Theor Appl Genet (1989) 78: 217-223

Correlated responses in development and distribution of fat depots in mice selected for body composition traits

H. Prasetyo * **and E. J. Eisen**

Animal Science Department, North Carolina State University, Raleigh, NC 27695-7621, USA

Received February 8, 1989; Accepted March 17, 1989
Communicated by G. Wenzel

Summary. Development of adipose tissue in five depots was investigated in mice selected for high or low 12-week epididymal fat pad weight as a percentage of body weight (HF and LF lines), or high or low 12-week hind carcass weight as a percentage of body weight (HL and LL lines). An unselected control line (RC) was maintained. Hind carcass (HC) and fat pads from subcutaneous hindlimb, subcutaneous forelimb, gonads, kidneys and mesentery were dissected and weighed at 4, 6, 9, 12 or 15 weeks of age. Generally, body weight (BW), daily gain (DG), feed intake (FI), feed efficiency (FE) and feed intake/metabolic body weight (FC) were higher ($P \leq 0.05$) in HF than in LF, and in LL than in HL. HF had more fat (as a percentage of BW) than LF in all depots ($P \leq 0.01$), and asymmetry ($P \leq 0.01$) was detected for gonadal fat. LL consistently had a higher ($P \leq 0.01$) fat percentage than HL, and asymmetry ($P \leq 0.01$) was observed for perirenal fat. At age of selection, ranking of fat depot weights as a percentage of total fat depot weight was not changed by selection; however, gonadal fat accounted for more of the total fat in HF and LL compared with RC, while the opposite was found in LF and HL. HC percentage was higher ($P \leq 0.01$) in HL than LL, and higher ($P \leq 0.01$) in LF than HF. Growth rate of each fat depot relative to BW was not affected by selection. These results demonstrated that selection for proportion of fat in one depot or for HC percentage changed fat percentage in other depots. However, the rate of fat deposition in each depot relative to body weight gain was not altered.

Key words: Correlated responses – Fat depots – Lean tissue – Body composition – Mice

* Present address: Balai Penelitian Ternak, P.O. Box 123, Bogor, Indonesia

Introduction

The demand for lean meat free of excessive fat tissue continues to be a major concern in livestock production. Adipose tissue is energetically more expensive to deposit than lean because of a higher content of water in muscle than in fat (Webster 1977), thereby reducing the efficiency of meat production. The energetic expense of fat deposition along with the labor required to trim excessive carcass fat makes fat levels above what are acceptable by the consumer wasteful (Allen and McCarthy 1980).

The low unit cost and short generation length of mice favor their use as a model for studying the genetics of body composition in livestock species. Eisen (1987a) found that selection for increased postweaning gain in mice not only changed the proportion of fat in each depot examined, but also modified maturing patterns of fat depots. Selection for growth rate also can affect the relative rate of fat deposition in different sites (Allen and McCarthy 1980). The developmental pattern of fat deposition was not affected by selection for high and low body weight at 5 weeks, but selection at 10 weeks affected the level of fat at low carcass weights and the relative rate at which fat was deposited (Allen and McCarthy 1980); selection also had a preferential effect on faster-growing fat depots. These results demonstrate that growth of fat varies among fat depots in mice, and selection for growth traits may induce differential correlated responses in the distribution of fat. Therefore, direct selection for a change in a single fat depot may lead to differential responses in other fat depots (Eisen 1987a).

The present study was designed to evaluate correlated responses due to single-trait divergent selection for epididymal fat pad percentage or for hind carcass percentage at 12 weeks of age on development and distribution of fat depots in five sites, at five different ages.

Materials and methods

Formation of lines

Mice were sampled from lines derived by divergent single-trait selection for fat percentage or for lean tissue percentage at 12 weeks of age (Eisen 1987b). Right epididymal fat pad weight as a percentage of body weight was used as a measure of body fat percentage because of a high phenotypic correlation between the traits (Eisen and Leatherwood 1978). High and low lines were designated as HF and LF. Lean tissue percentage was measured as hind carcass weight as a percentage of body weight. High and low lines were identified as HL and LL. These indirect measures of fat and lean tissue percentages are highly heritable and genetically negatively correlated (Eisen 1987b). A contemporary control line (RC) was maintained by random selection. At generation 13, selection was relaxed. Parents of mice used in the present study were from generation 14.

General husbandry

Female breeders were fed Purina Mouse Chow (Purina Mills, St. Louis/MO) from mating to weaning of their litters. Following weaning, mice had free access to feed (Purina Laboratory Chow 5001) and water. The laboratory environment was maintained at 22 °C, 55% relative humidity and 12 h light–12 h dark cycle. Pups were permanently identified at 12 days of age.

