While one source of such heat will be the chemical reactions involved in protein synthesis, it seems likely that the differential demands of laying down lean and fat may account for only a part, perhaps a small part, of the total energetic input. The alternative outlets for energy may have swamped the system. As one example, since the mice selected for efficiency tended to be smaller at the start of the test period, their maintenance requirements associated with protein turnover may have been less. If this were the case, selection over a fixed age period (as was done here) may not be directly comparable to selection over a fixed weight range, as is frequently done with domestic livestock. The selected mice also tended to be fatter at the start of the test period, possibly leading to a reduced maintenance requirement while on test. This observation poses a cautionary note: the effects of selection for efficiency cannot be fully assessed without monitoring changes in metabolic demands outside the test period.

The second unexpected feature of the experiment was the total lack of interaction between feeding regime and the response to selection. This differs from the results of Hetzel (1978), who selected mice for gain both under ad libitum and on a fixed intake. The fixed intake part of his experiment is identical to that part of ours, but the two characters (gain and efficiency) on ad libium are not directly comparable. Hetzel found an interaction between his selection responses and feeding regime: weight gain on each feeding regime was most improved by selection on that regime. The food intake of his line selected on a fixed amount was marginally decreased when tested on ad libitum and neither was the fat percentage of that line significantly altered on either feeding regime. In our case, neither appetite nor carcass composition differed between the two selection methods. The question therefore shifts: why did appetite not change when it was given a free role when selecting on ad libitum feeding? Perhaps the first point to note is that except for the pig, the connection between appetite and efficiency is not very clear (Yüksel 1979). Even so, if there is any genetic variation in efficiency, animals that secured the same weight gain on less food would be selected, and it was precisely this concern that prompted us to introduce the two feeding methods when designing the experiment. However, we probably did not entirely exclude variation in appetite under the fixed regime, since some mice may have failed to eat all of the feed offered but were charged with it anyway. Subjectively, we were not aware of extensive refusals, but they were not measured. But if they occurred, this would be another source of interaction rather than an explanation of a lack of interaction. To the extent that our results may be generalized, the debate among pig breeders about optimal feeding schemes under test might prove to be superfluous.

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