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# Restricted selection index in mice designed to change body fat without changing body weight: correlated responses *

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**Summary.** Correlated responses were studied in lines of mice selected for eight generations based on the criterion of a restricted selection index. Two replicate lines were selected in each treatment as follows: HE, high epididymal fat pad weight (EF) with zero change in body weight (BW) at 12 weeks of age; LE; low EF with zero change in BW; and RS, randomly. Correlated responses showed considerable variation between replicates, suggesting that genetic drift was important. Further, correlated responses for most traits were relatively small, probably because of low selection intensity. The HE line responded as expected in component traits of the restricted index. Associated compositional traits in HE responded as predicted since traits correlated with adiposity increased and hind carcass weight did not change significantly. Feed intake increased and feed efficiency (weight gain/feed intake) decreased in HE, as predicted. In contrast, the LE line did not respond in component traits as predicted since EF did not decrease and BW increased. Consequently, LE exhibited little change in traits associated with adiposity, but hind carcass weight, feed intake and feed efficiency increased. Of the correlated responses scored for fitness traits (littering rate, number of days from pairing of mate to littering, litter size and preweaning pup survival rate), significant effects were found for decreased littering rate in LE and increased prenatal survival rate in HE. In summary, correlated responses to restricted index selection generally agreed with expectation when responses in component traits of the index were considered.

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## Introduction

Single-trait selection experiments for growth, body composition or feed efficiency in livestock, poultry or rodents are likely to result in an array of correlated responses in these and other growth-related traits and in fitness traits (Hetzer and Miller 1970, 1973; Yüksel 1979; Siegel and Dunnington 1987; Mrode 1988; Eisen 1989; Sholtz et al. 1990; Thompson 1990). Many modern livestock selection programs are based on the use of a selection index to improve a multiple of traits. Yet, apart from a few studies with swine and beef cattle (see reviews by Vangen and Kolstad 1986; Mrode 1988), there is little information on correlated responses to index selection for production traits in livestock. This type of information is important as breeders attempt to predict selection progress.

The mouse has been used as a mammalian model for livestock in selection studies to ascertain direct and correlated responses to selection for traits such as growth and body composition (Malik 1984; Eisen 1989). In the study reported here correlated responses in an array of growth and fitness traits are evaluated in replicate lines of mice that have been selected based on a restricted index for high or low fat content while holding body weight unchanged. Direct responses to selection have been reported in an earlier paper (Eisen 1992).

## Materials and methods

### *Selected lines*

The base population and selection treatments used in this study were described previously (Eisen 1992). Briefly, replicate lines were selected as follows: high (HE1, HE2) or low (LE1, LE2) 12-week right epididymal fat pad weight (EF) while holding 12-week body weight (BW) unchanged; and randomly (RS1, RS2). Omission of the replicate number indicates pooling of replicates. Selection within full-sib families was practiced for eight generations. Replicate lines were maintained with 15 pair-matings per generation, litters were standardized to ten mice at 1 day of age and pups were weaned at 3 weeks of age. Mice were fed ad libitum Purina Laboratory Chow 5001, Purina Mills, Richmond, Indiana, from weaning through the 16-day mating period. Females were fed ad libitum Purina Mouse Chow 5015 from the day they were separated from their mate until their litters were weaned.

### *Correlated traits*

Following the 16-day mating period, males were caged individually. At 12 weeks of age males were weighed and then killed by cervical dislocation. The EF (Eisen and Leatherwood 1978) and right hind-limb subcutaneous fat pad (SF) (Smith et al. 1983) were dissected and weighed. The hind carcass was also dissected and carefully trimmed of skin, viscera and external fat as described by Bhuvanakumar et al. (1985) and weighed. SF was used as a correlated response in a second fat depot. EF was used as an indirect measure of total body fat (Eisen and Leatherwood 1978). The hind carcass as a percentage of body weight (HC%) is highly negatively correlated genetically and phenotypically with epididymal fat pad weight as a percentage of body weight (Eisen 1987a; Eisen and Prasetyo 1988).

About 15 male hind carcasses (1 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 in the hind carcass as a percentage of hind carcass weight (WA%) was calculated as the difference between fresh (HC) and dry (HCD) weight divided by HC. Water percentage in the hind carcass was used as a measure of fat percentage in the hind carcass, the two traits being highly negatively correlated (Eisen 1987a).