Experimental procedure

Twenty-two males and 22 females of each line, varying in age from 8 to 10 weeks, were randomly pair-mated. After 16 days, males were removed and females were caged separately and checked daily for litters, beginning on day 19. Litters were standardized to ten pups at 1 day of age, and weaned at 3 weeks. Two male and two female siblings were chosen randomly from each litter at weaning, and two like-sexed siblings were caged together.

Individual body weights (BW) were recorded weekly from weaning to 15 weeks or until mice were killed. Weight gain (DG), feed intake (FI) (average of two mice per cage), gross feed efficiency (FE) (weight gain/feed intake) and feed intake/metabolic body weight (FC) ($kg/kg^{0.75}$) were calculated. Ten males and ten females were randomly assigned to be killed with CO_2 at 4, 6, 9, 12 or 15 weeks of age. Immediately afterwards, fat pads from regions of the subcutaneous hindlimb (SUBCHL) and forelimb (SUBCFL), gonads (GONAD), mesentery (MESEN) and kidneys (PRENAL) were dissected and weighed. Right and left fat pads were pooled and weighed together. The hind carcass (HC) was also dissected and weighed, following the method used during selection (Eisen 1987b).

Statistical analyses

Least-squares procedures were used to estimate means of each trait based on the following statistical model:

$$Y_{ijkl} = \mu + L_i + A_j + (LA)_{ij} + D_{k\,(ij)} + S_l + (LS)_{il} + (AS)_{jl} + (LAS)_{ijl} + e_{ijkl}.$$

where Y_{ijkl} is the mean of two mice in the k^{th} litter of the i^{th} line, j^{th} age and l^{th} sex, μ is the overall mean, L_i is a fixed line effect, A_j is a fixed age effect, $D_{k\,(ij)}$ is a random litter effect, S_l is a fixed sex effect, e_{ijkl} is a random residual effect and the remaining terms are corresponding interaction effects. Line, age and line × age mean squares were tested against the litter mean square, and sex and interactions with sex were tested against the residual mean square. Preliminary analyses indicated that line × sex and line × sex × age interactions were not significant, except the line × sex interaction for GONAD as a percentage of body weight (see Results).

Means were compared using Duncan's multiple comparison procedure. Planned linear contrasts included HF−LF = divergence between lines selected for high and low fat percentage HF + LF − 2 RC = asymmetry for HF and LF, HL−LL = divergence between lines selected for high and low lean percentage, HL + LL − 2 RC = asymmetry for HL and LL and (HF−LF)−(LL−HL) = difference between divergence in lines selected for fat percentage and divergence in lines selected for lean percentage.

Growth rate of each fat depot and the hind carcass (y) relative to body weight (x) was analyzed by transforming $y = ax^b$ to natural logarithms, $\ln y = \ln a + b \ln x$, where a is an intercept and b is a regression of $\ln y$ on $\ln x$ (Huxley 1932). The regression coefficients among lines were found to be homogeneous. Line differences in ln fat depot and hind carcass weights, adjusted for ln body weight, were similar to line differences in component weights as a percentage of body weight; therefore, these data are not presented.

Results

Body growth traits

Weekly BW means for the five lines, averaged over sex, are presented in Fig. 1. HF was consistently larger ($P \leq 0.05$) than LF, and LL was larger ($P \leq 0.05$) than HL, while RC was intermediate.

DG, FI, FC and FE between 3 and 6 weeks, 6 and 12 weeks and 12 and 15 weeks are in Table 1. Males were larger ($P \leq 0.05$) than females in all periods for DG and FI and in the first two periods for FE, whereas no sex differences were found for FC. Line differences in DG were highest from 3 to 6 weeks, with RC being intermediate between the faster-gaining HF and LL lines and the slower-gaining LF and HL lines. At later ages, DG was reduced and line differences decreased. FI increased greatly in all lines between 3 and 6 weeks; at later ages,

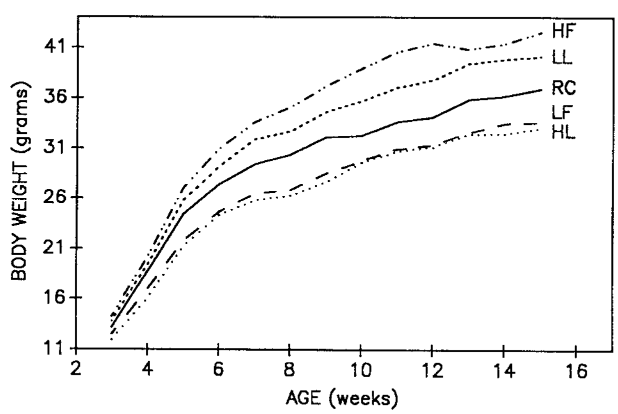

Fig. 1. Growth curves, averaged over sexes, of lines selected for high and low fat percentage (HF and LF), high and low lean percentage (HL and LL) and controls (RC). Standard errors for successive weekly body weights from 3 to 15 weeks were 0.2, 0.4, 0.6, 0.5, 0.6, 0.6, 0.6, 0.8, 0.9, 0.9, 1.2, 1.2 and 1.1

