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# Selection for components related to body composition in mice: correlated responses*

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**Summary.** Correlated responses were estimated in each of two replicate lines of mice selected within full-sib families for high (HF) or low (LF) 12-week epididymal fat pad weight as a percentage of body weight (epididymal fat pad percentage), or high (HL) or low (LL) 12-week hind carcass weight as a percentage of body weight (hind carcass percentage). Two replicate control lines (RC) were maintained. Correlated traits were measured in each of the 10 generations of selection. Realized ($r_{GR}$) and offspring-sire genetic correlations generally were in agreement. In HF and LF, 3–6 week postweaning gain ($r_{GR} = 0.36 \pm 0.04$) and feed intake ($r_{GR} = 0.50 \pm 0.13$) had positive correlated responses, but feed efficiency and feed intake/metabolic body size did not change. Positive correlated responses were found for subcutaneous fat pad percentage, body weight-adjusted subcutaneous fat pad weight and fat percentage in the hind carcass ($r_{GR}$'s were $1.04 \pm 0.13$, $0.93 \pm 0.13$ and $0.90 \pm 0.08$). In the hind carcass, fat-free dry (protein + ash) percentage showed a small negative correlated response, and fat-free dry weight did not change. In HL and LL, the correlated responses for the above traits were generally opposite to those observed in HF and LF. Litter size, percentage of infertile matings, and preweaning mortality showed no consistent correlated responses in any of the lines, but an index of fitness combining the three traits showed a decrease in all four selection treatments.

**Key words:** Correlated responses – Mice – Body composition – Growth – Fat

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## Introduction

Selection experiments for growth rate or feed efficiency generally result in correlated responses in body composition. The mouse has been used extensively as a model for livestock to clarify the complex physiological factors controlling body composition changes resulting from selection for growth rate, feed consumption or feed efficiency (Eisen 1974; Roberts 1979; McCarthy 1982; Malik 1984). However, only one study in mice has examined correlated responses in growth, feed intake and feed efficiency following selection for components related to body composition (Bishop and Hill 1985).

Correlated responses in fitness traits are important to consider in all selection experiments (Falconer 1981). A reduction in fitness, whether the result of lowered reproductive performance or decreased survival, has a detrimental effect on overall productivity of the selected population. Brien et al. (1984) reported negligible correlated responses in reproductive performance of mice following single-trait selection for traits associated with body composition.

The objective of the present study was to evaluate correlated responses to selection for the following components related to body composition: (1) growth rate, feed consumption and feed efficiency; (2) body composition traits; and (3) fitness traits. Direct responses to selection are reported in a companion paper by Eisen (1987).

## Materials and methods

### *Selected lines*

The base population and selection treatments used in this study were described previously (Eisen 1987). Briefly, replicate lines were selected as follows: high (HF1, HF2) or low (LF1,

LF2) right epididymal fat pad weight as a percentage of body weight (epididymal fat pad percentage); high (HL1, HL2) or low (LL1, LL2) hind carcass weight as a percentage of body weight (hind carcass percentage); and randomly (RC1, RC2). Omission of the replicate number denotes pooling of replicates. Within full-sib family selection was practiced for 10 generations, and the correlated traits reported were measured in each generation. Replicate lines were maintained with 15 pair-matings per generation, litters were standardized to ten mice at one day of age, and pups were weaned at three weeks. Mice were fed ad libitum Purina Laboratory Chow 5001, Ralston Purina Co., St. Louis, MO, from weaning through the mating period. Dams were fed ad libitum Purina Mouse Chow from the time they were separated from their mates until they weaned their litters.

*Correlated traits*

At weaning, two male full sibs from each litter were randomly caged together to obtain feed consumption from 3 to 6 weeks of age. This procedure was followed because mice caged singly grow less rapidly than grouped mice (Bakker et al. 1976), which may affect body composition. Following weaning, the remaining males and all females were combined, four to a cage within sex and replicate line. Body weights at 3 and 6 weeks of age were recorded, and 3–6 week weight gain was used as a measure of postweaning growth rate. Feed efficiency from 3 to 6 weeks was defined as 100 × (weight gain)/(feed consumption). Feed intake per unit metabolic body size was defined as (3–6 week feed intake)/$(W_3^{0.75}+W_6^{0.75})/2$, where $W_3$ and $W_6$ are 3- and 6-week body weight means in kilograms of the two male sibs.

Following a 16-day mating period, males were caged individually. At 12 weeks of age they were killed by cervical dislocation and naso-anal body length and body weight were obtained. The right hind-limb subcutaneous fat pad (Smith et al. 1983) and right epididymal fat pad (Eisen and Leatherwood 1978) were dissected and weighed. The hind carcass was also dissected and was carefully trimmed of external fat as described by Bhuvanakumar et al. (1985) and weighed. Responses in 12-week body weight and epididymal fat pad and hind carcass weights and percentages of body weight were described by Eisen (1987). Body length provided an estimate of linear growth. The subcutaneous fat pad was measured to determine the correlated response in a second fat depot. A modified lean index (Sharp et al. 1984), 12-week body weight − 16 × (epididymal fat pad weight), was calculated as a correlated trait.

Fifteen male hind carcasses (one from each litter) from each replicate line-generation subclass were identified with a chick wingband and frozen at −18 °C until they were analyzed. When hind carcasses were removed from the freezer, they were lyophilized for 48 h and then weighed. Weight of water was calculated as the difference between fresh and dry hind carcass weight. Approximately 15 dry hind carcasses were placed in a soxhlet extraction tube with a solvent containing 78% chloroform and 22% methanol by volume, and the fat content was extracted by heating the tube for 24 h under a fume hood. Residual solvent in the carcasses was allowed to evaporate overnight under a fume hood, and the hind carcasses were relyophilized for 3 h to remove any moisture before they were weighed. Fat weight was estimated as the difference between the dry and fat-free dry hind carcass weights. Traits analyzed were fat, water and fat-free dry (protein + ash) weights as percentages of hind carcass weight, and fat-free dry hind carcass weight. Fat-free dry weight as a percentage of hind carcass dry weight is not presented because the correlation between it and fat weight as a percentage hind carcass weight was essentially minus one.

Fitness traits were defined as percentage of infertile matings, first parity litter size at birth, and percentage of preweaning mortality. Postweaning mortality was negligible and, therefore, was not included although it is recognized to be a fitness trait.

