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

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**Summary.** Replicated within full-sib family single-trait selection was conducted for 10 generations in mice for (1) high or low 12-week epididymal fat pad percentage (100 × epididymal fat pad weight/body weight) or (2) high or low 12-week hind carcass percentage (100 × hind carcass weight/body weight). Pooled realized heritabilities based on high, low and divergent selection were $0.66 \pm 0.09$, $0.65 \pm 0.13$ and $0.66 \pm 0.05$ for epididymal fat pad percentage and $0.48 \pm 0.08$, $0.33 \pm 0.08$ and $0.40 \pm 0.04$ for hind carcass percentage. The pooled realized genetic correlation ($r_{GR}$) between epididymal fat pad percentage and hind carcass percentage based on divergence was $-0.67 \pm 0.04$. Other estimates of $r_{GR}$ were: epididymal fat pad percentage with body weight ($0.57 \pm 0.05$); epididymal fat pad percentage with epididymal fat pad weight ($1.17 \pm 0.05$); hind carcass percentage with body weight ($-0.61 \pm 0.09$); hind carcass percentage with hind carcass weight ($-0.05 \pm 0.11$). Indirect measures of fat and lean tissue percentages were highly heritable, and $r_{GR}$ between them would be desirable from the standpoint of analogous types of traits in livestock. In the same context, undesirable $r_{GR}$'s were found between epididymal fat pad percentage and body weight and between hind carcass percentage and body weight.

**Key words:** Mice – Fat – Lean tissue – Selection – Heritability – Genetic correlation

## Introduction

Consumer demand for lean meat free of excessive fat tissue has led animal breeders to emphasize selection for increased lean tissue growth rate and (or) reduced fat deposition in livestock and poultry (Webb 1986). More detailed information is needed on genetic variation in components associated with body composition. The dynamics of genetic change in protein synthesis, lipogenesis, appetite control, feed efficiency and reproductive performance can be studied in lines selected divergently for either lean tissue growth rate or fat deposition. The mouse is a useful laboratory animal model for this purpose because of its short generation interval and low unit cost. Although considerable data are available on correlated responses in body composition resulting from selection for growth, few studies have involved direct selection for components related to body composition.

The objectives of this experiment were to use replicated single-trait divergent selection to estimate (1) realized heritabilities of components related to fat and lean tissue growth, (2) realized genetic correlations between the two components and (3) correlated responses in other traits. The present report will emphasize the first two objectives, apart from correlated responses in closely associated traits. Preliminary findings were presented earlier (Eisen 1986). Correlated responses in an array of other traits are presented in another paper (Eisen 1988).

## Materials and methods

### *Formation of base population*

The base population of mice used for this study was formed by reciprocally crossing two lines of diverse genetic origin. One

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line, originating from an ICR base, had been selected for rapid 3–6 week postweaning gain (M16) and had become moderately obese (Eisen 1975; Eisen et al. 1977; Eisen and Leatherwood 1978). The second line, originating from a 4-way cross of inbred lines (A/Jax, Balb/c, DBA/2Jax, AKR), had been selected for small 6-week body weight and had no appreciable correlated responses in body composition (Legates 1969; Lang and Legates 1969). The composite population was mated randomly with about 75 sire-dam pairs per generation for two generations to permit recombination to occur. In the $F_3$ generation two replicates were formed, each consisting of four selected lines and a control line.

*Selection procedures*

Each line was maintained with 15 pair-matings per generation. Intra-line selection was conducted within full-sib families to minimize inbreeding and maternal effects. Matings were at random except sib matings were avoided. The expected effective population size was 60 in each line.

The criterion used to select for body fat content was the right epididymal fat pad as a percentage of body weight (epididymal fat pad percentage). This trait was used because the time and cost involved in using proximate analysis to measure total body fat content of all males would be prohibitive. The epididymal fat pad is easily dissected and is phenotypically highly correlated ($r = 0.84$) with total body fat percentage in adult mice (Eisen and Leatherwood 1981).

Hind carcass weight as a percentage of body weight (hind carcass percentage) was used as an indirect selection criterion for lean tissue content (Bhuvanakumar et al. 1985). The hind carcass was defined as the skinned and eviscerated tissue mass posterior to the lumbo-sacral joint and anterior to the first coccigial vertebra, less the tissue dorsal to the tibio-tarsal joint (Bhuvanakumar et al. 1985). The phenotypic correlation between hind carcass percentage and epididymal fat pad percentage was found to be negative ($r = -0.57$) in a preliminary study. If this is indicative of a negative genetic correlation, then selection for hind carcass percent would be an alternative approach to selection for a change in body fat content.

Divergent single-trait selection was carried out for epididymal fat pad percentage and hind carcass percentage at 12 weeks old in two replicates for ten generations. Replicate high and low epididymal fat pad percentage lines are designated HF1, HF2 and LF1, LF2 respectively. Replicate high and low hind carcass percentage lines are identified as HL1, HL2 and LL1, LL2 respectively. Replicate unselected control lines are referred to as RC1 and RC2. Omission of the replicate number, e.g. RC, indicates pooling of replicates.