Table 1. Least-squares means with standard errors of weight gain, feed intake and feed efficiency for each of five lines and two sexes

Traits [1]	Lines						Sexes		
	HF	LF	HL	LL	RC	SE [2]	M	F	SE [2]
WG3-6, g/d	0.79^{a}	0.57^{d}	0.59^{d}	0.73^{b}	0.68^{c}	0.02	0.77^{a}	0.58^{b}	0.02
WG6-12, g/d	0.25^{a}	0.15^{c}	0.15^{c}	0.19^{b}	0.17^{bc}	0.01	0.23^{a}	0.14^{b}	0.01
WG12-15, g/d	0.14^{a}	0.08^{b}	0.06^{b}	0.09^{ab}	0.08^{b}	0.02	0.11^{a}	0.07^{b}	0.01
FI3-6, g/d	5.08^{a}	4.20^{c}	4.17^{c}	4.72^{b}	4.59^{b}	0.09	4.71^{a}	4.39^{b}	0.07
FI6-12, g/d	5.88^{a}	5.21^{b}	5.13^{b}	5.53^{ab}	5.19^{b}	0.13	5.79^{a}	4.98^{b}	0.12
FI12-15, g/d	5.45^{ab}	5.65^{a}	5.11^{b}	5.57^{ab}	5.15^{ab}	0.16	5.82^{a}	4.95^{b}	0.08
FE3-6, g/g	0.156^{a}	0.137^{d}	0.140^{cd}	0.154^{ab}	0.147^{bc}	0.003	0.162^{a}	0.131^{b}	0.003
FE6-12, g/g	0.043^{a}	0.028^{b}	0.029^{b}	0.034^{b}	0.032^{b}	0.002	0.039^{a}	0.027^{b}	0.002
FE12-15, g/g	0.026^{a}	0.015^{ab}	0.012^{b}	0.016^{ab}	0.015^{ab}	0.004	0.019^{a}	0.015^{a}	0.002
FC3-6, $kg/d/kg^{0.75}$	0.086^{a}	0.082^{b}	0.084^{ab}	0.083^{b}	0.084^{ab}	0.001	0.083^{a}	0.084^{a}	0.001
FC6-12, $kg/d/kg^{0.75}$	0.070^{b}	0.075^{a}	0.075^{a}	0.070^{b}	0.070^{b}	0.001	0.072^{a}	0.073^{a}	0.001
FC12-15, $kg/d/kg^{0.75}$	0.060^{c}	0.074^{a}	0.067^{b}	0.063^{c}	0.063^{c}	0.001	0.064^{a}	0.066^{a}	0.001

[1] WG*i-j* = weight gain/mouse/day from i^{th} to j^{th} week
FI*i-j* = feed intake/mouse/day from i^{th} to j^{th} week
FE*i-j* = feed efficiency (gain/intake) from i^{th} to j^{th} week
FC*i-j* = adjusted feed intake (daily feed intake/average metabolic body weight) from i^{th} to j^{th} week
[2] Approximate standard errors
[a, b, c, d] For line and sex separately, means with no superscripts in common are different ($P \leq 0.05$)

Table 2. Estimates of line divergence, asymmetry and sex difference for percentages of fat pads and hind carcass weights, averaged across ages. Traits are: HC – hind carcass; fat pads from the specified regions: SUBCHL – subcutaneous hindlimb; SUBCFL – subcutaneous forelimb; GONAD – gonads; PRENAL – kidneys; MESEN – mesentary; TFAT – total of the five fat depots

Traits	HF−LF	HF+LF −2 RC	HL−LL	HL+LL −2 RC	(HF−LF) −(LL−HL)	Male − female
As a percentage of body weight						
SUBCHL	0.91**	0.15^{NS}	−0.40**	-0.21^{NS}	0.51**	−0.09*
SUBCFL	0.71**	0.18^{NS}	−0.36**	-0.14^{NS}	0.35**	−0.19**
GONAD	3.28**	1.15**	−1.26**	-0.23^{NS}	2.02**	−0.22**
PRENAL	0.67**	0.00^{NS}	−0.24**	−0.32**	0.43**	0.11**
MESEN	0.95**	0.07^{NS}	−0.40**	-0.18^{NS}	0.55**	−0.08*
TFAT	6.53**	1.55**	−2.67**	-1.09^{NS}	3.86**	−0.46**
HC	−1.25**	−0.84**	1.84**	0.61**	0.58**	−0.19**
As a percentage of total fat depot weight						
SUBCHL	−4.04**	0.15^{NS}	2.10**	-0.07^{NS}	-1.94^{NS}	−0.76*
SUBCFL	−5.65**	1.59^{NS}	1.44^{NS}	0.70^{NS}	−4.22**	−3.82**
GONAD	15.07**	0.69^{NS}	−7.13**	0.16^{NS}	7.94**	2.29**
PRENAL	2.30**	−2.50*	-0.89^{NS}	−3.42**	1.42^{NS}	2.02**
MESEN	−7.68**	0.07^{NS}	4.47**	2.63^{NS}	-3.21^{NS}	-0.72^{NS}