In generations five and seven, correlated responses in feed intake and feed efficiency were estimated on samples of male mice. Two full sibs from each litter within a line-replicate class were randomly caged together at weaning. Body weights at 3 and 6 weeks of age (BW3, BW6) were recorded, and 3–6 week postweaning gain (PWG) was subsequently calculated. Feed intake (FEED) and gross feed efficiency (EFF = weight gain/feed intake) from 3 to 6 weeks of age were analyzed on a per cage basis and then converted to an individual mouse basis. Feed intake was also expressed per unit of body weight by dividing feed intake by the means of 3- and 6-week body weights for the two mice in each cage (FEED/$\overline{BW}$).

Four fitness traits were recorded in each generation. Littering rate (LR) was defined as the number of females giving birth as a percentage of the number of females mated. The number of days from exposure to a male to littering (CH) is a measure of how rapidly a successful mating occurred. Litter size (LS) is the number of live plus dead young born, and preweaning pup survival (PS) provides a measure of preweaning viability.

### *Statistical analysis*

Within each generation, least-squares means were estimated from a model which included an overall mean, a fixed selection criterion effect, a random replicate effect, a selection criterion × replicate effect, a random litter effect for traits that included more than one observation per litter and a random residual effect. Realized correlated responses for those traits measured across generations were estimated from the regressions of correlated response generation mean on generation number (Falconer 1989). Correlated responses in each generation were based on means of selected line deviated from those of controls. Divergence was estimated as the difference between the slopes for high and low lines. Asymmetry was calculated as the sum of the slopes for high and low lines, both adjusted for environmental effects. Empirical standard errors were based on the variation between replicates to account for genetic drift effects (Hill 1972).

## Results

### *Control lines*

Means, phenotypic standard deviations and coefficients of variation pooled within replicate controls and generations are presented in Table 1. Absolute fat pad weights and fat pad weights as a percentage of body weight had characteristically high coefficients of variation (CV), whereas water as a percentage of hind carcass weight and hind carcass traits had relatively low CV. Fitness traits also had high CV. Means and standard deviations were similar to those reported in the original control populations used to develop the RS controls (Eisen 1987a, b). Of the 11 traits monitored across generations, SF%, HC% and PS showed small but significant ($P<0.05$) trends (Table 1). These changes were probably due to genetic drift effects, and their relatively small magnitude is not likely to have an impact on the interpretation of correlated responses.

**Table 1.** Means, phenotypic standard deviations ($\sqrt{V_p}$), coefficients of variation (CV) and regression coefficients (b ± SE) of generation means on generation number for traits pooled within control line (RS1, RS2) replicates

| Trait[a] | Mean[b] | $\sqrt{V_p}$[b] | CV[b] | b ± SE[c] |
|---|---|---|---|---|
| SF (mg) | 186.00 | 63.98 | 34.40 | 3.2 ± 2.0 |
| HC (mg) | 4,857.00 | 502.23 | 10.34 | 44.3 ± 23.4 |
| HCD (mg) | 1,549.00 | 164.08 | 10.59 | 14.6 ± 8.7 |
| EF% | 0.77 | 0.245 | 31.82 | −0.013 ± 0.010 |
| SF% | 0.49 | 0.152 | 31.02 | 0.010 ± 0.004* |
| WA% | 68.00 | 1.267 | 1.86 | −0.049 ± 0.050 |
| HC% | 12.84 | 0.948 | 7.38 | 0.16 ± 0.06* |
| LR (%) | 96.71 | 0.798 | 0.83 | −0.10 ± 0.04 |
| CH (days) | 22.38 | 2.37 | 10.58 | 0.10 ± 0.09 |
| LS | 10.67 | 2.38 | 22.34 | −0.05 ± 0.04 |
| PS (%) | 98.86 | 0.47 | 0.48 | −0.28 ± 0.11* |

* $P<0.05$

[a] SF, Hind-limb subcutaneous fat pad weigth; HC, hind carcass weight; HCD, dry hind carcass weight; EF%, 100 · (epididymal fat pad wt)/(body wt); SF%, 100 · SF/(body wt); WA%, 100 · (water wt in hind carcass)/body wt); HC%, 100 · HC/(body wt); LR, littering rate; CH, number of days from pairing of mates to littering; LS, litter size at birth; PS, preweaning pup survival rate

[b] Pooled within replicate controls and generations ($n=1068$ for SF, HC, EF%, SF% and HC%; $n=287$ for HCD and WA%; $n=1020$ for LR, CH, LS and PS)

[c] Pooled within replicates

*Correlated responses in indicator traits of body composition*

Regressions of correlated responses in compositional weight traits on generation number are given in Table 2. Correlated response in epididymal fat pad weight was given in the paper describing direct responses in the restricted index lines (Eisen 1992). Pooled estimates of correlated responses in the HE lines were not significant for subcutaneous fat pad weight and fresh and dry hind carcass weight, although individual replicates varied considerably. The LE lines decreased ($P<0.01$) in subcutaneous fat pad weight and increased ($P<0.05$) in fresh and dry hind carcass weight; the correlated responses in the latter two traits were similar in direction to correlated responses for body weight (Eisen 1992). There was a suggestion of asymmetry for subcutaneous fat pad weight and fresh and dry hind carcass weight, but asymmetry was significant ($P<0.01$) for dry hind carcass weight only.