*Statistical analysis*

Within each generation, least-squares means were obtained from a statistical model which included an overall mean, a fixed selection criterion effect, a random replicate effect, a selection criterion × replicate interaction, a random litter effect for traits which included more than one observation per litter, and a random residual effect. The model for 3- and 6-week body weights and 3–6 week postweaning gain also included a fixed effect of sex and interactions with sex. The model for 3-week body weight included the number of pups weaned as a covariate. Subcutaneous fat pad weight was analyzed with and without the addition of 12-week body weight as a covariate in the model.

Realized correlated responses were estimated from the regression of generation mean on generation number. Adjustment for environmental effects was obtained by two least-squares methods. Method 1 was based on the use of generation means for all lines (Richardson et al. 1968), and Method 2 used deviations of selected from control line means (Falconer 1981). Divergence was estimated as the difference between the high and low line slopes. Asymmetry was estimated as the sum of the high and low line slopes, both adjusted for environmental effects.

Realized genetic correlations were estimated by the following formula (Rutledge et al. 1973):

$$r_{G_R} = b_{G_{ij}} (h_j^2 V_{P_j} / h_i^2 V_{P_i})^{1/2},$$

where $b_{Gij}$ is the realized genetic regression of the $i^{th}$ unselected trait on the $j^{th}$ selected trait, $h_j^2$ and $h_i^2$ are the respective heritabilities of the selected and unselected traits, and $V_{P_j}$ and $V_{P_i}$ are the respective phenotypic variances. Heritabilities of the selected traits were obtained from the realized heritabilities of the present experiment (Eisen 1987), and heritabilities of the correlated traits were estimated from twice the regressions of offspring on sire in the replicate control lines (Eisen and Prasetyo 1988). The phenotypic variances were pooled from residual sums of squares within replicate control line-generation subclasses.

## Results

*Control line*

Least-squares means, phenotypic standard deviations, and coefficients of variation estimated in the control lines are presented in Table 1. The means represent a base for evaluating the degree of correlated responses in the selected lines. The regression coefficients of control line generation mean on generation number were not significant ($P > 0.05$) for any trait (data not shown), indicating that environmental trends and/or genetic drift did not have a major effect on the traits measured.

**Table 1.** Least-squares means, phenotypic standard deviations ($\sqrt{V_p}$) and coefficients of variation (CV) for correlated traits[a]

| Trait | Mean | $\sqrt{V_p}$ | CV (%) | DF[b] |
|---|---|---|---|---|
| 3-wk body wt (g)[c] | 12.7 | 1.62 | 12.8 | 3,678 |
| 6-wk body wt (g) | 27.3 | 3.19 | 11.7 | 3,634 |
| 3–6 wk postweaning gain (g/d) | 0.69 | 0.117 | 16.9 | 3,634 |
| 3–6 wk feed intake (g/d)[d] | 5.2 | 0.56 | 10.8 | 357 |
| 3–6 wk feed intake/metabolic body wt ($kg/kg^{0.75}$)[d] | 95.5 | 7.85 | 8.2 | 357 |
| 3–6 wk feed efficiency (100 g/g)[d] | 15.0 | 2.17 | 14.4 | 357 |
| 12-wk body length (cm) | 10.8 | 0.33 | 3.0 | 996 |
| Subc. fat pad wt/body wt (%) | 0.46 | 0.111 | 23.9 | 996 |
| Subc. fat pad wt (mg) | 170 | 50.0 | 29.4 | 996 |
| Adj. subc. fat pad wt (mg)[e] | 177 | 39.7 | 22.4 | 996 |
| Lean index (g) | 30.1 | 2.85 | 9.5 | 996 |
| Fat wt/hind carcass wt (%) | 3.84 | 1.169 | 30.46 | 351 |
| Water wt/hind carcass wt (%) | 67.99 | 0.980 | 1.44 | 351 |
| Fat-free dry wt/hind carcass wt (%) | 28.17 | 0.658 | 2.34 | 351 |
| Fat-free dry hind carcass wt (g) | 1.22 | 0.120 | 9.90 | 351 |
| Infertile matings (%) | 3.7 | 0.95 | 25.6 | 396 |
| Litter size at birth (no.) | 10.6 | 3.10 | 29.2 | 383 |
| Preweaning pup mortality (%) | 0.9 | 0.16 | 18.3 | 3,712 |

[a] Estimates were obtained by pooling within generation data from replicate control lines. Three-wk body wt, 6-wk body wt and 3–6 wk postweaning gain are averaged over males and females; all other traits are measured only in males
[b] Residual degrees of freedom
[c] Adjusted for number weaned by covariance analysis within generations
[d] Experimental unit is the mean of two male litter-mates
[e] Adjusted for 12-wk body wt by covariance analysis within generations

*Correlated responses in growth, feed intake and efficiency*

Regression coefficients of correlated responses on generation number for growth, feed consumption and feed efficiency between 3 and 6 weeks of age are presented in Tables 2 and 3. In general, the two methods of estimating response gave similar slopes, but in these and subsequent tables there were some discrepancies.

Lines selected for high and low epididymal fat pad percentage showed divergent correlated responses ($P<0.01$) and no asymmetry ($P>0.05$) for weaning weight, 6-week body weight, and 3–6 week postweaning gain (Table 2). Pooled across replicates, HF responded positively ($P<0.01$) and LF negatively ($P<0.01$), but replicate heterogeneity was apparent in some cases. Lines HF and LF also diverged ($P<0.01$) for 3–6 week feed consumption. Divergence in feed intake between HF and LF may be explained by divergence in body weight between the two selection treatments, resulting in a change in maintenance requirements. Evidence supporting this contention was the nonsignificant divergence in feed intake per unit metabolic weight. Feed efficiency did not show any significant correlated response. Therefore, increased growth rate in HF was offset by increased feed intake, and similarly decreased growth rate was offset by decreased feed intake in LF.

Selection for high and low hind carcass percentage led to divergence ($P<0.01$) in weaning weight, 6-week body weight, postweaning gain, and feed intake (Table 3). For each trait, HL decreased ($P<0.01$) and LL increased ($P<0.01$). Feed intake/metabolic body weight decreased nonsignificantly ($P>0.05$) in HL and increased significantly ($P<0.05$) in LL, with divergence being significant ($P<0.01$). Thus, the correlated responses in feed consumption in HL and LL could not be explained completely by correlated responses in body weight, as was the case in HF and LF. Feed efficiency exhibited no significant correlated responses in HL and LL when averaged across replicates. Asymmetry was not important for any of these traits.

*Correlated responses in body composition traits*

Correlated responses in HF and LF are displayed in Table 4. Selection in HF and LF resulted in divergence ($P<0.01$) for body length, subcutaneous fat pad percentage and weight, lean index, and fat and water percentages of the hind carcass. Divergence in subcutaneous fat pad weight was reduced after adjustment to a constant body weight. Fat-free dry (protein + ash) percentage of the hind carcass showed significant ($P<0.05$) divergence based on Method 1, but not Method 2. Asymmetry ($P<0.01$) was found for body length and subcutaneous fat pad weight (Method 1).