In all, 60 8- to 10-week old male-female pairs in the selected lines and 30 pairs in the control lines were cohabited for 16 days. During this period, Purina Laboratory Chow 5001 was fed ad libitum. Males were progeny from 15 full-sib families with a mean of four full brothers per family in selected lines and two in control lines. Following the mating period, males were caged singly until 12 weeks old, when they were weighed and killed by cervical dislocation. The right epididymal fat pad and the hind carcass were dissected and weighed immediately.

One male was selected within each of the 15 full-sib families based on the selection criterion of the line. If a selected male could not be used because of an infertile mating, litter mortality or insufficient male progeny, then the second best male was selected.

Females were fed ad libitum Purina Mouse Chow from the time they were separated from their mate until they weaned their litter. Litters were standardized to ten pups when 1 day old. Foster pups in augmented litters were identified and discarded at weaning (21 days old).

*Statistical analysis*

Within each generation, least-squares means were obtained for the selected traits (epididymal fat pad percentage and hind carcass percentage) and correlated traits (12-week body weight, epididymal fat pad weight and hind carcass weight) based on a statistical model which included an overall mean, a fixed selection criterion effect, a random replicate effect, a selection criterion × replicate interaction effect, a random litter effect and a random residual effect. In addition, 12-week body weight was added as a covariate to the models for epididymal fat pad weight and hind carcass weight.

Selection differentials were calculated by taking each selected male's performance minus his full-sib family mean, averaging over all 15 families and dividing by 2. It was assumed that selection pressure was attributable to male parents only. A preliminary analysis indicated that weighting the selected male's performance by the number of its progeny scored for the selected trait in the next generation did not affect the selection differential. Therefore, only unweighted selection differentials are reported.

Control replicates were evaluated for trends in each trait by regressing generation mean on generation number. The model included an overall mean, a replicate control line effect, regression of each replicate control line mean on generation number and a residual effect.

Realized responses or realized heritabilities were estimated from the regression of generation mean response on generation number or cumulative selection differential, respectively. Responses were corrected for environmental effects by three least-squares statistical methods. Method 1 used generation means from all lines (Richardson et al. 1968), method 2 used deviations of selected from control line means (Falconer 1981) and method 3 was based on the divergence between high and low lines (Falconer 1981). Hill (1972a, b) has shown that the least-squares estimates of realized heritability are unbiased, but that the least-squares standard errors are biased downward because of genetic drift. To avoid this bias, standard errors were estimated by methods proposed by Hill (1972a, b) and by using the variation between replicates. Realized heritability was based on within full-sib family differences. Therefore, individual heritabilities were calculated as $h^2 = h_R^2(1-t)/(1-r)$, where $h_R^2$ = estimated realized heritability, t = estimated intraclass correlation among full sibs and r = Wright's relationship coefficient between full sibs (1/2).

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

$$r_{GR} = (b_{G_{ij}}\, b_{G_{ji}})^{1/2} \quad (1)$$

and

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

where $b_{G_{ij}}$ and $b_{G_{ji}}$ are realized genetic regressions of the unselected trait on the selected trait, $h_j^2$ and $h_i^2$ are heritabilities and $V_{P_j}$ and $V_{P_i}$ are phenotypic variances of the selected and unselected traits. Formula (1) was used to estimate $r_{GR}$ from the double selection experiment, assuming symmetry of the genetic correlation; i.e. the same $r_{GR}$ is being estimated regardless of which of the two traits is selected directly (Falconer 1981). As the direction of response for epididymal fat pad percent and hind carcass percent was the same in HF and LL and in LF and HL, these respective lines were paired to obtain estimates of $r_{GR}$ from formula (1). Formula (2) was used to determine if $r_{GR}$ between epididymal fat pad percentage and hind carcass

percentage was symmetric and to estimate $r_{GR}$ between the selected traits and other correlated traits.

The parameters in formula (2) were estimated as follows: heritability of the selected trait ($h_j^2$) from the realized heritability in the present study, heritability of the correlated trait from regression of offspring on sire in the replicate control lines (Eisen and Prasetyo 1988) and phenotypic variances from residual sums of squares within replicate control line-generation subclasses. Standard errors of $r_{GR}$ were estimated by procedures of Hill (1971) and from variation between replicates.

## Results

### *Control lines*

Base population means, phenotypic variances and coefficients of variation in male mice were estimated by pooling data from RC1 and RC2 from generations 0 to 10 (Table 1). Considerably more variation was apparent for the epididymal fat depot than for the hind carcass. Regression coefficients of generation means on generation number were not significantly different from zero in the replicate controls for any trait (Table 2), indicating that drift effects and (or) environmental trends in the laboratory were probably not important for these traits.