**Table 2.** Regression coefficients $\pm$SE of correlated responses in fat pad and hind carcass weights on generation number in restricted index selected lines

| Line | Trait[c] | | |
|---|---|---|---|
| | SF (mg) | HC (mg) | HCD (mg) |
| HE1[a] | 1.2±2.9 | −40.0±20.4* | 1.0± 8.4 |
| HE2[a] | 11.8±2.9 | 28.7±20.4 | 17.6± 8.4* |
| Pooled[b] | 6.5±5.3 | −5.7±34.4 | 9.3± 8.3 |
| LE1[a] | −1.1±2.9 | 70.4±20.4** | 27.5± 8.4** |
| LE2[a] | −1.7±2.9 | 25.0±20.4 | 9.6± 8.4 |
| Pooled[b] | −1.4±0.3** | 47.7±22.7* | 18.6± 9.0* |
| Divergence 1[a] | 2.3±2.1 | −110.4±15.1** | −26.5± 6.0** |
| Divergence 2[a] | 13.2±2.1** | 3.7±15.1 | 8.0± 6.0 |
| Pooled[b] | 7.8±5.4 | −53.4±57.1 | −9.3±17.3 |
| Asymmetry[a] | 5.1±3.6 | 42.0±26.1 | 27.8±10.3** |

* $P<0.05$, ** $P<0.01$
[a] Standard errors calculated by least-squares
[b] Standard errors calculated from variation between replicates
[c] SF, hind-limb subcutaneous fat pad weight; HC, hind carcass weight; HCD, dry hind carcass weight

Correlated responses in indicator traits of body composition, expressed as percentages, are listed in Table 3. EF% increased ($P<0.01$) in HE, but not in LE ($P<0.05$), resulting in significant ($P<0.05$) asymmetry; similar correlated responses were also observed for absolute weights of the epidiymal fat pad (Eisen 1992). Correlated responses in SF% paralleled that observed for EF%, although asymmetry was not significant. Correlated response in WA% was negative ($P<0.01$) in the HE lines, while no change was found in LE. No significant correlated responses were detected for HC% in the HE and LE lines.

*Correlated responses in feed intake and feed efficiency*

Male mice were sampled from each replicate line in generations five and seven to estimate changes in feed intake and feed efficiency (Table 4). Results from the two generations were in fair agreement, and correlated responses were generally small. In generation 5, but not in generation 7, HE exhibited a positive correlated response in 3-week body weight. Line differences in 6-week body weight were not present in generation 5, but LE mice had

**Table 3.** Regression coefficients±SE of correlated responses in percentages of body components on generation number in restricted index selected lines

| Line | Trait[c] | | | |
|---|---|---|---|---|
| | EF% | SF% | WA% | HC% |
| HE1[a] | 0.037±0.015* | 0.009±0.006 | −0.203±0.063** | 0.020±0.053 |
| HE2[a] | 0.057±0.015** | 0.026±0.006** | −0.168±0.063** | −0.078±0.053 |
| Pooled[b] | 0.047±0.010** | 0.018±0.008** | −0.185±0.018** | −0.029±0.049 |
| LE1[a] | 0.008±0.015 | −0.008±0.006 | 0.040±0.063 | 0.054±0.053 |
| LE2[a] | −0.019±0.015 | −0.010±0.006 | −0.042±0.063 | −0.070±0.053 |
| Pooled[b] | −0.006±0.013 | −0.009±0.001** | −0.001±0.041 | −0.008±0.062 |
| Divergence 1[a] | 0.029±0.011* | 0.017±0.004** | −0.245±0.043** | −0.034±0.040 |
| Divergence 2[a] | 0.076±0.011** | 0.036±0.004** | −0.126±0.043** | −0.008±0.040 |
| Pooled[b] | 0.053±0.024* | 0.027±0.009** | −0.185±0.060** | −0.021±0.013 |
| Asymmetry | 0.041±0.019* | 0.008±0.007 | −0.186±0.073* | −0.036±0.069 |

