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Direct and Correlated Responses to Selection for Efficiency of Lean Gain in Mice¹

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ABSTRACT: Improvement in feed efficiency when selection is based on gain:feed ratio has often been accompanied by a reduction in feed intake. The following four criteria were used in mass selection for improved lean gain efficiency in mice with an objective of evaluating changes in lean gain and intake: 1) gain deviation, animals selected had the greatest gain in fat-free mass (FFM) after adjustment to a constant intake; 2) intake deviation, mice selected had the least feed intake after adjustment to a constant gain in FFM; 3) intrinsic efficiency, similar to the second criterion except that adjustment was also made for average weight maintained during the period; and 4) a positive control that used the ratio of gain in FFM: feed intake as the selection criterion. A fifth line, in which a male and a female were selected at random from each litter, served as a negative control. Experimental animals were outbred mice of the CF1 strain. Two replicates of the five lines were included in

the study. Twelve males and females were pair-mated within each line-replicate combination each generation. Feed disappearance was measured from 25 to 42 d. Mice were scanned to obtain an electrical conductivity measurement for prediction of FFM. After six generations of selection, realized heritabilities for gain:feed, gain deviation, intake deviation, and intrinsic efficiency were .00 \pm .04, .04 \pm .29, .35 \pm .08, and $.28 \pm .06$, respectively. There were no differences among lines for gain:feed ratio. The correlated response in feed intake reduction was significant in the intake deviation and intrinsic efficiency lines $(-.17 \pm .05 \text{ and } -.21 \pm .04 \text{ g}\cdot\text{d}^{-1}\cdot\text{generation}^{-1}, \text{ respec-}$ tively). The realized genetic correlations between the ratio and gain deviation, intake deviation, and intrinsic efficiency were .83 \pm .15, .01 \pm .04, and .21 \pm .12, respectively. Litter size was depressed in all selected lines.

Key Words: Mice, Body Lean Mass, Selection

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Introduction

In swine herds, feed cost for the slaughter animal accounts for about 45% of the production cost for lean tissue (Tess et al., 1983). Selection programs that improve the efficiency of feed utilization are expected to be beneficial to the swine industry. Despite reports that feed conversion ratio (**FCR**) is moderately heritable, direct selection for the trait has been largely unsuccessful (Webb and King, 1983). Improvements in FCR have, however, resulted from selection that used an index based on growth rate and backfat (Cleveland et al., 1982) or growth rate, backfat, and FCR (Ellis et al., 1988).

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A consequence of achieving an improvement in feed efficiency in most of the studies cited has been a reduction in appetite. The latter may limit response in

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reduction in appetite. The latter may limit response in the overall selection goal and growth rate. Meat quality and reproduction may suffer as well. The objectives of this study were to evaluate the

response in efficiency of feed utilization for four methods of selecting for lean efficiency as well as to evaluate resulting correlated responses in reproductive performance and metabolic rate.

Materials and Methods

Population and Management

Experimental animals were outbred mice of the CF1 strain. The base population was produced by reciprocally mating CF1 males and females from two commercial sources. One generation of random mating was practiced before selection was initiated. Two replicates of five selection lines were included in the experiment. Fifteen pairs of animals within each line

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and replicate were mated at approximately 60 d of age. Mating was permitted for a period of 21 d. Progeny from the 12 highest ranking litters (based on their parents' records) were measured in the subsequent generation. Matings were initiated on the same day within a replicate. Matings for Replicate 2 were not initiated until matings for Replicate 1 were completed within any generation in order to more evenly distribute labor requirements.

All mice had ad libitum access to a pelleted diet (23% crude protein and 4.5% fat; Lab Diet 5001, PMI Feeds, St. Louis, MO) and distilled water. From d 17 of pregnancy until litters were weaned, females were housed in polycarbonate cages measuring $28 \times 17 \times 12$ cm. Litters remained in these cages until 25 d of age. During the test period, mice were individually housed in stainless steel hanging wire cages measuring $24 \times 10 \times 13$ cm. Animal rooms were maintained at $22 \pm 2^{\circ}$ C with a relative humidity of 50 \pm 10% and illuminated from 0700 to 1900 daily.