### *Direct response in epididymal fat pad percentage*

Divergent response to selection for high and low epididymal fat pad percentage was observed (Fig. 1). Regression coefficients of generation mean on generation number for epididymal fat pad percentage and tests of significance for divergence (HF-LF) and asymmetry (HF+LF2-RC) are given in Table 3. The two methods of estimating response generally were in good agreement. Responses to high, low and divergent selection were significant ($P<0.01$). Asymmetry of response was indicated by method 2 ($P<0.05$) and to a lesser degree by method 1 ($P<0.10$). Cumulative responses over ten generations of selection were 87% and −56% of the control mean in HF and LF respectively. Responses in additive genetic standard deviations were 2.9 and −1.8 for HF and LF.

Cumulative selection differentials for epididymal fat pad percentage were higher in HF than in LF (Table 4). The difference was large enough to account for the asymmetric response in epididymal fat pad percentage. The difference in selection differentials may have resulted from a positive correlation between mean and variance across generations. To investigate this possibility, the regression coefficient of phenotypic variance on generation number was estimated in each replicate line. The regression coefficients were not heterogeneous ($P>0.10$) between replicate lines, and the pooled regression coefficients were $0.0093\pm0.0031$ (%)$^2$ ($P<0.01$) in HF and $-0.0086\pm0.0031$ (%)$^2$ ($P<0.01$) in LF.

**Table 1.** Means, phenotypic standard deviations ($\sqrt{V_p}$) and phenotypic coefficients of variation (CV) in male mice 12 weeks old[a]

| Trait | Mean | $\sqrt{V_p}$ | CV (%) |
|---|---|---|---|
| Epididymal fat pad wt/body wt (%) | 1.00 | 0.375 | 37.5 |
| Hind carcass wt/body wt (%) | 11.98 | 0.723 | 6.0 |
| 12-wk body wt (g) | 36.4 | 3.85 | 10.6 |
| Epididymal fat pad wt (mg) | 372 | 166 | 44.6 |
| Adj. epididymal fat pad wt (mg)[b] | 386 | 123 | 31.8 |
| Hind carcass wt (mg) | 4,348 | 418 | 9.6 |
| Adj. hind carcass wt (mg)[b] | 4,383 | 239 | 5.4 |

[a] Pooled within replicate control lines and generations; df=996

[b] Adjusted for body weight by covariance analysis within generations

**Table 2.** Regression coefficients ±SE of generation mean on generation number in replicate control lines (RC1, RC2)

| Trait | RC1 | RC2 |
|---|---|---|
| Epididymal fat pad wt/body wt (%) | 0.020± 0.017 | −0.006± 0.017 |
| Hind carcass wt/body wt (%) | −0.045± 0.027 | −0.040± 0.027 |
| 12-wk body wt (g) | 0.20 ± 0.12 | 0.09 ± 0.12 |
| Epididymal fat pad wt (mg) | 10.0 ± 7.5 | −1.4 ± 7.5 |
| Adj. epididymal fat pad wt (mg)[a] | 11.1 ± 6.9 | 0.4 ± 6.9 |
| Hind carcass wt (mg) | 8.4 ±11.4 | −3.1 ±11.4 |
| Adj. hind carcass wt (mg)[a] | 8.0 ±10.5 | 9.8 ±10.5 |

[a] Adjusted for body weight by covariance analyses within generations

Realized heritability estimates for epididymal fat pad percentage are presented in Table 5. Estimates of $h_R^2$ in lines selected for high epididymal fat pad percentage were in good agreement between replicates and between methods of estimation. In lines selected for low epididymal fat pad percentage, $h_R^2$ between replicates and between methods of estimation did not agree as well. The two replicates had similar estimates of $h_R^2$ based on divergence. Pooled $h_R^2$ estimates were similar for upward, downward and divergent selection. These results support the conclusion that asymmetric responses were caused by differences in selection differentials.

Pooled realized heritabilities, converted to an individual basis, ranged from 0.61 to 0.67 with an $h_R^2$ of $0.66\pm0.05$ estimated from divergence. The heritability of epididymal fat pad percentage estimated from regression of offspring on sire was $0.50\pm0.09$ (Eisen and