Body length was also measured to determine if body weight/(body length)$^2$ would respond to selection for epididymal fat pad percentage (Eisen and Prasetyo 1988). In human studies, body weight/height$^2$ has been

**Table 2.** Regression coefficients ± SE of correlated responses on generation number for growth, feed intake and feed efficiency in lines selected for high (HF1, HF2) or low (LF1, LF2) epididymal fat pad wt/body wt

| Trait | Method[a] | HF1 | HF2 | Pooled | LF1 | LF2 | Pooled | Divergence | Asymmetry |
|---|---|---|---|---|---|---|---|---|---|
| 3-wk body wt (g)[b,c] | 1 | 0.020±0.034 | 0.167±0.034** | 0.093±0.024** | −0.094±0.034** | −0.009±0.034 | −0.052±0.024* | 0.145±0.024** | 0.042±0.042 |
| | 2 | 0.038±0.034 | 0.149±0.034** | 0.094±0.024** | −0.094±0.034** | −0.046±0.034 | −0.070±0.024** | 0.164±0.024** | 0.024±0.042 |
| 6-wk body wt (g)[b] | 1 | 0.20 ±0.06** | 0.29 ±0.06** | 0.24 ±0.04** | −0.27 ±0.06** | −0.09 ±0.06 | −0.18 ±0.04** | 0.42 ±0.04** | 0.06 ±0.07 |
| | 2 | 0.20 ±0.06** | 0.30 ±0.06** | 0.25 ±0.04** | −0.23 ±0.06** | −0.10 ±0.06 | −0.16 ±0.04** | 0.41 ±0.04** | 0.09 ±0.07 |
| 3–6 wk post-weaning gain ×10 (g/d)[b] | 1 | 0.083±0.022** | 0.058±0.022** | 0.071±0.016** | −0.086±0.022** | −0.040±0.022 | −0.063±0.016** | 0.134±0.016** | 0.008±0.028 |
| | 2 | 0.069±0.022** | 0.074±0.022** | 0.071±0.016** | −0.064±0.022** | −0.026±0.022 | −0.045±0.016** | 0.116±0.016** | 0.025±0.028 |
| 3–6 wk feed intake ×10 (g/d)[d] | 1 | 0.16 ±0.19 | 0.28 ±0.19 | 0.22 ±0.14 | −0.32 ±0.19 | −0.27 ±0.19 | −0.30 ±0.14* | 0.52 ±0.14** | −0.08 ±0.24 |
| | 2 | 0.21 ±0.19 | 0.46 ±0.19* | 0.34 ±0.14* | −0.31 ±0.19 | 0.01 ±0.19 | −0.15 ±0.14 | 0.49 ±0.14** | 0.19 ±0.24 |
| 3–6 wk feed intake/metabolic wt ($kg/d/kg^{0.75}$)[d,e] | 1 | −0.09 ±0.28 | −0.17 ±0.28 | −0.13 ±0.20 | −0.05 ±0.28 | −0.38 ±0.28 | −0.21 ±0.20 | 0.08 ±0.20 | −0.34 ±0.35 |
| | 2 | −0.09 ±0.28 | 0.13 ±0.28 | 0.02 ±0.20 | −0.09 ±0.28 | −0.01 ±0.28 | −0.05 ±0.20 | 0.07 ±0.20 | −0.03 ±0.35 |
| 3–6 wk feed efficiency (100 g/d)[d] | 1 | 0.116±0.073 | −0.042±0.073 | 0.037±0.052 | −0.086±0.073 | 0.002±0.073 | −0.041±0.052 | 0.078±0.052 | −0.004±0.090 |
| | 2 | 0.114±0.073 | −0.078±0.073 | 0.018±0.052 | −0.053±0.073 | 0.057±0.073 | 0.003±0.052 | 0.015±0.052 | 0.021±0.090 |

* $P<0.05$; ** $P<0.01$

[a] 1 = method of Richardson et al. (1968); 2 = deviation from control (Falconer 1981)

[b] Adjusted for sex effect

[c] Adjusted for number weaned by covariance analysis within generations

[d] Based on mean of two male litter-mates per cage

[e] Metabolic body weight = ½ ($W_3^{0.75} + W_6^{0.75}$) where $W_3$ and $W_6$ are the mean body weights (kg) at 3 and 6 weeks of age, respectively, of the two males in the same cage

**Table 3.** Regression coefficients ± SE of correlated responses on generation number for growth, feed intake and feed efficiency in lines selected for high (HL1, HL2) or low (LL1, LL2) hind carcass wt/body wt

| Trait | Method[a] | HL1 | HL2 | Pooled | LL1 | LL2 | Pooled | Divergence | Asymmetry |
|---|---|---|---|---|---|---|---|---|---|
| 3-wk body wt (g)[b,c] | 1 | −0.212±0.034** | 0.014±0.034 | −0.100±0.024** | 0.024±0.034 | 0.152±0.034** | 0.088±0.024** | −0.188±0.024** | −0.012±0.042 |
| | 2 | −0.211±0.034** | −0.005±0.034 | −0.108±0.024** | 0.034±0.034 | 0.130±0.034** | 0.082±0.024** | −0.190±0.024** | −0.026±0.042 |
| 6-wk body wt (g)[b] | 1 | −0.39 ±0.06** | −0.10 ±0.06 | −0.25 ±0.04** | 0.26 ±0.06** | 0.36 ±0.06** | 0.31 ±0.04** | −0.56 ±0.04** | 0.06 ±0.07 |
| | 2 | −0.33 ±0.06** | −0.16 ±0.06** | −0.25 ±0.04** | 0.21 ±0.06** | 0.27 ±0.06** | 0.24 ±0.04** | −0.49 ±0.04 | −0.01 ±0.07 |
| 3–6 wk post-weaning gain ×10 (g/d)[b] | 1 | −0.085±0.022** | −0.057±0.022** | −0.071±0.016** | 0.113±0.022** | 0.099±0.022** | 0.106±0.016** | −0.178±0.016** | 0.035±0.028 |
| | 2 | −0.059±0.022** | −0.074±0.022** | −0.067±0.016** | 0.082±0.022** | 0.068±0.022** | 0.075±0.016** | −0.142±0.016** | 0.008±0.028 |
| 3–6 wk feed intake ×10 (g/d)[d] | 1 | −0.73 ±0.19** | −0.32 ±0.19 | −0.53 ±0.14** | 0.57 ±0.19** | 0.68 ±0.19** | 0.62 ±0.14** | −1.15 ±0.14** | 0.09 ±0.24 |
| | 2 | −0.64 ±0.19** | −0.21 ±0.19 | −0.42 ±0.14** | 0.56 ±0.19** | 0.65 ±0.19** | 0.61 ±0.14** | −1.03 ±0.14** | 0.19 ±0.24 |
| 3–6 wk feed intake/metabolic wt kg/d/kg$^{0.75}$)[d,e] | 1 | −0.21 ±0.28 | −0.32 ±0.28 | −0.26 ±0.20 | 0.55 ±0.28* | 0.35 ±0.28 | 0.45 ±0.20* | −0.67 ±0.20** | 0.19 ±0.35 |
| | 2 | −0.06 ±0.28 | −0.05 ±0.28 | −0.06 ±0.20 | 0.56 ±0.28* | 0.39 ±0.28 | 0.47 ±0.20* | −0.53 ±0.20** | 0.41 ±0.35 |
| 3–6 wk feed efficiency (100 g/d)[d] | 1 | −0.010±0.073 | −0.110±0.073 | −0.060±0.052 | 0.032±0.073 | −0.020±0.073 | 0.006±0.052 | −0.066±0.052 | −0.054±0.090 |
| | 2 | 0.017±0.073 | −0.208±0.073** | −0.095±0.052 | 0.006±0.073 | −0.053±0.073 | −0.023±0.052 | −0.072±0.052 | −0.118±0.090 |