Total number of pups born in each litter was recorded, and experimental animals were reared in litters standardized, as nearly as possible, to four males and four females. Standardization was done 1 d after birth. Number born and number weaned were recorded. Litters were weaned at 21 d of age and pups weighed. At 25 d of age, mice were again weighed, placed in individual cages, and recording of feed intake was initiated. Body weights and feed intake were recorded at 31, 37, and 42 d of age. Intake for each recording period was estimated by calculating feed disappearance, defined as total weight of feed placed in the cage minus that present in the cage at the end of the recording period. Animals were fed daily an amount expected to slightly exceed that consumed.

At 45 d of age, mice were weighed and anesthetized by intraperitoneal injection of a solution of 2.5% Avertin (Hogan et al., 1986) at a dose rate of .015 mL/ g of body weight. An EM-SCAN SA-2 instrument (EM-SCAN, Springfield, IL) was used to obtain a measure of electrical conductivity (\mathbf{E}) in triplicate. The mean of the three measures was calculated and FFM at 45 d estimated by using the equation (Holder and Lamberson, 1996)

FFM = -3.732 + .578 body weight + 2.967 E^{.5}

The prediction equation for FFM was estimated by fitting the average of duplicate measures of FFM of mice obtained by using an ether extract procedure in a Soxhlet apparatus to a series of models including the effects of body weight, body length, and E. Eighty mice of both sexes and ranging in weight from 9.8 to 50 g were included in the calibration procedure. Each model was run five times with random samples of 54 of the 80 mice. The resulting equations were then used to predict the FFM of the remaining 26 mice. Body length was not found to contribute significantly to the prediction equation. The model that resulted in the highest R^2 included the effects of body weight and $E^{.5}$. Fat-free masses of all animals in the group were then fitted to the model to obtain the final prediction equation.

A fixed fat percentage of 12% at 25 d was assumed for calculation of gain in FFM. This percentage was based on earlier chemical analyses conducted in our laboratory. The assumption was made because the model of TOBEC instrument used in this study was not highly accurate at lower body weights (<10 g). Furthermore, fat percentage at the initial point of measurement was not anticipated to be a significant correlated response to short-term selection in this experiment. A total of 6,500 mice were measured in the present study.

Selection Criteria

Five lines were included in the selection experiment. A line in which a male and female were selected at random from each litter served as a negative control. This line served to measure fluctuations and trends in the environment. A line in which the selection criterion was weight of FFM gained divided by feed intake between 25 and 42 d of age (gain:feed ratio) was the positive control line. This selection criterion represented the standard from past experiments. Three experimental criteria represented alternatives to selection on the gain:feed ratio. The first criterion was denoted as gain deviation. Animals selected on this criterion were those with the highest residual for gain of FFM when gain of FFM was fitted to a model including the effect of intake. This is equivalent to selection on greatest gain of FFM after adjustment to a constant intake. The second experimental criterion was intake deviation. Animals selected on this criterion were those with the greatest negative residual for intake when it was fitted to a model including the effect of gain of FFM. This is equivalent to selection on least intake after adjustment to a constant gain of FFM. The final criterion was intrinsic efficiency. It was similar to intake deviation except that the effect of average weight maintained between 25 and 42 d of age in addition to gain of FFM were fitted as effects in the model for intake deviation. Mass selection was used in choosing parents for replacement in select lines. Mating was at random except that mating of full-sibs was avoided.