**Table 3.** Regression coefficients ± SE of direct and correlated responses on generation number 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 |
|---|---|---|---|---|---|---|---|---|---|
| Epid. fat pad wt/body wt (%)[b] | 1 | 0.079 ± 0.016** | 0.096 ± 0.016** | 0.087 ± 0.011** | −0.069 ± 0.014** | −0.042 ± 0.011** | −0.056 ± 0.009** | 0.143 ± 0.011** | 0.031 ± 0.019 |
| | 2 | 0.084 ± 0.016** | 0.100 ± 0.016** | 0.092 ± 0.011** | −0.066 ± 0.014** | −0.023 ± 0.010** | −0.045 ± 0.009** | 0.137 ± 0.011** | 0.047 ± 0.019* |
| Hind carcass wt/body wt (%)[c] | 1 | −0.108 ± 0.025** | −0.084 ± 0.026** | −0.096 ± 0.018** | 0.075 ± 0.022** | 0.082 ± 0.023** | 0.078 ± 0.016** | −0.174 ± 0.021** | −0.018 ± 0.036 |
| | 2 | −0.103 ± 0.025** | −0.080 ± 0.026* | −0.091 ± 0.018** | 0.079 ± 0.022** | 0.078 ± 0.023** | 0.079 ± 0.016** | −0.170 ± 0.021** | −0.012 ± 0.036 |
| 12-wk body wt (g)[c] | 1 | 0.49 ± 0.10** | 0.41 ± 0.10** | 0.45 ± 0.07** | −0.26 ± 0.10** | −0.05 ± 0.10 | −0.15 ± 0.07* | 0.60 ± 0.07** | 0.30 ± 0.12* |
| | 2 | 0.50 ± 0.10** | 0.42 ± 0.10** | 0.46 ± 0.07** | −0.27 ± 0.10** | −0.06 ± 0.10 | −0.17 ± 0.07** | 0.63 ± 0.07** | 0.29 ± 0.12* |
| Epid. fat pad wt (mg)[c] | 1 | 38.1 ± 5.2** | 41.5 ± 5.2** | 39.8 ± 3.7** | −28.6 ± 5.2** | −15.9 ± 5.2** | −22.2 ± 3.7** | 62.0 ± 3.7** | 17.6 ± 6.4** |
| | 2 | 42.4 ± 5.2** | 44.4 ± 5.2** | 43.2 ± 3.7** | −28.0 ± 5.2** | −9.6 ± 5.2 | −18.8 ± 3.7** | 62.0 ± 3.7** | 24.4 ± 6.4** |
| Adj. epid. fat pad wt (mg)[c,d] | 1 | 20.5 ± 3.5** | 30.0 ± 3.5** | 25.3 ± 2.4** | −23.1 ± 3.5** | −15.1 ± 3.5** | −19.1 ± 2.4** | 44.4 ± 2.4** | 6.2 ± 4.2 |
| | 2 | 21.2 ± 3.5** | 32.8 ± 3.5** | 27.0 ± 2.4** | −24.0 ± 3.5** | −8.3 ± 3.5* | −16.2 ± 2.4** | 43.2 ± 2.4* | 10.8 ± 4.2* |
| Hind carcass wt (mg)[c] | 1 | 13.5 ± 8.5 | 15.2 ± 8.5 | 14.4 ± 6.0* | −3.7 ± 8.5 | 23.8 ± 8.5** | 10.0 ± 6.0 | 4.4 ± 6.0 | 24.4 ± 10.4* |
| | 2 | 12.6 ± 8.5 | 16.9 ± 8.5* | 14.7 ± 6.0* | −3.9 ± 8.5 | 20.1 ± 8.5* | 8.1 ± 6.0 | 6.6 ± 6.0 | 22.8 ± 10.4* |
| Adj. hind carcass wt (mg)[c,d] | 1 | −27.1 ± 8.1** | −21.7 ± 8.1** | −24.4 ± 5.7** | 21.6 ± 8.1** | 31.5 ± 8.1** | 26.5 ± 5.7** | −50.9 ± 5.7** | 2.1 ± 9.9 |
| | 2 | −25.0 ± 8.1** | −21.5 ± 8.1** | −23.3 ± 5.7** | 23.4 ± 8.1** | 29.7 ± 8.1** | 26.5 ± 5.7** | −49.8 ± 5.7** | 3.2 ± 9.9 |

* $P < 0.05$
** $P < 0.01$
[a] 1 = method of Richardson et al. (1968); 2 = deviation from control (Falconer 1981)
[b] Direct response
[c] Correlated response
[d] Adjusted for body weight by covariance analysis within generations

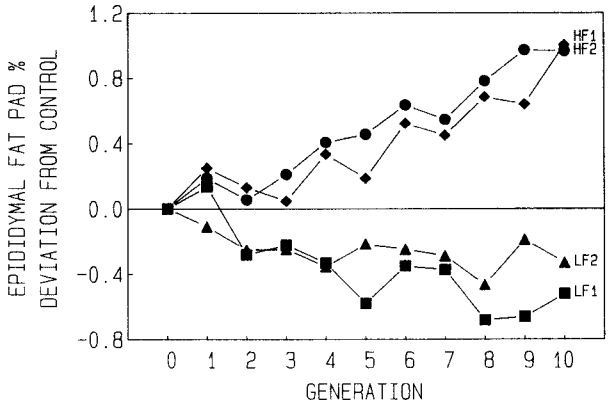


**Fig. 1.** Generation means of epididymal fat pad percentage deviated from control means in lines selected for high (HF1, HF2) or low (LF1, LF2) epididymal fat pad percentage

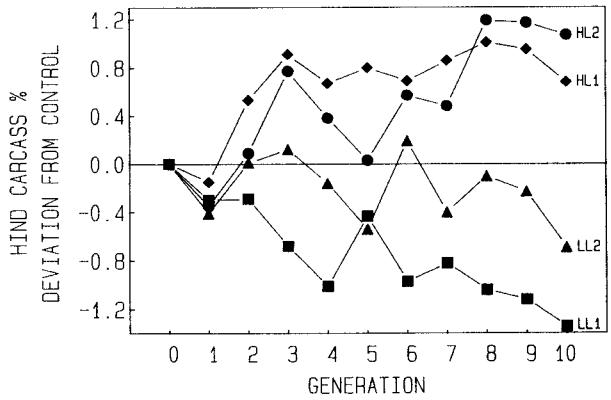


**Fig. 2.** Generation means of hind carcass percentage deviated from control means in lines selected for high (HL1, HL2) or low (LL1, LL2) hind carcass percentage

Prasetyo 1988), which was not significantly different from the pooled individual realized heritability based on divergence.