* $P<0.05$, ** $P<0.01$
[a] Standard errors calculated by least squares
[b] Standard errors calculated from variation between replicates
[c] EF%, 100 · (epididymal fat pad wt)/(body wt); SF%, 100 · (hind-limb subcutaneous fat pad wt)/(body wt); WA%, 100 · (water wt in hind carcass)/(hind carcass wt); HC%, 100 · (hind carcass wt)/(body wt)

larger ($P<0.05$) 6-week body weights than RS mice in generation 7. In generation 5 there were no significant line differences in feed intake and feed intake/body weight, and HE had a lower feed efficiency than LE and RS.

**Table 4.** Least-squares line means, pooled across replicates, for body weight, feed intake and feed efficiency of males

| Trait[a] | Generation | Line | | | |
|---|---|---|---|---|---|
| | | HE | LE | RS | SE[e] |
| BW3 | 5 | 13.3[b] (68)[d] | 12.6[c] (71) | 12.7[c] (70) | 0.20 |
| | 7 | 12.0[b] (72) | 12.5[b] (72) | 12.1[b] (70) | 0.18 |
| BW6 | 5 | 32.2[b] (67) | 32.3[b] (68) | 31.3[b] (65) | 0.43 |
| | 7 | 29.6[b] (72) | 31.8[c] (69) | 29.3[b] (68) | 0.40 |
| PWG (g/day) | 5 | 0.90[b] | 0.94[c] | 0.89[b] | 0.016 |
| | 7 | 0.84[b] | 0.91[c] | 0.82[b] | 0.016 |
| FEED (g/day) | 5 | 5.48[b] (33) | 5.32[b] (33) | 5.26[b] (32) | 0.115 |
| | 7 | 5.20[b] (36) | 5.18[b] (34) | 4.75[c] (34) | 0.103 |
| FEED/$\overline{BW}$ (g/g) | 5 | 0.242[b] | 0.237[b] | 0.242[b] | 0.0034 |
| | 7 | 0.250[b] | 0.234[c] | 0.230[c] | 0.0032 |
| EFF (g/g) | 5 | 0.164[b] | 0.179[c] | 0.169[b] | 0.0031 |
| | 7 | 0.161[b] | 0.177[c] | 0.176[c] | 0.0035 |

[a] BW3, 3-week body weight; BW6, 6-week body weight; PWG, 3- to 6-week postweaning gain; FEED, 3- to 6-week feed intake; FEED/$\overline{BW}$, (FEED)/0.5 (BW3+BW6); EFF, PWG/FEED
[b,c] Means within the same row with no superscripts in common are different ($P<0.05$)
[d] Number of mice for first set of three traits and number of pairs of mice for second set of three traits are in parentheses
[e] Approximate standard error of the mean

*Correlated responses in fitness traits*

Correlated responses in components of fitness in the restricted index selected lines are displayed in Table 5. Littering rate decreased ($P<0.01$) in LE and did not show a significant trend in HE. Number of days from pairing of mates to littering did not exhibit any significant correlated responses. Divergence ($P<0.05$) was observed for litter size in replicate one with HE1 decreasing and LE1 increasing in litter size, but litter size showed no significant correlated responses when pooled across replicates. Prenatal pup survival rate increased ($P<0.01$) in HE and decreased ($P<0.05$) in LE, leading to divergence ($P<0.01$) between the restricted index lines.

## Discussion

Divergent restricted index selection for epididymal fat pad weight holding body weight unchanged led to considerable variation between replicates in correlated responses, which may be explained by genetic drift. Correlated responses for most traits were generally relatively small, probably because selection intensity was relatively weak due to within-family selection on males only.

Asymmetry of response in component traits of the restricted index was reported earlier (Eisen 1992). Responses in component traits were as expected in the HE line where EF increased and BW did not change significantly, whereas responses in the LE line were contrary to expectation because EF did not change and BW increased.