* $P<0.05$; ** $P<0.01$

[a] 1 = method of Richardson et al. (1968); 2 = deviation from control (Falconer 1981)

[b] Adjusted for sex effect

[c] Adjusted for number weaned by covariance analysis within generations

[d] Based on mean of two male litter-mates per cage

[e] Metabolic body weight = ½ ($W_3^{0.75}$ + $W_6^{0.75}$) where $W_3$ and $W_6$ are the mean body weights (kg) at 3 and 6 weeks of age, respectively, of the two males in the same cage

**Table 4.** Regression coefficients ± SE of correlated responses on generation number for body composition traits at 12 weeks of age in replicate lines selected for high (HF1, HF2) or low (LF1, LF2) epididymal fat pad wt/body wt

| Trait | Method[a] | HF1 | HF2 | Pooled | LF1 | LF2 | Pooled | Divergence | Asymmetry |
|---|---|---|---|---|---|---|---|---|---|
| 12-wk body length (mm) | 1 | 0.34 ±0.08** | 0.35 ±0.08** | 0.35 ±0.06** | −0.08 ±0.08 | 0.21 ±0.08** | 0.07 ±0.06 | 0.28 ±0.06** | 0.42 ±0.10** |
| | 2 | 0.34 ±0.08** | 0.41 ±0.08** | 0.37 ±0.06** | −0.01 ±0.08 | 0.24 ±0.08** | 0.09 ±0.06 | 0.28 ±0.06** | 0.46 ±0.10** |
| Subc. fat pad wt/body wt (%) | 1 | 0.019±0.0034** | 0.020±0.0034** | 0.020±0.0024** | −0.016±0.0034** | −0.016±0.0034** | −0.016±0.0024** | 0.036±0.0024** | 0.004±0.0041 |
| | 2 | 0.023±0.0034** | 0.019±0.0034** | 0.021±0.0024** | −0.014±0.0034** | −0.013±0.0034** | −0.014±0.0024** | 0.035±0.0024** | 0.007±0.0041 |
| Subc. fat pad wt (mg) | 1 | 10.3 ±1.6** | 10.2 ±1.6** | 10.2 ±1.2** | −7.4 ±1.6** | −5.9 ±1.6** | −6.6 ±1.2** | 16.8 ±1.2** | 3.6 ±2.1 |
| | 2 | 12.6 ±1.6** | 10.0 ±1.6** | 11.3 ±1.2** | −6.8 ±1.6** | −5.1 ±1.6** | −5.5 ±1.2** | 16.8 ±1.2** | 5.8 ±2.1** |
| Adj. subc. fat pad wt (mg)[b] | 1 | 4.8 ±1.1** | 6.9 ±1.1** | 5.9 ±0.8** | −5.5 ±1.1** | −5.0 ±1.1** | −5.3 ±0.8** | 11.2 ±0.8** | 0.6 ±1.4 |
| | 2 | 5.9 ±1.1** | 6.8 ±1.1** | 6.4 ±0.8** | −5.2 ±1.1** | −3.7 ±1.1** | −4.4 ±0.8** | 10.8 ±0.8** | 2.0 ±1.4 |
| Lean index (g)[c] | 1 | −0.118±0.066 | −0.253±0.066** | −0.185±0.047** | 0.195±0.066** | 0.205±0.066** | 0.200±0.047** | −0.385±0.047** | 0.015±0.081 |
| | 2 | −0.175±0.066** | −0.285±0.066** | −0.230±0.047** | 0.177±0.066** | 0.088±0.066 | 0.132±0.047** | −0.362±0.047** | −0.098±0.081 |
| Fat wt/hind carcass wt (%) | 1 | 0.125±0.047** | 0.207±0.048** | 0.164±0.037** | −0.190±0.045** | −0.166±0.048** | −0.178±0.037** | 0.342±0.037** | −0.014±0.064 |
| | 2 | 0.206±0.046** | 0.191±0.046** | 0.198±0.032** | −0.150±0.046** | −0.141±0.046** | −0.146±0.032** | 0.344±0.032** | 0.052±0.056 |
| Water wt/hind carcass wt (%) | 1 | −0.133±0.042** | −0.183±0.044** | −0.157±0.034** | 0.170±0.042** | 0.087±0.043* | 0.130±0.034** | −0.287±0.034** | −0.027±0.060 |
| | 2 | −0.174±0.044** | −0.140±0.044** | −0.157±0.031** | 0.196±0.044** | 0.108±0.044* | 0.152±0.031** | −0.309±0.032** | −0.005±0.054 |
| Fat-free dry wt/hind carcass wt (%) | 1 | 0.008±0.032 | −0.024±0.034 | −0.007±0.024 | 0.021±0.032 | 0.079±0.032* | 0.048±0.024* | −0.055±0.024* | 0.041±0.042 |
| | 2 | −0.034±0.029 | −0.051±0.029 | −0.042±0.021* | −0.049±0.029 | 0.033±0.029 | −0.008±0.021 | −0.034±0.021 | −0.050±0.036 |
| Fat-free dry wt (g) | 1 | 0.005±0.004 | 0.005±0.004 | 0.004±0.004 | −0.000±0.002 | 0.014±0.004** | 0.000±0.004 | −0.002±0.004 | 0.010±0.006 |
| | 2 | 0.002±0.003 | 0.005±0.003 | 0.003±0.003 | −0.005±0.003 | 0.012±0.003** | 0.004±0.003 | −0.001±0.003 | 0.007±0.005 |

* $P<0.05$; ** $P<0.01$

[a] 1 = method of Richardson et al. (1968); 2 = deviation from control (Falconer 1983)

[b] Adjusted for 12-wk body wt by covariance analysis within generations

[c] Sharp et al. (1984)

used as an index of obesity (Keyes et al. 1972). Body weight/(body length)$^2$ showed no significant divergence or asymmetry (data not shown).