*Direct response in hind carcass percentage*

Response to selection for hind carcass percentage was found for all lines except LL2 (Fig. 2). Regression coefficients of generation mean on generation number for hind carcass percentage were similar for methods 1 and 2 (Table 6). For upward selection, the replicate slopes ($P < 0.01$) were in close agreement, whereas for downward selection LL1 decreased ($P < 0.01$) but LL2 did not ($P > 0.05$). Pooled divergence was significant ($P < 0.01$) and no asymmetry was detected ($P > 0.05$). Cumulative responses over ten generations of selection were 9.3% and −7.3% of the control mean in HL and LL respectively. These responses were equivalent to 2.4 and −1.9 additive genetic standard deviations in HL and LL.

**Table 4.** Cumulative selection differentials

| Trait | Line[a] | | | |
|---|---|---|---|---|
| | HF1 | HF2 | LF1 | LF2 |
| Epid. fat pad wt/body wt (%) | 1.83 | 1.61 | −0.99 | −0.93 |
| | HL1 | HL2 | LL1 | LL2 |
| Hind carcass wt/body wt (%) | 3.15 | 2.81 | −2.97 | −2.82 |

[a] Lines selected for high (HF1, HF2) or low (LF1, LF2) epididymal fat pad percentage and high (HL1, HL2) or low (LL1, LL2) hind carcass percentage

Cumulative selection differentials for hind carcass percentage were similar for high and low selection (Table 4). Realized heritabilities for hind carcass percentage were similar among methods and for all replicates except LL2 (Table 7). There was no evidence that the pooled $h^2_R$ estimates in the high and low lines were different, and the pooled $h^2_R$ based on divergence was $0.32 \pm 0.03$. Estimates of pooled realized individual heritability ranged from 0.33 to 0.48, with individual heritability of divergence being $0.40 \pm 0.04$. These heritability estimates were similar to the offspring-sire regression estimate of $0.42 \pm 0.09$ in the controls (Eisen and Prasetyo 1988).

*Correlated responses in epididymal fat pad percentage and hind carcass percentage*

Hind carcass percentage had significant negative correlated responses in HF and LF (Table 3), equivalent to −8.0% and 6.5% respectively of the control mean. Negative correlated responses were evident for epididymal fat pad percentage in HL and LL (Table 6); the correlated response in LL2 was not significant, as was the case for the direct response described previously. As a percentage of the control line mean, correlated responses in epididymal fat pad percentage were −44% in HL and 30% in LL.

Realized genetic correlations between epididymal fat pad percentage and hind carcass percentage are listed in Table 8. Although always negative, estimates of $r_{GR}$ were variable. Single selection line estimates from formula (2) provide an indication of whether $r_{GR}$ is symmetric. There was a suggestion that selection for epididymal fat pad percentage resulted in a higher realized genetic correlation than selection for hind carcass percentage. This trend was evident in both replicates. Therefore, it is less likely to be a drift effect. Thus, the estimate of $r_{GR}$ from formula (1) may be questioned, but

**Table 5.** Realized heritability estimates ± SE (%) for epididymal fat pad weight/body weight

| Line | Method[a] | Rep. 1 ± SE | Rep. 2 ± SE | Pooled ± SE | Pooled individual ± SE[d] |
|---|---|---|---|---|---|
| HF | 1 | 44 ± 9[b] | 53 ± 10[b] | 49 ± 7[b] (5)[c] | 61 ± 9[b] (6)[c] |
| | 2 | 47 ± 9 | 58 ± 10 | 53 ± 7 (8) | 66 ± 9 (10) |
| LF | 1 | 64 ± 16 | 43 ± 12 | 54 ± 10 (11) | 67 ± 13 (13) |
| | 2 | 74 ± 16 | 29 ± 11 | 52 ± 10 (22) | 65 ± 13 (28) |
| Divergence | 3 | 56 ± 6 | 48 ± 6 | 52 ± 4 (4) | 66 ± 5 (5) |

[a] 1 = method of Richardson et al. (1968), 2 = deviation from control (Falconer 1981), 3 = difference between high and low lines (Falconer 1981)
[b] Standard error calculated by methods of Hill (1972a, b)
[c] Standard error in parentheses calculated from variation between replicates
[d] Individual heritability = $\hat{h}^2_R (1-\hat{t})/(1-r)$ where $\hat{h}^2_R$ = realized heritability based on within full-sib family selection, $\hat{t}$ = intraclass correlation between full sibs and r = Wright's relationship between full sibs

it does provide a joint estimate which can be compared with the base population estimate. The replicate estimates of $r_{GR}$ based on formula (1) were in reasonably good agreement, given the high sensitivity of $r_{GR}$ to fluctuations in gene frequency caused by selection (Bohren et al. 1966). Pooled estimates of $r_{GR}$ from the double selection experiment ranged from −0.57 to −0.69 and were in excellent agreement with the base population estimate of $-0.61 \pm 0.09$ (Eisen and Prasetyo 1988).