[NS] Not significant
* $P \leq 0.05$
** $P \leq 0.01$

FI decreased slightly in HF, LL and RC and increased slightly in LF and HL (data not shown). Significant divergence between HF and LF was found between 3 and 6 weeks and between 6 and 12 weeks, but not between 12 and 15 weeks. FI was greater in LL than HL, but the difference was only significant between 3 and 6 weeks. FC had considerably reduced line differences compared to FI. The smaller body weight lines (HL, LF) had significantly higher FC between 6 and 12 weeks and between 12 and 15 weeks than the larger lines (LL, HF). FE was greatest in all lines between 3 and 6 weeks and decreased with age. FE between 3 and 6 weeks was higher in HF and LL than in LF and HL.

Fat pads and hind carcass weights as a percentage of body weight

Development of fat pad weights as a percentage of BW is presented in Fig. 2, and estimates of divergence and asymmetry, averaged across sex and age, are in Table 2.

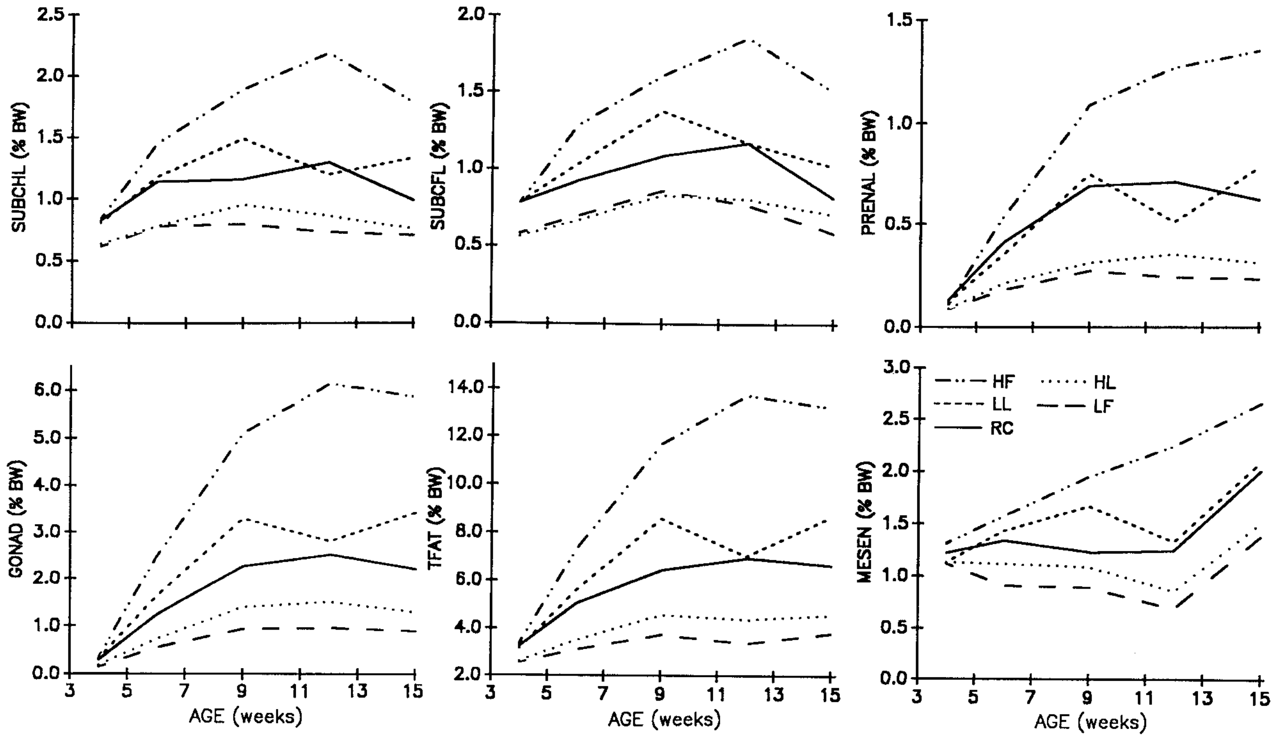

Fig. 2. Least-squares means of each fat depot as a percentage of body weight at 4, 6, 9, 12 and 15 weeks for each line, averaged across sexes. Standard errors of line × age means were 0.09, 0.09, 0.28, 0.09, 0.14 and 0.56 for SUBCHL, SUBCFL, GONAD, PRENAL, MESEN and TFAT

Fat pad weights in all depots (except PRENAL) and HC weight, as a percentage of body weight, were larger in females than in males. There was no significant interaction between sexes and lines, except in GONAD ($P \leq 0.01$), where the fat percentage was higher in females for HF and LL lines and not different for the other lines; however, the ranking of lines was the same for males and females (data not shown).