Positive ($P<0.01$) correlated responses in HF and LF were found for adjusted and unadjusted subcutaneous fat pad weight, subcutaneous fat pad percentage, and fat percentage of the hind carcass and in HF for body length. Correlated responses in HF and LF were negative ($P<0.01$) for lean index, water percentage of the hind carcass and, to a lesser extent, fat-free dry percentage of the hind carcass (HF decreased, $P<0.05$ based on Method 2; LF increased, $P<0.05$ based on Method 1). Fat-free dry weight of the hind carcass showed no consistently significant correlated responses.

Correlated responses in body composition traits of HL and LL are listed in Table 5. Divergence ($P<0.01$) was apparent for all traits except fat-free dry weight and percentage of hind carcass weight. The only traits exhibiting asymmetry were body length ($P<0.01$, Method 1 and $P<0.05$, Method 2) and lean index ($P<0.05$, Method 1). No divergence or asymmetry was found for body weight/(body length)$^2$ (data not shown).

Selection for increased hind carcass percentage yielded negative ($P<0.01$) correlated responses for subcutaneous fat pad percentage, adjusted and unadjusted subcutaneous fat pad weights, and fat percentage of the hind carcass. Fat-free dry weight and percentage of the hind carcass did not show significant correlated responses in HL and LL. Lean index failed to respond significantly in HL, but responded negatively in LL, although replicate heterogeneity was present.

*Correlated responses in fitness traits*

Correlated changes in the three fitness traits – infertile matings, litter size at birth and preweaning mortality – were generally inconsistent between selection treatments, between replicates within selection treatments, and between methods of estimation (Table 6). Line HF showed an increased frequency of infertile matings. Line LF declined in litter size when estimated by Method 1, but only one replicate declined. A negative correlated response in litter size was apparent in HL. Infertile matings increased in LL1, but not in LL2. Preweaning pup mortality showed no important trends in any of the selected lines.

An index of fitness was defined for each line as the product of litter size, proportion of fertile matings and proportion of preweaning survival. Thus, the index provides a measure of the combined ability of each line to reproduce and survive. The fitness index was calculated as 10.1 in the controls. Using this mean fitness index as a base, the estimated total declines in fitness index over ten generations of selection were 13%, 7%, 11% and 5% in HF, LF, HL and LL, respectively. Therefore, negative responses in an index of fitness were found, even though any one component of fitness did not exhibit consistent decreases with selection.

*Realized genetic correlations*

Estimates of realized genetic correlations ($r_{G_R}$) between 12-week epididymal fat pad percentage and correlated traits are presented in Table 7. Estimates were pooled within replicates and direction of selection, except where estimates for each direction were discrepant. Comparisons were made with genetic correlations estimated from offspring-sire covariances ($r_{G_S}$) in the base population (Eisen and Prasetyo 1988).

Estimates of heritabilities of hind carcass body composition traits needed to compute $r_{G_R}$ have not been previously published. These heritabilities, estimated as twice the regression of offspring on sire in the control replicates ($df=146$), were as follows: fat percentage ($0.49\pm0.16$), water percentage ($0.56\pm0.17$), fat-free dry percentage ($0.00\pm0.16$), and fat-free dry weight ($0.61\pm0.16$).

Only $r_{G_R}$ between epididymal fat pad percentage and body length appeared to differ between direction of selection, being about 0.5 for upward selection and not significantly different from zero for downward selection. The former correlation agreed with $r_{G_S}$.

The pooled realized genetic correlations of epididymal fat pad percentage with 3- and 6-week body weight and 3–6 week postweaning gain were positive. The $r_{G_R}$ with 3–6 week feed intake also was positive, while $r_{G_R}$ with 3–6 week feed efficiency was close to zero. The realized genetic correlations with other fat depot measurements were all approximately one, while $r_{G_R}$ between epididymal fat percentage and water percentage of the hind carcass was about minus one. The genetic correlation between fat percentage and water percentage of the hind carcass, estimated from sire-offspring covariances in the control replicates, was also approximately minus one. The $r_{G_R}$ between epididymal fat pad percentage and fat-free dry hind carcass weight was zero. No realized genetic correlation could be calculated with fat-free dry percentage of the hind carcass because the estimated heritability of this trait was zero. Epididymal fat pad percentage and litter size had an $r_{G_R}$ that was not different from zero.

Estimates of $r_{G_R}$ and $r_{G_S}$ were in agreement with the exception of those involving lean index and body length (in LF). The four estimates of $r_{G_R}$ between epididymal fat pad percentage and lean index were in remarkably close agreement. This suggests the possibility that $r_{G_S}$ between lean index and body length may have been underestimated.

**Table 5.** Regression coefficients ± SE of correlated responses on generation number for body composition traits at 12 weeks of age in replicate lines selected for high (HL1, HL2) or low (LL1, LL2) hind carcass wt/body wt