*Correlated responses in numerator and denominator of the primary traits*

The primary traits selected, epididymal fat pad percentage or hind carcass percentage, are a ratio of two traits, the right epididymal fat pad weight or hind carcass weight in the numerator and body weight in the denominator. The numerator and denominator of the primary traits were expected to show correlated responses, partly because of the part-whole relationship (Sutherland 1965; Eisen 1966). In addition, epididymal fat pad weight or hind carcass weight adjusted for body weight by covariance analysis provides an alternative to percentages in assessing responses at a fixed body weight.

The correlated responses in HF and LF are given in Table 3. Selection in HF and LF resulted in divergence ($P < 0.01$) for 12-week body weight and epididymal fat pad weight. The correlated responses were asymmetrical, being larger in HF than in LF. Compared with unadjusted responses, epididymal fat pad weight adjusted for body weight reduced the correlated response in HF and had no effect in LF. Correlated responses in ad-

**Table 6.** Regression coefficients ± SE of direct and correlated responses on generation number in replicate lines selected for high (HL1, HL2) or low (LL1, LL2) hind carcass weight/body weight

| Trait | Method[a] | HL1 | HL2 | Pooled | LL1 | LL2 | Pooled | Divergence | Asymmetry |
|---|---|---|---|---|---|---|---|---|---|
| Epid. fat pad | 1 | −0.065±0.015** | −0.022±0.015 | −0.044±0.011** | 0.038±0.015* | 0.030±0.015 | 0.034±0.010** | −0.078±0.011** | −0.010±0.019 |
| body wt (%)[b] | 2 | −0.059±0.015** | −0.019±0.015 | −0.039±0.011** | 0.035±0.015* | 0.022±0.015 | 0.029±0.010** | −0.068±0.011** | −0.010±0.019 |
| Hind carcass | 1 | 0.114±0.026** | 0.107±0.027** | 0.111±0.019** | −0.136±0.027** | −0.038±0.020 | −0.087±0.017** | 0.198±0.018** | 0.024±0.031 |
| body wt (%)[c] | 2 | 0.083±0.024** | 0.130±0.029** | 0.107±0.019** | −0.113±0.027** | −0.034±0.020 | −0.074±0.017** | 0.181±0.018** | 0.033±0.031 |
| 12-wk body | 1 | −0.44 ±0.10** | −0.19 ±0.10 | −0.32 ±0.07** | 0.41 ±0.10** | 0.57 ±0.10** | 0.49 ±0.07** | −0.81 ±0.07** | 0.17 ±0.12 |
| wt (g)[b] | 2 | −0.45 ±0.10** | −0.28 ±0.10** | −0.36 ±0.07** | 0.30 ±0.10** | 0.45 ±0.10** | 0.38 ±0.07** | −0.74 ±0.07** | 0.02 ±0.12 |
| Epid. fat pad | 1 | −28.1 ±5.2** | −10.0 ±5.2 | −19.1 ±3.7** | 19.7 ±5.2** | 17.3 ±5.2** | 18.6 ±3.7** | −37.7 ±3.7** | −0.5 ±6.4 |
| wt (mg)[b] | 2 | −25.9 ±5.2** | −9.7 ±5.2 | −17.8 ±3.7** | 17.8 ±5.2** | 13.8 ±5.2** | 15.8 ±3.7** | −33.6 ±3.7** | −2.0 ±6.4 |
| Adj. epid. fat | 1 | −18.3 ±3.5** | −5.0 ±3.5 | −11.7 ±2.4** | 6.9 ±3.5 | 0.1 ±3.5 | 3.5 ±2.4 | −15.2 ±2.4** | −8.2 ±4.2 |
| pad wt (mg)[b,d] | 2 | −16.9 ±3.5** | −2.9 ±3.5 | −9.9 ±2.4** | 6.2 ±3.5 | −2.3 ±3.5 | 1.9 ±2.4 | −11.8 ±2.4** | −8.0 ±4.2 |
| Hind carcass | 1 | −12.7 ±8.5 | 15.0 ±8.5 | 1.1 ±6.0 | −6.7 ±8.5 | 51.6 ±8.5** | 22.5 ±6.0** | −21.4 ±6.0** | 23.6 ±10.4* |
| wt (mg)[b] | 2 | −25.6 ±8.5** | 12.1 ±8.5 | −6.8 ±6.0 | −11.9 ±8.5 | 36.6 ±8.5** | 12.3 ±6.0* | −19.1 ±6.0** | 5.5 ±10.4 |
| Adj. hind carcass | 1 | 29.9 ±8.1** | 36.4 ±8.1** | 33.1 ±5.7** | −40.5 ±8.1** | 0.2 ±8.1 | −20.2 ±5.7** | 53.3 ±5.7** | 12.9 ±9.9 |
| wt (mg)[b,d] | 2 | 18.9 ±8.1* | 43.3 ±8.1** | 31.1 ±5.7** | −33.0 ±8.1** | −1.2 ±8.1 | −17.1 ±5.7** | 48.2 ±5.7** | 14.0 ±9.9 |