SUBCHL and SUBCFL had similar developmental patterns; HF was higher ($P \leq 0.01$) than LF and LL was higher ($P \leq 0.01$) than HL, beginning at 4 weeks, with no significant asymmetry. For GONAD and PRENAL, the high (HF, HL) and low lines (LF, LL) started to diverge significantly at 6 weeks. Asymmetric response was observed between HF and LF for GONAD, and between HL and LL for PRENAL. MESEN had a different pattern of development in that LF and HL decreased in fat percentage until 12 weeks. At 15 weeks all lines showed an increase. Total fat depot weight (sum of the five fat depot weights) as a percentage of body weight was higher ($P \leq 0.01$) in HF than LF and was higher ($P \leq 0.01$) in LL than HL. Asymmetric response ($P \leq 0.01$) was detected between HF and LF. The difference in divergence between the lines selected on the basis of fat and those selected on the basis of lean was large ($P \leq 0.01$).

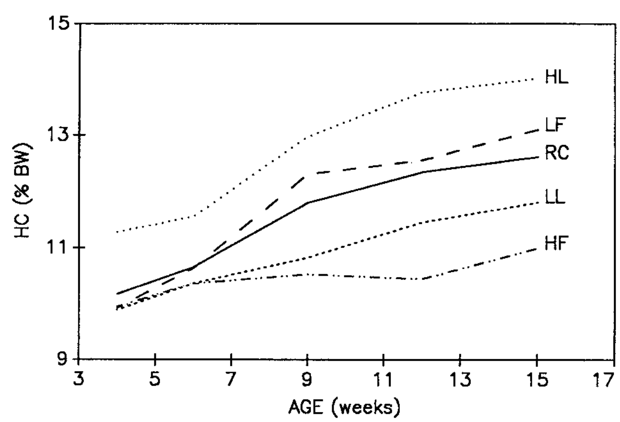

Fig. 3. Least-squares means of hind carcass weight as a percentage of body weight at 4, 6, 9, 12 and 15 weeks in the selected and control lines, averaged across sexes. Standard error for each line × age mean was 0.22

HC percentage showed differences in development among lines (Fig. 3 and Table 2), which were opposite to those of depot fat percentages. HL and LL started to diverge significantly in HC at 4 weeks of age, while HF and LF did not begin to diverge significantly until 9 weeks (Fig. 3).