| Trait | Method[a] | HL1 | HL2 | Pooled | LL1 | LL2 | Pooled | Divergence | Asymmetry |
|---|---|---|---|---|---|---|---|---|---|
| 12-wk body length (mm) | 1 | −0.15 ±0.08 | −0.02 ±0.08 | −0.09 ±0.06 | 0.40 ±0.08** | 0.58 ±0.08** | 0.49 ±0.06** | −0.58 ±0.06** | 0.40 ±0.10** |
| | 2 | −0.13 ±0.08 | −0.10 ±0.08 | −0.12 ±0.06* | 0.29 ±0.08** | 0.44 ±0.08** | 0.37 ±0.06** | −0.49 ±0.06** | 0.25 ±0.10* |
| Subc. fat pad wt/body wt (%) | 1 | −0.015±0.0034** | −0.008±0.0034* | −0.012±0.0024** | 0.012±0.0034** | 0.007±0.0034* | 0.009±0.0024** | −0.021±0.0024** | −0.003±0.0041 |
| | 2 | −0.012±0.0034** | −0.009±0.0034* | −0.010±0.0024** | 0.013±0.0034** | 0.003±0.0034 | 0.008±0.0024** | −0.018±0.0024** | −0.002±0.0041 |
| Subc. fat pad wt (mg) | 1 | −7.5 ±1.6** | −3.8 ±1.6* | −5.7 ±1.2** | 6.8 ±1.6** | 5.8 ±1.6** | 6.3 ±1.2** | −12.0 ±1.2** | 0.6 ±2.1 |
| | 2 | −6.5 ±1.6** | −4.5 ±1.6** | −5.5 ±1.2** | 7.0 ±1.6** | 3.8 ±1.6* | 5.4 ±1.2** | −10.9 ±1.2** | −0.1 ±2.1 |
| Adj. subc. fat pad wt (mg)[b] | 1 | −4.0 ±1.1** | −2.2 ±1.1* | −3.1 ±0.8** | 3.2 ±1.1** | 0.9 ±1.1 | 2.0 ±0.8* | −5.1 ±0.8** | −1.1 ±1.4 |
| | 2 | −2.7 ±1.1* | −2.0 ±1.1 | −2.4 ±0.8** | 3.5 ±1.1** | −0.6 ±1.1 | 1.4 ±0.8 | −3.8 ±0.8** | −1.0 ±1.4 |
| Lean index (g)[c] | 1 | 0.011±0.066 | −0.033±0.066 | −0.011±0.047 | 0.090±0.066 | 0.297±0.066** | 0.193±0.047** | −0.204±0.047** | 0.182±0.081* |
| | 2 | −0.036±0.066 | −0.122±0.066 | −0.080±0.047 | 0.018±0.066 | 0.229±0.066** | 0.123±0.047** | −0.203±0.047** | 0.043±0.081 |
| Fat wt/hind carcass wt (%) | 1 | −0.215±0.045** | −0.112±0.048* | −0.166±0.036** | 0.118±0.045* | 0.073±0.047 | 0.097±0.037** | −0.263±0.036** | −0.064±0.063 |
| | 2 | −0.166±0.046** | −0.117±0.046* | −0.142±0.032** | 0.128±0.046** | 0.060±0.046 | 0.094±0.032** | −0.236±0.032** | −0.048±0.056 |
| Water wt/hind carcass wt (%) | 1 | 0.186±0.042** | 0.083±0.042* | 0.137±0.034** | −0.111±0.042** | −0.082±0.044 | −0.097±0.034** | 0.234±0.034** | 0.040±0.060 |
| | 2 | 0.152±0.044** | 0.126±0.044** | 0.139±0.031** | −0.095±0.044* | −0.068±0.044 | −0.082±0.031** | 0.221±0.031** | 0.057±0.054 |
| Fat-free dry wt/hind carcass wt (%) | 1 | 0.029±0.032 | 0.029±0.032 | 0.029±0.024 | −0.006±0.032 | 0.007±0.033 | 0.000±0.024 | 0.029±0.024 | 0.029±0.042 |
| | 2 | 0.013±0.029 | −0.009±0.029 | 0.002±0.021 | −0.038±0.029 | 0.005±0.029 | −0.016±0.021 | 0.018±0.021 | −0.014±0.036 |
| Fat-free dry wt (g) | 1 | −0.004±0.004 | 0.008±0.004* | 0.002±0.003 | −0.002±0.004 | 0.016±0.004** | 0.006±0.004 | 0.004±0.003 | 0.008±0.005 |
| | 2 | −0.010±0.003** | 0.005±0.003 | −0.003±0.003 | −0.005±0.003 | 0.010±0.003** | 0.002±0.003 | 0.005±0.003 | 0.000±0.005 |

* $P<0.05$; ** $P<0.01$

[a] 1 = method of Richardson et al. (1968); 2 = deviation from control (Falconer 1983)

[b] Adjusted for 12-wk body wt by covariance analysis within generations

[c] Sharp et al. (1984)

**Table 6.** Regression coefficients ± SE of correlated responses on generation number for fitness traits in lines selected for high (HF1, HF2) or low (LF1, LF2) epididymal fat pad wt/body wt or high (HL1, HL2) or low (LL1, LL2) hind carcass wt/body wt

| Trait | Method[a] | HF1 | HF2 | Pooled | LF1 | LF2 | Pooled | Divergence | Asymmetry |
|---|---|---|---|---|---|---|---|---|---|
| Infertile matings (%) | 1 | 0.77 ±0.40 | 0.63 ±0.40 | 0.70 ±0.28* | 0.01 ±0.40 | −0.13 ±0.40 | −0.06 ±0.98 | 0.76 ±0.28** | 0.64 ±0.48 |
| | 2 | 1.17 ±0.40** | 0.61 ±0.40 | 0.89 ±0.28** | 0.14 ±0.40 | −0.06 ±0.40 | 0.04 ±0.28 | 0.85 ±0.28** | 0.81 ±0.48 |
| Litter size at birth | 1 | −0.10 ±0.06 | −0.02 ±0.06 | −0.06 ±0.04 | −0.16 ±0.06** | −0.02 ±0.06 | −0.09 ±0.04* | 0.03 ±0.04 | −0.15 ±0.07* |
| | 2 | −0.03 ±0.06 | −0.04 ±0.06 | 0.03 ±0.04 | −0.00 ±0.06 | −0.08 ±0.06 | −0.04 ±0.04 | 0.01 ±0.04 | −0.07 ±0.07 |
| Preweaning pup mortality (%) | 1 | 0.037±0.118 | −0.008±0.118 | 0.015±0.083 | 0.007±0.118 | 0.009±0.118 | 0.008±0.083 | 0.007±0.083 | 0.023±0.144 |
| | 2 | 0.192±0.118 | −0.022±0.118 | 0.085±0.083 | 0.105±0.118 | 0.118±0.118 | 0.111±0.083 | −0.026±0.083 | 0.196±0.144 |
| Trait | Method[a] | HL1 | HL2 | Pooled | LL1 | LL2 | Pooled | Divergence | Asymmetry |
| Infertile matings (%) | 1 | −0.06 ±0.40 | 0.04 ±0.40 | −0.01 ±0.28 | 0.87 ±0.40* | −0.31 ±0.40 | 0.28 ±0.28 | −0.29 ±0.28 | 0.27 ±0.48 |
| | 2 | 0.16 ±0.40 | 0.06 ±0.40 | 0.11 ±0.28 | 1.17 ±0.40** | −0.03 ±0.40 | 0.57 ±0.28* | −0.46 ±0.28 | 0.68 ±0.48 |
| Litter size at birth | 1 | −0.16 ±0.06** | −0.09 ±0.06 | −0.13 ±0.04** | −0.09 ±0.06 | 0.07 ±0.06 | −0.01 ±0.04 | −0.14 ±0.04** | 0.12 ±0.07 |
| | 2 | −0.02 ±0.06 | −0.15 ±0.06* | −0.08 ±0.04* | 0.01 ±0.06 | −0.01 ±0.06 | 0.00 ±0.04 | −0.08 ±0.04* | −0.08 ±0.07 |
| Preweaning pup mortality (%) | 1 | 0.030±0.118 | −0.043±0.118 | −0.007±0.083 | 0.016±0.118 | −0.001±0.118 | 0.007±0.083 | −0.014±0.083 | 0.000±0.144 |
| | 2 | 0.299±0.118* | −0.003±0.118 | 0.148±0.083 | 0.214±0.118 | 0.082±0.118 | 0.148±0.083 | 0.000±0.083 | 0.296±0.144* |