* $P<0.05$
** $P<0.01$
[a] 1 = method of Richardson et al. (1968); 2 = deviation from control (Falconer 1981)
[b] Correlated response
[c] Direct response
[d] Adjusted for body weight by covariance analysis within generations

**Table 7.** Realized heritability estimates ±SE (%) for hind carcass weight/body weight

| Line | Method[a] | Rep. 1±SE | Rep. 2±SE | Pooled ±SE | Pooled individual ±SE[d] |
|---|---|---|---|---|---|
| HL | 1 | 34±8[b] | 37±10[b] | 36±6[b] (2)[c] | 45±8 (6) |
| | 2 | 28±7 | 48±10 | 38±6 (10) | 48± 8 (13) |
| LL | 1 | 42±9 | 12± 7 | 27±6 (15) | 34±8 (19) |
| | 2 | 41±9 | 12± 7 | 27±6 (15) | 33±8 (18) |
| Divergence | 3 | 35±4 | 30± 4 | 32± 3 (3) | 40± 4 (4) |

[a, b, c, d] See respective footnotes in Table 5

**Table 8.** Realized genetic correlation estimates ± SE (×100) between epididymal fat pad weight/body weight and hind carcass weight/body weight

| Criterion | Rep. 1 | Rep. 2 | Pooled |
|---|---|---|---|
| HF[a] | −89 | −54 | −72±18[c] |
| LL | −50 | −41 | −46± 5 |
| LF | −89 | −137 | −113±24 |
| HL | −79 | −22 | −51±28 |
| HF, LL[b] | −67 | −47 | −57±10 |
| HL, LF | −84 | −55 | −69±14 |
| Divergence | −73 | −56 | −67±12 |

[a] Estimate of $r_{G_R}$ from formula (2) in text
[b] Estimate of $r_{G_R}$ from formula (1) in text
[c] Standard error calculated from variation between replicates

justed epididymal fat pad weight were significant ($P<0.01$) in HF and LF, accounting for 66% and −49% of control line means respectively. Hind carcass weight had an asymmetric correlated response ($P<0.05$) with a positive trend in HF ($P<0.05$) and LF ($P>0.05$). Heterogeneity between replicates in downward selection was noted, however. Correlated response in adjusted hind carcass weight was positive ($P<0.01$) for HF and negative ($P<0.01$) for LF, with no evidence of asymmetry.

Presented in Table 6 are the correlated responses in HL and LL. Body weight at 12 weeks decreased ($P<0.01$) in HL and increased ($P<0.01$) in LL, and asymmetry was not significant. Hind carcass weight did not change significantly in HL, but there was an increase in LL. Lines selected for small hind carcass percentage showed a heterogeneous correlated response in hind carcass weight as they did for the primary trait; hind carcass weight declined nonsignificantly ($P>0.05$) in LL1 and significantly ($P<0.01$) in LL2. The correlated responses indicate that LL1 responded downward in hind carcass percentage by increasing body weight (denominator) and slightly decreasing hind carcass weight

**Table 9.** Realized ($r_{G_R}$) and offspring-sire ($r_{G_S}$) genetic correlations ($\times 100$) between epididymal fat pad weight/body weight or hind carcass weight/body weight and correlated traits

| Epididymal fat pad wt/body wt with: | $r_{G_R}$ | | | | | $r_{G_S}$[a] |
|---|---|---|---|---|---|---|
| | HF1 | HF2 | LF1 | LF2 | Pooled | |
| 12-wk body wt | 71 | 52 | 57 | 51 | 57± 5[b] | 66± 7 |
| Epididymal fat pad wt | 131 | 116 | 112 | 109 | 117± 5 | 98± 1 |
| Adj. epididymal fat pat wt | 102 | 135 | 128 | 134 | 125± 8 | 88[c] |
| Hind carcass wt | 13 | 22 | 11 | −29 | 4±11 | 35±12 |
| Adj. hind carcass wt | −81 | −53 | −89 | −163 | −97±23 | −47[c] |
| **Hind carcass wt/body wt with:** | $r_{G_R}$ | | | | | $r_{G_S}$[a] |
| | HL1 | HL2 | LL1 | LL2 | Pooled | |
| 12-wk body wt | −67 | −38 | −56 | −83 | −61± 9[b] | −52±10 |
| Epididymal fat pad wt | −89 | −29 | −67 | −64 | −62±12 | −63± 8 |
| Adj. epididymal fat pad wt | −73 | −11 | −34 | 8 | −28±17 | −47[c] |
| Hind carcass wt | −18 | 18 | 9 | −28 | −5±11 | −10±15 |
| Adj. hind carcass wt | 91 | 122 | 108 | 91 | 103± 8 | 71[c] |

[a] From Eisen and Prasetyo (1988)
[b] Standard error calculated from replicate variation
[c] Based on formulas of Osborne (1957)

(numerator), whereas LL2 failed to respond in hind carcass percentage because both numerator and denominator increased. Hind carcass weight adjusted for body weight increased ($P<0.01$) in HL. The downward selected lines again showed heterogeneity with a decrease ($P<0.01$) in LL1 and no change in LL2.