An important question is whether correlated responses in indicator traits of body composition followed

**Table 5.** Regression coefficients ±SE of correlated responses in fitness traits on generation number in restricted index selection lines

| Line | Trait[c] | | | |
|---|---|---|---|---|
| | LR (%) | CH (days) | LS | PS (%) |
| HE1[a] | $0.027 \pm 0.078$ | $-0.014 \pm 0.106$ | $-0.096 \pm 0.072$ | $0.099 \pm 0.285$ |
| HE2[a] | $-0.107 \pm 0.078$ | $-0.084 \pm 0.106$ | $-0.017 \pm 0.072$ | $0.187 \pm 0.285$ |
| Pooled[b] | $-0.040 \pm 0.067$ | $-0.049 \pm 0.035$ | $-0.056 \pm 0.040$ | $0.143 \pm 0.044$** |
| LE1[a] | $-0.145 \pm 0.078$† | $0.090 \pm 0.106$ | $0.096 \pm 0.072$ | $-0.337 \pm 0.285$ |
| LE2[a] | $-0.096 \pm 0.078$ | $-0.119 \pm 0.106$ | $-0.057 \pm 0.072$ | $-0.037 \pm 0.285$ |
| Pooled[b] | $-0.121 \pm 0.025$** | $-0.015 \pm 0.105$ | $0.020 \pm 0.076$ | $-0.187 \pm 0.150$ |
| Divergence 1[a] | $0.172 \pm 0.054$* | $-0.104 \pm 0.076$ | $-0.192 \pm 0.051$** | $0.436 \pm 0.196$* |
| Divergence 2[a] | $-0.011 \pm 0.054$ | $0.035 \pm 0.076$ | $0.040 \pm 0.051$ | $0.224 \pm 0.196$ |
| Pooled[b] | $0.081 \pm 0.091$ | $-0.034 \pm 0.070$ | $-0.076 \pm 0.116$ | $0.330 \pm 0.106$** |
| Asymmetry[a] | $-0.161 \pm 0.093$† | $-0.064 \pm 0.131$ | $-0.036 \pm 0.088$ | $-0.044 \pm 0.339$ |

† $P<0.10$, * $P<0.05$, ** $P<0.01$
[a] Standard errors calculated by least squares
[b] Standard errors caclulated from variation between replicates
[c] LR, littering rate; CH, number of days from pairing of mates to littering; LS, litter size at birth; PS, preweaning pup survival rate

the pattern predicted from the genetic correlations involving EF and BW, respectively, with indicator traits of body composition. Clearly, EF% and WA% showed correlated responses in the HE line as expected based on base population genetic correlations between EF% and EF ($0.98 \pm 0.01$) (Eisen and Prasetyo 1988) and between EF% and WA% ($-0.89 \pm 0.09$) (Eisen 1987a). Further, SF and SF% increased in HE, although to a smaller extent than expected based on the genetic correlations between EF and SF ($0.86 \pm 0.03$) and between EF and SF% ($0.63 \pm 0.07$) (Eisen and Prasetyo 1988). On average, HC and HC% did not change in HE, a result expected because BW showed no genetic change. Therefore, the restricted selection index was able to restrict traits correlated with the component trait EF despite sizable genetic correlations: $0.49 \pm 0.10$ between EF and HC and $-0.63 \pm 0.08$ between EF and HC% (Eisen and Prasetyo 1988). In the LE line, the positive correlated response in HC and HCD and the absence of any major correlated responses in SF, SF%, EF and WA% were in agreement with the positive correlated response in BW and the negligible correlated response in EF. It was concluded, therefore, that compositional traits changed in the expected direction based on the observed gains in component traits of the restricted index.

The second group of correlated responses examined included feed intake and feed efficiency. Appetite increased in both HE and LE. The genetic correlation between feed intake and index units was $-0.23$. Noting that a decrease in index units is expected to result in an increase in fat content, the positive feed intake response in HE agrees with expectation. The direction of feed intake response in LE was contrary to expectation, and may be explained by the positive response in body weight.

Feed efficiency in the HE line declined as would be expected because of the relative inefficiency of fat growth (Webster 1977). The positive genetic correlation of 0.66 between feed efficiency and index units predicted this outcome. The increased feed efficiency in the LE line may have occurred because of increased 6-week body weight, a consequence of accelerated postweaning gain. Previous studies had shown positive correlated responses in feed efficiency as a result of selection for EF%, but this was due, in part, to a positive correlated response in body weight (Sharp et al. 1984; Prasetyo and Eisen 1989).

Few instances of significant correlated responses in fitness traits were observed. A noted exception was the decrease in littering rate in the LE replicates. Generally, traits related to fitness are expected to be reduced as a correlated response to selection for quantitative traits (Falconer 1989). Absence of any large decreases in fitness traits may be associated with the rather mild selection applied in this study as mentioned earlier.

In summary, correlated responses to restricted index selection generally agreed with expectation when responses in component traits of the index were taken into account. Therefore, breeders should be able to predict correlated responses as long as component traits of the index are carefully monitored across generations (Eisen 1992).

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