* $P < 0.05$; ** $P < 0.01$

[a] 1 = method of Richardson et al. (1968); 2 = deviation from control (Falconer 1981)

**Table 7.** Realized ($r_{G_R}$) and sire-offspring ($r_{G_S}$) genetic correlations (× 100) between epididymal fat pad wt/body wt and correlated traits

| Epididymal fat pad wt/body wt with: | $r_{G_R}$ | | | | | $r_{G_S}$[a] |
|---|---|---|---|---|---|---|
| | HF1 | HF2 | LF1 | LF2 | Pooled | |
| 3-wk body wt | 31 | 120 | 85 | 116 | 88±21[b] | 98±1 |
| 6-wk body wt | 24 | 43 | 41 | 36 | 36±4 | −46±10 |
| 3–6 wk postweaning gain | 18 | 25 | 25 | 15 | 21±3 | 34±10 |
| 3–6 wk feed intake | 13 | 73 | 66 | 46 | 50±13 | 63±11 |
| 3–6 wk feed efficiency | 27 | −26 | 21 | −6 | 4±12 | 6±17 |
| Body length | 45 | 58 | 12 | −33 | 52±7[c]<br>−11±22 | 54±10 |
| Subc. fat pad wt/body wt | 108 | 76 | 96 | 136 | 104±13 | 71±6 |
| Subc. fat pad wt | 135 | 90 | 102 | 130 | 114±11 | 88±3 |
| Adj. subc. fat pad wt | 77 | 77 | 85 | 133 | 93±13 | 61[d] |
| Lean index | −37 | −48 | −36 | −42 | −41±3 | −1±15 |
| Fat wt/hind carcass wt | 95 | 70 | 86 | 108 | 90±8 | 85±10 |
| Water wt/hind carcass wt | −96 | −57 | −124 | −129 | −101±17 | −89±9 |
| Fat-free dry hind carcass wt | 3 | 6 | 12 | −21 | 0±7 | 5±18 |
| Litter size | −2 | −12 | 7 | 35 | 7±10 | – |

[a] From Eisen and Prasetyo (1988) or the present paper
[b] Standard errors calculated from variation among lines
[c] Calculated separately for HF (upper value) and LF (lower value) because of asymmetric correlated responses
[d] Based on formulas of Osborne (1957)

**Table 8.** Realized ($r_{G_R}$) and sire-offspring ($r_{G_S}$) genetic correlations (× 100) between hind carcass wt/body wt and correlated traits

| Hind carcass wt/body wt with: | $r_{G_R}$ | | | | | $r_{G_S}$[a] |
|---|---|---|---|---|---|---|
| | HL1 | HL2 | LL1 | LL2 | Pooled | |
| 3-wk body wt | −115 | 2 | −17 | −28 | −40±26[b] | −119 |
| 6-wk body wt | −46 | −23 | −39 | −41 | −37±5 | −46±11 |
| 3–6 wk postweaning gain | −19 | −24 | −37 | −28 | −27±4 | −29±11 |
| 3–6 wk feed intake | −59 | −38 | −79 | −115 | −73±16 | −53±13 |
| 3–6 wk feed efficiency | 1 | −26 | −20 | 23 | −6±11 | 12±16 |
| Body length | −9 | −18 | −62 | −73 | −14±5[c]<br>−68±6 | −43±12 |
| Subc. fat pad wt/body wt | −72 | −36 | −66 | −48 | −56±8 | −53±10 |
| Subc. fat pad wt | −83 | −42 | −83 | −83 | −73±10 | −67±8 |
| Adj. subc. fat pad wt | −48 | −20 | −53 | −19 | −35±9 | −45[d] |
| Lean index | −1 | −24 | −10 | −51 | −22±11 | −10±15 |
| Fat wt/hind carcass wt | −90 | −46 | −54 | −64 | −64±10 | −79±10 |
| Water wt/hind carcass wt | 110 | 53 | 49 | 45 | 64±15 | 58±12 |
| Fat-free dry hind carcass wt | −10 | 6 | 4 | −5 | −1±4 | 31±15 |
| Litter size | −31 | −36 | −06 | 39 | −9±17 | – |

[a] From Eisen and Prasetyo (1988) or the present paper
[b] Standard errors calculated from variation among lines
[c] Calculated separately for HF (upper value) and LF (lower value) because of asymmetric correlated responses
[d] Based on formulas of Osborne (1957)

Realized genetic correlations between hind carcass percentage and correlated traits are given in Table 8. The $r_{G_R}$ of hind carcass percentage with 3- and 6-week body weight and postweaning gain were negative, and $r_{G_R}$ with feed efficiency was close to zero. All measures of fat were negatively correlated with hind carcass percentage, but water percentage of the hind carcass and hind carcass percentage were positively correlated. The $r_{G_R}$ between hind carcass percentage and fat-free dry hind carcass weight was essentially zero. A small negative realized genetic correlation was found between hind carcass percentage and lean index. Again, the $r_{G_R}$ involving body length appeared to depend on the direction of selection, being a large negative in LL and a small negative in HL. In general, $r_{G_R}$ and $r_{G_S}$ were in good agreement.

## Discussion

### *HF and LF lines*

Selection for 12-week epididymal fat pad percentage led to positive correlated responses in 3- and 6-week body weight and 3–6 week postweaning gain. The $r_{G_R}$ with 6-week body weight ($0.36 \pm 0.04$) was lower than that with 12-week body weight ($0.57 \pm 0.05$; Eisen 1987). Ordinarily, higher genetic correlations are expected between physical measurements taken at the same age than at different ages. The exceptionally high $r_{G_R}$ with 3-week body weight ($0.88 \pm 0.21$) may be the result of an additional positive correlation associated with maternal effects. Bishop and Hill (1985) also reported high-low positive divergence in body weight as a correlated response to selection for epididymal fat pad percentage, although an earlier report on the same lines did not reveal significant differences (Sharp et al. 1984). The results from both studies agree with earlier reports of positive correlated responses in body fat content in the majority of lines of mice selected for postweaning body weight or weight gain (Malik 1984).