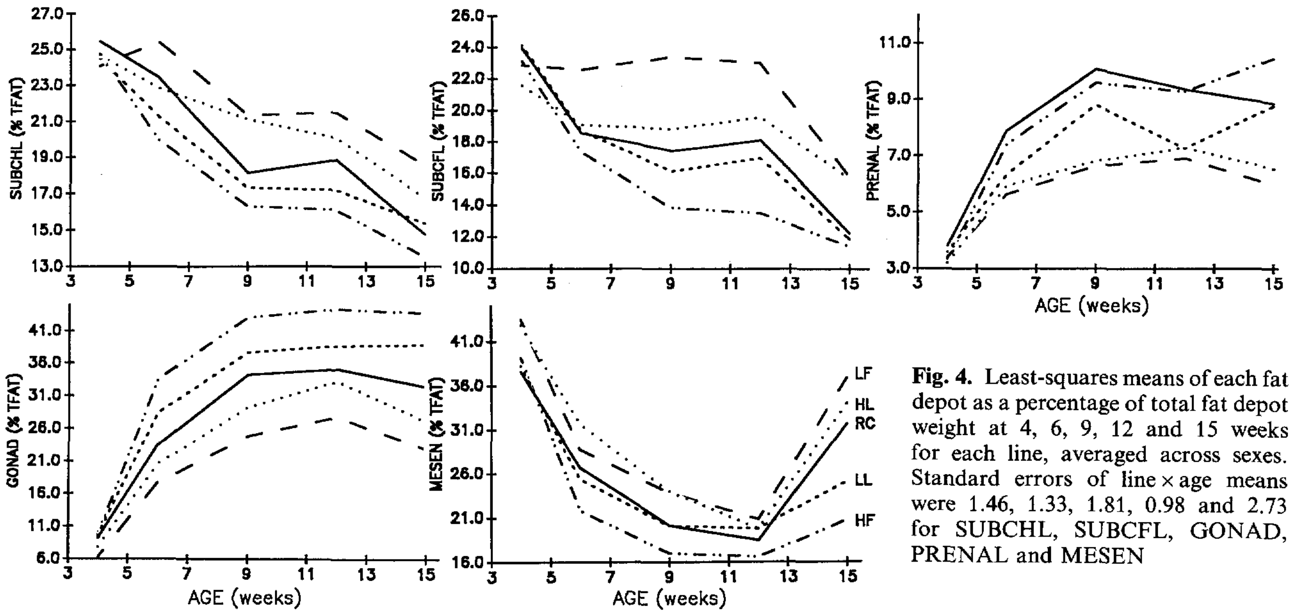

Fig. 4. Least-squares means of each fat depot as a percentage of total fat depot weight at 4, 6, 9, 12 and 15 weeks for each line, averaged across sexes. Standard errors of line × age means were 1.46, 1.33, 1.81, 0.98 and 2.73 for SUBCHL, SUBCFL, GONAD, PRENAL and MESEN

Fat pad weights as a percentage of total fat depot weight

Different patterns were shown by the five fat depots when analyzed as a percentage of total fat depot weight (TFAT) (Fig. 4). Sex differences were found in all fat depots except MESEN (Table 2).

SUBCHL and SUBCFL as a percentage of TFAT decreased with age. LF had a higher ($P \leq 0.01$) fat percentage than HF, and HL was higher than LL. As a percentage of TFAT, GONAD and PRENAL increased rapidly with age until 9 weeks. HF was higher ($P \leq 0.01$) than LF for both depots, while LL was higher than HL but significant only for GONAD. Asymmetry was not significant for either selection criteria in GONAD, but asymmetry was significant ($P \leq 0.05$) in PRENAL. Divergence between HF and LF was much higher than divergence between HL and LL in GONAD, but this contrast was not significant in PRENAL. MESEN showed a different pattern from other depots. LF had a higher ($P \leq 0.01$) fat percentage than HF, and HL was higher ($P \leq 0.01$) than LL, with no asymmetry.

At age of selection (12 weeks), GONAD made up the largest and PRENAL the smallest percentage of TFAT in the control line (RC), while SUBCHL, SUBCFL and MESEN were intermediate (Fig. 5). Divergent selection in HF and LF did not change the ranking. There was, however, a redistribution of fat, with a greater percentage of TFAT in HF being distributed to GONAD and a lesser percentage to SUBCHL, SUBCFL and MESEN compared to RC. The reverse was true in LF; additionally, PRENAL showed a decrease relative to the control. The trends in LL and HL were similar to HF and LF, respectively, but were not as large.

Discussion

Divergent selection for fat percentage in HF and LF resulted in positive correlated responses in BW and DG. Bishop and Hill (1985) reported similar findings. These results are as expected since body fat percentage and body weight are positively genetically correlated (Eisen and Prasetyo 1988). Positive correlated responses in growth rate from selection for fat percentage agree with positive correlated changes in body fat content resulting from selection for postweaning body weight or weight gain in mice (Hayes and McCarthy 1976; McPhee and Neil 1976; Allen and McCarthy 1980).

Divergent selection for lean tissue percentage in HL and LL led to negative correlated responses in BW, especially from 6 to 15 weeks. These findings confirm that hind carcass percentage as a measure of lean tissue percentage is negatively genetically correlated with BW (Eisen 1987b, c; Eisen and Prasetyo 1988). The negative correlation is, in part, mathematically induced because BW is the denominator of lean tissue percentage. Bishop and Hill (1985) selected mice divergently for a lean index defined as body weight − 8 × (epididymal fat pad weight), a phenotypic predictor of fat-free mass. Selection on the lean index resulted in positive correlated responses in body weight (Bishop and Hill 1985). Clearly, the selection criterion used as a measure of lean tissue determined the direction of the correlated response in body weight.

Divergent selection for epididymal fat percentage led to positive correlated responses in FI, while negative correlated responses occurred when selection was for hind carcass percentage. In selection for epididymal fat pad