Selection Differentials and Realized Heritabilities and Genetic Correlations

Weighted selection differentials were calculated by subtracting the mean performance of the parent generation from the weighted mean of the selected individuals. Each parent was weighted by the number of offspring it contributed for measurement in the offspring generation. For each generation, the weighted selection differentials were calculated separately for each sex within lines and then averaged to give the weighted selection differentials for respective lines. Selection differentials for the select lines were corrected for unintended selection in the random control line. These weighted selection differentials were then summed across generations to yield the cumulative selection differentials for the traits.

Selection was practiced for six generations. Realized heritability estimates for gain:feed ratio, gain deviation, intake deviation, and intrinsic efficiency were calculated from the regression of cumulative response on weighted cumulative selection differentials. Empirical standard errors of the realized heritability estimates were calculated from variation between replicates and, thus, include drift error (Hill, 1972). Response means were calculated as deviations from the negative control. The assumption was that environmental differences affected the selected and control lines alike; therefore, the difference between them provided an estimate of the genetic improvement made by selection (Falconer, 1989).

Realized genetic correlations between the ratio and each of the other selected traits were calculated using the method of Falconer (1989):

$$r_{g}^{2} = (CR_{x} \cdot CR_{y})/(R_{x} \cdot R_{y})$$

where r_{g}^{2} is the square of the pooled genetic correlation between traits x and y, CR refers to the correlated response, and R the direct response for the trait denoted by the subscript. Standard errors were estimated from replicate variance.

Correlated responses in first-parity litter size for the four selected lines and random control were determined by regressing line-generation means on generation number.

Terminal Evaluation

Reproductive performance was evaluated after six generations of selection and one generation of withinline random mating. Twenty pairs per line were mated at random. A single male and female per cage were left together for a period of 100 d beginning when they were 45 d of age. A total of 268 litters were produced. Traits recorded included age at first parturition, average parturition interval, number of litters born and weaned per mated pair, total number and total weight of offspring born alive, and total number and total weight of offspring weaned during the 100-d mating period.

One male offspring chosen at random from the first litter of each of 12 females per line underwent measurement of resting metabolic rate (**RMR**). Following weaning, mice were placed in individual wire cages and trained in stocks for 30 min on at least four occasions in the week preceding measurement to minimize elevation in RMR due to excitation. Tests were conducted at 55 d of age and were performed in a water-jacketed metabolic chamber with four horizontal cylinders for individual animals. Each animal was weighed and fitted with a thermocouple inserted approximately 30 mm beyond the anal sphincter to record colonic temperature. Once in the chamber, animals were allowed to rest for 1 h before measurements were taken. Intended ambient temperature was 31°C, a value within the thermoneutral zone of mice (Gordon, 1993). Actual ambient temperature (31.04 \pm .02°C) was calculated as the average of temperatures recorded continuously in four different points of the chamber. Oxygen consumption was measured using an open-flow system. Room air was dried by passage through a calcium sulfate container and circulated at a flow rate of 338 mL/min. Oxygen content of the effluent air was analyzed with a Rosemount Model 755 O₂ analyzer (Rosemount, Eden Prairie, MN), interfaced with a microcomputer. Resting metabolic rates were estimated from rates of O2 consumption using a respiratory quotient of .83.

All traits were analyzed by least squares methods using the GLM procedure of SAS (1985). Models included the effects of line and sire within line. Models for litter birth weight and litter weaning weight (**LWW**) included litter size as a covariate. When line effect was significant (P < .05), preplanned orthogonal contrasts were used to compare means. Contrasts included the four selected lines versus random control, gain:feed ratio versus gain deviation, intake deviation and intrinsic efficiency, gain deviation versus intake deviation and intrinsic efficiency, and intake deviation versus intrinsic efficiency.

Results

Realized Heritabilities and Genetic Correlations

Realized heritability estimates for gain:feed ratio, gain deviation, intake deviation, and intrinsic efficiency were .00 \pm .04, .04 \pm .29, .35 \pm .08, and .28 \pm .06, respectively.

Cumulative selection differentials for the four selected traits, expressed in standard deviation units, are shown in Table 1. Selection differentials were highest for the intake deviation and intrinsic efficiency lines and lowest for the ratio.