The HF and LF lines showed distinct changes in 3–6 week feed consumption ($r_{G_R} = 0.50 \pm 0.13$), but 3–6 week feed consumption/metabolic body size did not change. The correlated responses in feed consumption were probably the result of a change in maintenance requirements acting through changes in body weight. In contrast to the present results, high–low divergence in 4–6 week feed intake and feed intake adjusted for metabolic body size were similar for lines selected for epididymal fat pad percentage (Bishop and Hill 1985). The basis for the discrepancy is not clear, but may be related to genetic differences in the lines or differences in feed composition between the two experiments. Another difference between the two studies occurred for feed efficiency. The present results showed that $r_{G_R}$ between feed efficiency and epididymal fat pad percentage was essentially zero, whereas Bishop and Hill (1985) reported a moderately positive correlated response.

One goal of this experiment was to determine the extent of correlated responses in other fat depots as a consequence of selection for epididymal fat pad percentage. The high–low differences as a percentage of the control line mean were 76%, 61% and 90% for subcutaneous fat pad percentage, body weight-adjusted subcutaneous fat pad weight, and fat percentage in the hind carcass, respectively. Each of these differences was smaller than the 143% difference found for epididymal fat pad percentage (Eisen 1987). However, the respective $r_{G_R}$'s were $1.04 \pm 0.13$, $0.93 \pm 0.13$ and $0.90 \pm 0.08$. These high realized genetic correlations indicate that the loci determining additive genetic effects of fat content in the three sites are highly pleiotropic. In the only other study involving selection for epididymal fat pad percentage in mice, the high–low difference of total body fat content as a percent of the mean was 36%, compared with a difference of epididymal fat pad percentage of 64% (Sharp et al. 1984); however, the authors did not calculate a realized genetic correlation.

Correlated responses in the lean index were negative ($r_{G_R} = -0.41 \pm 0.03$), which contrasts markedly with the positive $r_{G_R}$ of 0.12 between epididymal fat pad percentage and lean index reported by Sharp et al. (1984). Both experiments were replicated, so the discrepancy is unlikely to be a result of genetic drift, although this cannot be ruled out completely.

In the hind carcass, water percentage mirrored the response in fat percentage ($r_{G_R} = -1.01 \pm 0.17$) whereas fat-free dry (protein + ash) percentage increased slightly in LF and decreased in HF. Fat-free dry hind carcass weight had no important correlated changes. Thus, the response in the hind carcass was primarily caused by responses in opposite directions for fat and water. Bishop and Hill (1985) reported similar findings for carcass composition in lines selected for epididymal fat pad percentage.

Litter size was not consistently affected by selection in HF or LF, in agreement with results in similarly selected lines (Brien et al. 1984). However, selection did result in a reduced index of fitness in HF and LF. Falconer (1981) pointed out that fitness must be reduced as a correlated response, unless the character selected is controlled entirely by genes with no effects on fitness. Inbreeding also may have contributed to the decrease in fitness. The decrease in fitness was not serious enough to interfere with selection because weighted and unweighted selection differentials were similar (Eisen 1987).

### *HL and LL lines*

Negative realized genetic correlations were found between hind carcass percentage and 3- and 6-week body weight and 3–6 week postweaning gain. The large negative $r_{G_R}$ between 3–6 week feed intake and hind carcass percentage was associated with the negative correlated response in body weight. However, the negative correlated responses in postweaning gain and feed intake had similar changes so that feed efficiency had a negligible correlated response. The parallel relations with the HF and LF lines are apparent, and an explanation for this is discussed below.

In general, selection for hind carcass percentage compared with epididymal fat pad percentage resulted in high–low correlated responses that were of opposite sign and smaller magnitude. Divergence in subcutaneous fat pad percentage, body weight-adjusted subcutaneous fat pad weight and fat percentage in the hind

carcass were −39%, −22% and −61%, respectively, of the control line mean, and corresponding $r_{G_R}$'s were $-0.56 \pm 0.08$, $-0.35 \pm 0.09$ and $-0.64 \pm 0.10$. Also, fat-free dry percentage and weight of the hind carcass had negligible correlated responses. These results are not surprising, since the realized genetic correlation between epididymal fat pad percentage and hind carcass percentage was high ($-0.67 \pm 0.04$; Eisen 1987).

The mechanism by which selection for hind carcass percentage changed fat percentage may be associated with the negative genetic correlation between hind carcass percentage and body weight ($r_{G_R} = -0.61 \pm 0.09$; Eisen 1987). Thus, because of this negative part-whole correlation, selection for larger proportional hind carcasses produced mice with smaller body weights. These mice also had less fat because of the positive genetic correlation between body weight and fat content; $r_{G_R} = 0.57 \pm 0.05$ between 12-week body weight and epididymal fat pad percentage (Eisen 1987). The opposite result was true when selection was for small hind carcass percentage.

Litter size decreased in HL, concomitant with a decrease in body weight, but litter size did not change in LL where there was a sizable positive change in body weight. However, both HL and LL exhibited a decreased fitness index. As noted for the HF and LF lines, the negative correlated response in fitness was not unexpected (Falconer 1981).

*General*

Correlated responses in growth rate, feed intake, and feed efficiency were similar in HF and LL and of opposite sign to those in LF and HL, which can be explained by the high negative genetic correlation between epididymal fat pad percentage and hind carcass percentage. Selection for increased (decreased) epididymal fat pad percentage or decreased (increased) hind carcass percentage at 12 weeks of age resulted in faster (slower) growth rate and greater (smaller) appetite from 3 to 6 weeks of age but no change in gross feed efficiency when compared with controls. The lack of response in gross feed efficiency differs from the positive correlated response when selecting for body weight or postweaning gain (Malik 1984). Correlated responses in energetic efficiency have not been examined.

Selection for epididymal fat pad weight as a proportion of body weight gave high realized genetic correlations with the hind limb subcutaneous fat pad/body weight and fat in the hind carcass as a proportion of hind carcass weight. Thus, many of the same loci control lipogenesis in at least two fat depots and in a major component of the carcass. It will be important to determine if the genetic change in fat content is a result primarily of change in cell number, cell size, or both, and whether the different fat depots develop at different rates.

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