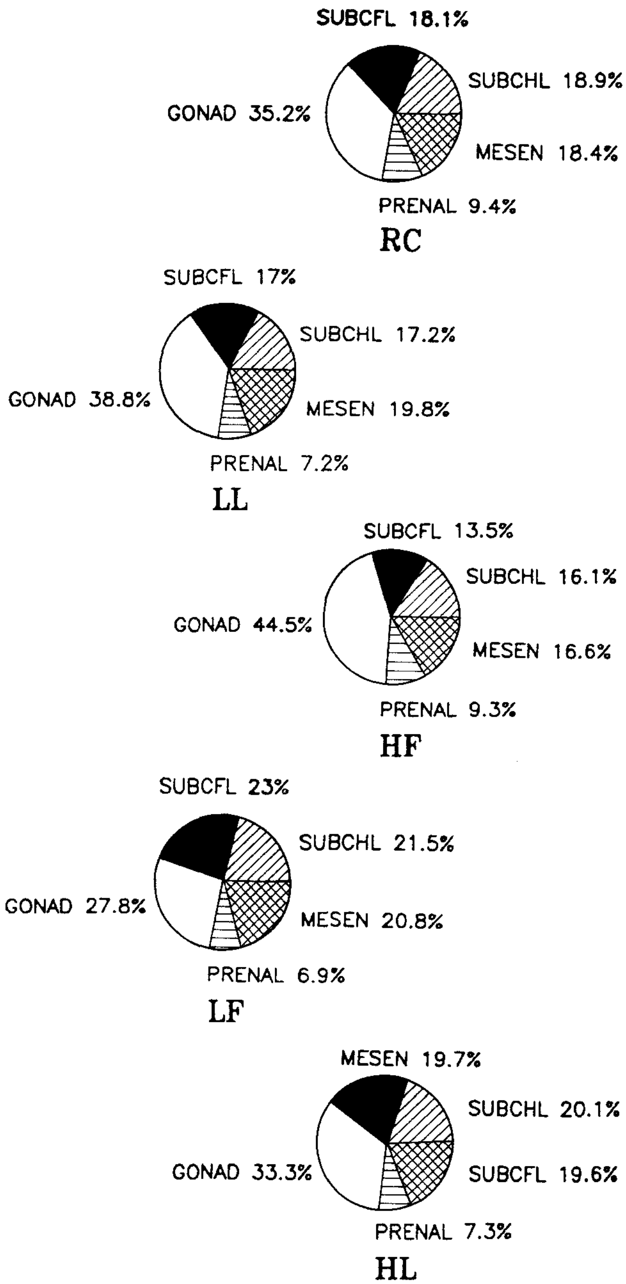

Fig. 5. Pie diagrams showing distribution of least-squares means of fat pads as a percentage of total fat depot weight for each line at age of selection (12 weeks), averaged across sexes. Standard errors are in the caption for Fig. 4

percentage or for lean index in mice, Bishop and Hill (1985) found large positive divergences in FI between high and low lines during the period associated with rapid postweaning growth, but as the mice approached maturity the divergence disappeared. McCarthy (1979) and Roberts (1981) reported positive correlated responses in FI due to selection for large body weight. The present data indicate that the direction of correlated response in FI due to selection for body composition traits under ad libitum feeding depends on the direction of change in body weight. One method of studying the genetic association between FI and body composition, independent of body weight, would be to select animals for an index designed to change body composition and hold body weight constant.

In the present study, selection did not alter FC between 3 and 6 weeks, confirming results obtained by Eisen (1987c). At later ages, high lean and low fat lines showed a higher FC compared to low lean and high fat lines. This finding agrees with results of Bishop and Hill (1985); selection for low fat showed a higher FC at later ages compared to selection for high fat, but not at earlier ages, whereas divergent selection for lean index did not show any change.

FE was also modified by selection, especially between HF and LF lines. An earlier report noted that FE did not show a significant correlated response (Eisen 1987c). Continued selection since the last report may explain the discrepancy. Roberts (1981) pointed out that higher FE in large mice is presumably due to lower maintenance requirements, which can be explained in terms of less surface area per unit of BW with its implications for thermo-regulation and its energetic cost.

As a percentage of body weight, all five fat depots responded positively to selection for epididymal fat pad percentage. The HF line reached maximum fat percentage at age of selection (12 weeks) in all depots, except MESEN. The largest divergence was in GONAD, which accounted for about half of the line divergence in total fat depot percentage. Correlated responses in the four other depots were in the same direction, but degree of divergence varied. Eisen (1987c) reported realized genetic correlations of approximately one between epididymal fat pad percentage and SUBCHL percentage and between epididymal fat pad percentage and fat as a percentage of hind carcass weight. Thus, selection for a single fat depot has resulted in high positive correlated responses in other fat depots and in hind carcass fat. These data indicate that there are high genetic correlations between different fat depots in amounts of fat deposited.

As correlated responses to selection for lean tissue percentage, HL contained smaller fat depot percentages than LL. These results differ from data of Bishop and Hill (1985); high lean index and control lines were similar in fat percentage until 10 weeks and the high line was lower at 17 weeks, while the low line had a higher fat percentage than control up to 10 weeks and then was similar at 17 weeks. Therefore, correlated reponses in fat percentages due to selection for lean tissue percentage depend upon the criterion used as a measure of lean tissue, i.e. lean tissue as a percentage of body weight or lean tissue mass.