Estimates obtained in the present study for the genetic correlation of gain:feed ratio with gain deviation, intake deviation, and intrinsic efficiency were .83 \pm .15, .01 \pm .04, and .21 \pm .12, respectively.

Correlated Responses

Line-generation means averaged over replicates for gain:feed ratio are presented in Figure 1. Considerable fluctuation among lines from generation to generation was evident.

Line-generation means averaged over replicates for feed intake are shown in Figure 2. Despite the lack of

Table 1. Cumulative selection differentials expressed in standard deviation units for the four selection lines: gain in fat-free mass/feed intake ratio (G:F), gain deviation (GD), intake deviation (ID), and intrinsic efficiency (IE)

Generation	Cumulative selection differentials ^a							
number	G:F	GD	ID	IE				
1	.52	.55	-1.05	76				
2	.52	1.67	-2.13	-1.97				
3	1.35	2.30	-2.87	-2.75				
4	1.93	2.93	-3.54	-3.10				
5	2.59	3.53	-4.16	-4.14				
6	3.11	4.36	-4.99	-5.07				

^aCumulative selection differentials were corrected for unintended selection in the random control prior to standardization.

response in gain:feed ratio, feed intake was reduced in the intake deviation and intrinsic efficiency lines relative to the control and gain:feed lines. The gain deviation line was intermediate and not significantly different from the other lines. Regressions of feed intake per day on generation as a deviation from control were $-.17 \pm .05 \text{ g}\cdot\text{d}^{-1}\cdot\text{generation}^{-1}$ for the intake deviation line and $-.21 \pm .04 \text{ g}\cdot\text{d}^{-1}\cdot\text{generation}^{-1}$ for the intrinsic efficiency line and were not different from zero for the gain:feed ratio and gain deviation lines.

Fluctuations in the response for gain in FFM are shown in Figure 3. There was no difference in the correlated response in lean gain among five lines. Numerically, the intrinsic efficiency and intake deviation lines had regressions that were small relative to the control, and this probably offset their favorable response in intake.

Regressions of litter size on generation for the selected lines during the six generations of selection ranged from $-.25 \pm .15$ to $-.42 \pm .20$ pups per generation. The regression of litter size on generation for the control line was $.01 \pm .17$ pups per generation. There were no significant differences in regression coefficients among the selected lines, and, when selected lines were pooled, litter size was reduced compared with the control (P < .05).

Terminal Evaluation

No differences were detected among lines for age at first parturition, average parturition interval, number of litters born and weaned, colonic temperature, or resting metabolic rate (Table 2). Decreases in number born alive (P < .01) and number weaned (P < .05) were observed in the selected lines when compared with the control (Table 2). The average number born alive and number weaned during the 100-d terminal evaluation period were 30.4 and 19.2, respectively, for the control line and 19.9 and 13.7, respectively, for the selected lines. Total weight of offspring born alive and

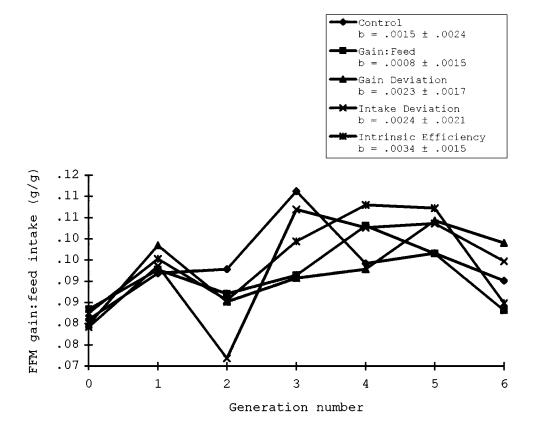


Figure 1. Line-generation means for the ratio of gain in fat-free mass (FFM) to feed intake.

litter weaning weight were greater in the gain deviation and gain:feed ratio lines when compared with the intake deviation and intrinsic efficiency lines (P < .01). Means for these traits in the gain lines (gain deviation and gain:feed) were 37.7 and 165.0 g, compared with 33.6 and 143.0 g in the intake reduction lines (intake deviation and intrinsic efficiency).