Realized ($r_{G_R}$) and offspring-sire ($r_{G_S}$) genetic correlations of the primary traits with correlated traits are compared in Table 9. The $r_{G_R}$ estimates were based on formula (2) and were pooled across replicate lines and direction of selection for each primary trait. The $r_{G_R}$ and $r_{G_S}$ of the primary ratio traits with numerator and denominator traits were in general agreement. The estimated genetic correlations between a selected trait and a trait adjusted by covariance analysis for body weight were obtained by deriving their expectation from formulas based on Osborne (1957) and substituting estimates of the parameters from Eisen and Prasetyo (1988). The $r_{G_R}$ between epididymal fat pad percentage and epididymal fat pad weight adjusted for body weight was essentially one, as was $r_{G_R}$ between hind carcass percentage and hind carcass weight adjusted for body weight.

## Discussion

Response to ten generations of replicated within full-sib family selection for high or low epididymal fat pad weight as a percentage of body weight resulted in a divergence equal to 143% of the control line mean. Epididymal fat pad percentage had a high proportion of additive genetic variance; the realized individual heritability based on divergence was $0.66\pm0.05$. Sharp et al. (1984) obtained similar results in mice selected divergently for the same trait although realized heritability was slightly lower (0.50). Selection for decreased body fat percentage in mice over six generations in two replicates gave a mean realized heritability of 0.32 although responses in the two replicates were heterogeneous (Hörstgen 1978).

Selection for components of body fat conducted in other species also indicates a moderately high heritability. In pigs, Hetzer and Harvey (1967) reported realized heritabilities ranging from 0.38 to 0.48 for backfat at 79.4 kg. Three generations of divergent selection for plasma triglycerides in broilers resulted in a realized heritability of 0.40 (Whitehead and Griffin 1985). Abdominal fat in poultry also has responded readily to selection (Leclercq et al. 1980; Lilburn et al. 1982; Cahaner and Krinsky 1985).

Selection yielded lower realized heritabilities for hind carcass percentage compared with epididymal fat pad percentage; realized individual heritability based on divergence was $0.40\pm0.04$. Failure of one of the low line replicates to respond significantly to selection may be the result of genetic drift (Falconer 1973). Divergence for hind carcass percentage amounted to 17% of the control line mean, which was much less than divergence for epididymal fat pad percentage. However, divergence in terms of additive genetic standard deviations was similar for both traits. Sharp et al. (1984) reported a realized individual heritability of 0.50 for a

lean index defined as body weight – 8 × epididymal fat pad weight in 10-week old male mice. The index is positively correlated with body weight, whereas hind carcass percentage is negatively correlated with body weight. Selection in mice for high and low protein weight at 60 days old led to a divergence of 29% of the control line after 12 generations (Horst et al. 1979). In rats, replicated selection among full-sib families for high protein gain and high protein efficiency gave responses of $0.19 \pm 0.10$ and $0.18 \pm 0.16$ per unit selection differential (Notter et al. 1976). After further selection, realized family heritabilities were 0.40 and 0.07 for protein gain and protein efficiency, respectively (Wang and Dickerson 1984).

The high negative realized genetic correlation of $-0.67 \pm 0.04$ estimated from divergence between the indirect measures of fat and lean mass as a percentage of body weight suggests a negative pleiotropic relationship between fat and protein deposition when expressed as a proportion of body weight. When viewed in the context of the goals of modern livestock breeding, this is a desirable relationship. However, selection for either trait had undesirable correlated responses.

The realized genetic correlation between epididymal fat pad percentage and 12-week body weight was high ($0.57 \pm 0.05$), whereas $r_{GR}$ was negligible between epididymal fat pad percentage and hind carcass weight ($0.04 \pm 0.11$). Similarly, the realized genetic correlation between hind carcass percentage and body weight was $-0.61 \pm 0.09$, whereas $r_{GR}$ between hind carcass percentage and hind carcass weight was essentially zero ($-0.05 \pm 0.11$). Thus, single-trait selection for either low epididymal fat pad percentage or high hind carcass percentage would reduce body weight and growth rate but not change hind carcass weight. Therefore a desired gains or restricted selection index would be necessary to minimize undesirable correlated responses in body weight and hind carcass weight (Eisen and Prasetyo 1988).

In conclusion, the indirect measures of fat and lean tissue percentage used in this study with mice were highly heritable. The negative sign of the genetic correlation between fat and lean percentages was compatible with present goals of selection in livestock and poultry. Undesirable correlated responses between epididymal fat pad percentage and hind carcass percentage on the one hand and growth rate and hind carcass weight on the other can be overcome by use of index selection.

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