The mechanism by which selection for hind carcass percentage caused negative correlated responses in fat percentages may be associated with the negative genetic correlation between hind carcass percentage and body weight (Eisen 1987c). Selection for large hind carcass percentage produced mice with smaller body weights and consequently less fat percentage, and the reverse was true in selection for low hind carcass percentage. In general, selection for hind carcass percentage resulted in correlated responses in fat depot percentages which were in the opposite direction and of smaller magnitude than selection for epididymal fat pad percentage.

Selection for hind carcass percentage resulted in significant direct responses, while significant negative correlated responses were found for hind carcass percentage based on selection for epididymal fat pad percentage. An interesting finding was that HL and LL lines started to diverge in hind carcass percentage at an earlier postweaning age than HF and LF. This result suggests that direct selection for hind carcass percentage may have caused differences in lean tissue development to be expressed at an earlier age compared with selection for adipose tissue.

Each fat depot weight as a percentage of TFAT was changed by selection. At age of selection, there was no change in ranking of the fat depot weights as a percentage of TFAT, but the percentages were redistributed primarily due to GONAD increasing in HF and LL and decreasing in HL and LF.

Selection did not change growth rate of fat depots relative to body growth (data not shown). In swine, Tess et al. (1986) did not observe any difference between Beltsville high fat and low fat lines in allometric coefficients for fat growth relative to empty body weight growth. In contrast, Allen and McCarthy (1980) found higher allometric growth coefficients for kidney and gonadal fat depots in lines of mice selected for large body weight than in controls. Eisen (1987a) also reported significant correlated responses in growth of fat depots relative to body weight growth in mice selected for high postweaning gain.

In conclusion, selection for epididymal fat pad weight as a percentage of body weight led to positive correlated responses in the proportion of other fat pad weights relative to body weight. These correlated responses were larger than those obtained as a result of selection for hind carcass weight as a percentage of body weight, but the latter selection criterion resulted in a larger change in lean tissue percentage. Both selection criteria failed to change rate of fat deposition in each depot relative to body weight growth. However, correlated responses were observed in fat depot weights at a constant body weight.

Acknowledgements. Paper No. 12023 of the Journal Series of the North Carolina Agricultural Research Service, Raleigh, NC, 27695-7643, USA. The use of trade names in this publication does not imply endorsement by the North Carolina Agricultural Research Service of the products named, nor criticism of similar ones not mentioned. The senior author was the recipient of a fellowship from the Indonesian government through a World Bank loan administered by Winrock International. The authors are grateful to Fields Gunsett, C. Clark Cockerham and W. J. Croom, Jr. for their comments on a draft of the manuscript. The assistance of S. Anderson, L. Hester and D. Pomp in data collection is acknowledged.

References

Allen P, McCarthy JC (1980) The effects of selection for high and low body weight on the proportion and distribution of fat in mice. Anim Prod 31:1–11

Bishop SC, Hill WG (1985) Effects of selection on growth, body composition, and food intake in mice. III. Correlated responses: growth, body composition, food intake, and efficiency and catabolism. Genet Res 46:57–74

Eisen EJ (1987a) Effects of selection for rapid postweaning gain on maturing patterns of fat depots in mice. J Anim Sci 64:133–147

Eisen EJ (1987b) Selection for components related to body composition in mice: direct responses. Theor Appl Genet 74:793–801

Eisen EJ (1987c) Selection for components related to body composition in mice: correlated responses. Theor Appl Genet 75:177–188

Eisen EJ, Leatherwood JM (1978) Adipose cellularity and body composition in polygenic obese mice as influenced by preweaning nutrition. J Nutr 108:1652–1662

Eisen EJ, Prasetyo H (1988) Estimates of genetic parameters and predicted selection responses for growth, fat and lean traits in mice. J Anim Sci 66:1153–1165

Hayes JF, McCarthy JC (1976) The effects of selection at different ages for high and low body weight on the pattern of fat deposition in mice. Genet Res 27:389–403

Huxley JS (1932) Problems of relative growth. Methuen, London

McCarthy JC (1979) Normal variation in body fat and its inheritance. In: Festing MFW (ed) Animal models of obesity. McMillan, London, pp 1–14

McPhee CP, Neill AR (1976) Changes in the body composition of mice selected for high and low eight-week weight. Theor Appl Genet 47:21–26

Roberts RC (1981) The growth of mice selected for large and small size in relation to food intake and the efficiency of conversion. Genet Res 38:9–24

Tess MW, Dickerson GE, Nienaber JA, Ferrell CL (1986) Growth, development and body composition in three genetic stocks of swine. J Anim Sci 62:968–979

Webster AJF (1977) Selection for leanness and the energetic efficiency of growth in meat animals. Proc Nutr Soc 36:53–59