Discussion

The realized heritability estimate for gain:feed ratio in this study is consistent with the lack of a response in FCR found in other studies in which direct selection for a ratio was practiced (Bernard and Fahmy, 1970; Jungst et al., 1981; Webb and King, 1983). Realized heritability estimates for intake deviation and intrinsic efficiency were moderate. In mice, Gunsett et al. (1981) reported a realized heritability of .73 for decreased feed intake on a constant gain in body weight. Chambers et al. (1994) reported an increase in realized heritability for efficiency when feed efficiency data for poultry were adjusted for differences in body weights. Similar findings have been reported by Wang et al. (1991).

Realized heritability for gain deviation was only .04 \pm .29, suggesting that the trait was not responsive to selection. The low estimate in this study and the lack of precision associated with it resulted from divergence of response in the two replicates. In the first replicate, response was negative. The regression of cumulative response on cumulative selection differential for the second replicate, however, yielded coefficients comparable with those obtained for the intake deviation and intrinsic efficiency lines, and to the estimate of .56 reported by Gunsett et al. (1981) for increased weight gain adjusted to a fixed feed intake.

Sutherland et al. (1970) reported estimates in mice of .91 and .52 for the genetic correlation between feed efficiency and weight gain, and between feed efficiency and feed intake, respectively. Estimates similar to those obtained in the present study have been reported for a beef cattle study by Koch et al. (1963). These researchers reported genetic correlations of .83 and .04 for the association between feed efficiency and live weight gain and between feed efficiency and feed intake, respectively. These findings suggest similar

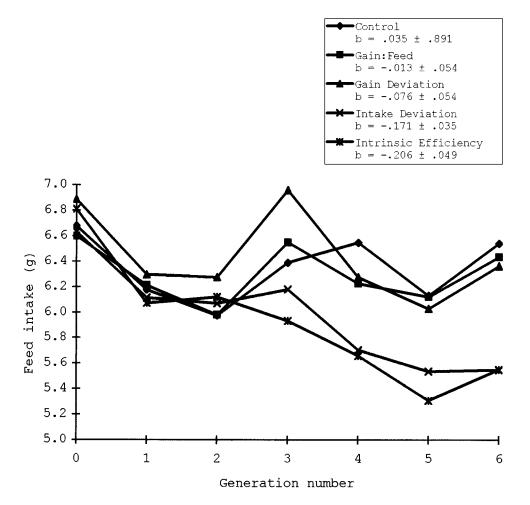


Figure 2. Line-generation means for daily feed intake.

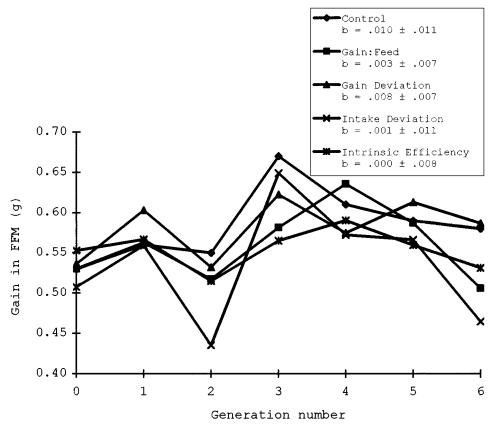


Figure 3. Line-generation means for daily gain in fat-free mass (FFM).

genetic relationships between lean gain and feed efficiency, and between live weight gain and feed efficiency, even when lean gain is corrected for feed intake.

Selection criteria similar to gain deviation and intake deviation were used by Gunsett et al. (1981). These scientists reported a high genetic correlation between the two traits ($r_g = -.94$) and concluded that selection on either criterion would be effective in changing the ratio. Correlated response in the ratio was not achieved in either the gain deviation or the intake deviation line in the present study. The

regression coefficients were similar in magnitude (.0023 \pm .0017 and .0024 \pm .0021, respectively) but not significantly different from zero.

Even though there was no significant difference in the correlated response in lean gain among the five lines, there was considerable fluctuation. The only significance that may be attributed to this response in lean gain is that there is variation in the population with respect to the trait and that exploiting this variation through selection depends in part on the amount of selection pressure exerted in reducing feed intake. The lack of a correlated response in the intake

Table 2. Least-squares means (LSM) and SE for reproductive traits, resting metabolic rate, and colonic temperature

Variable	Control		Gain:feed		Gain deviation		Intake deviation		Intrinsic efficiency	
	LSM	SE	LSM	SE	LSM	SE	LSM	SE	LSM	SE
Age at first parturition, d	82.2	1.4	77.9	1.5	78.9	1.3	78.2	1.8	80.7	1.4
Average parturition interval, d	32.3	2.0	28.0	2.0	30.2	1.8	32.8	2.4	31.1	1.9
No. of litters born	3.0	.2	2.8	.2	3.0	.2	2.7	.3	2.7	.2
No. of litters weaned	2.2	.2	2.3	.2	2.1	.2	2.3	.2	2.1	.2
Total born alive	30.2	1.5	20.8	2.7	19.0	2.5	20.6	2.8	17.1	2.8
Total weaned	18.7	2.1	15.0	2.0	12.3	2.2	18.5	2.0	11.9	2.2
Metabolic rate, watt·kg ⁻¹	14.0	1.0	13.2	1.0	14.5	1.0	14.1	1.1	11.5	1.0
Colonic temperature, °C	37.6	.1	37.6	.2	38.1	.1	37.7	.2	37.6	.1

deviation and intrinsic efficiency lines was expected because adjustment of intake to a constant gain in FFM would have reduced correlated selection emphasis on gain in FFM in these two lines. A similar result was reported by Chambers (1994) working with poultry. In that study, the correction of feed intake for test body weights contributed to a reduction in realized heritability of body weight at 28 d.

The correlated reduction in feed intake in the intake deviation and intrinsic efficiency lines is consistent with the selection pressure exerted on reducing feed appetite in these two lines. The intrinsic efficiency line differed from the intake deviation line only in that adjustment was also made for average weight maintained during the experiment.

Litter size was depressed in the present study as a result of selection. Inbreeding was not considered to be a contributing factor because inbreeding coefficients were low and similar in magnitude in all lines (range, .08 to .11). Nor could the unfavorable change in litter size be attributed to changes in weight of female because those changes were small and nearly identical across all lines. Nielsen et al. (1997) reported decreased litter size accompanying selection for decreased heat loss in mice. They suggested that the decrease in litter size might have resulted from decreased intake in the low-heat loss lines. Brien et al. (1984) had previously reported a similar relationship. A number of other mouse studies have reported small differences in favor of fat lines (Brien et al., 1984; Brien and Hill, 1986; Eisen, 1987; Hastings et al., 1991). The slight differences in favor of fat lines were attributed to differential survival of eggs and zygotes.

Unfortunately, no studies were found with correlated responses in reproduction to selection on efficiency of feed utilization. In swine, Berruecos et al. (1970) reported a significant decline of .3 pig per generation in litter size and pig weight after five generations of selection for carcass leanness. Johansson and Kennedy (1983) also found that the genetic correlations between leanness and litter size in pigs tended to be unfavorable.

Implications

Consistent decreases in reproductive rate associated with selection to improve efficiency of feed utilization in mice should be of concern to swine seedstock producers seeking to improve the latter trait. Caution is advised in practicing selection to improve the efficiency of lean gain, particularly in maternal lines, until studies can be completed evaluating correlated responses to selection using swine as the experimental animal.

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