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Body Composition and Energetic Efficiency in two Lines of Mice Selected for Rapid Growth Rate and their F_1 Crosses*

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Summary. Correlated responses to selection for increased growth rate were compared in two mouse populations (M16 and H_6) of distinct genetic origin. Traits studied were body composition, feed intake, constituent gains and energetic efficiency. When compared with their respective controls (ICR and C_2) at 6 and 9 weeks of age, body weight increased more in M16 (57% and 69% of the control mean) than in H_6 (40% and 34%). The M16 showed correlated responses in fat percent of 2.6% ($P < .05$), 8.4% ($P < .01$) and 11.2% ($P < .01$) at 3, 6 and 9 weeks, respectively, whereas corresponding values in H_6 were -2.4% ($P < .05$), 3.3% ($P < .05$) and 2.09% ($P > .05$). The correlated responses in fat percent were 2.7 and 4.7 times higher in M16 than H_6 at 6 and 9 weeks. The regression of *ln* fat weight on *ln* empty body weight was larger in M16 ($P < .05$) compared to ICR and larger ($P < .01$) in H_6 compared to C_2. Both M16 and H_6 exhibited positive correlated responses from 3 to 6 weeks of age in feed intake and gain and efficiency in fat, protein, calories and ash; fat and caloric gain and efficiency exhibited higher correlated responses in M16 than H_6. During the 6- to 9-week interval, the M16 population continued to evince positive correlated responses in gains and efficiencies of fat, protein and calories, whereas H_6 did not. Several possible explanations are presented to account for the differences in correlated responses between the selected populations. Partitioning of correlated response differences between M16 and H_6 into average direct and average maternal genetic effects indicated that average direct genetic effects, favoring M16, were responsible for the major difference between the selected populations. Direct heterosis in F_1 crosses of the selected populations were generally not significant, although there was a tendency for fat percent and fat weight to show heterosis.

Introduction

Selection experiments for growth rate in laboratory species such as mice and rats have clearly demonstrated the feasibility of rapidly increasing postweaning body weight by genetic manipulation (Roberts 1965; Eisen 1974). From a quantitative genetic standpoint, the architecture of body weight has been adequately described by essential genetic parameters such as maternal and non-additive genetic variances and realized heritabilities. Recent refinements have demonstrated the importance of considering effective population size, genetic drift and selection intensity in assessing response to selection for body weight (Hanrahan, Eisen and Legates 1973; Falconer 1973; Eisen 1975; Baker, Chapman and Wardell 1975). Components of growth which may have changed as a consequence of selection for body weight or postweaning gain have been less intensely studied to date (Sutherland, Biondini and Ward 1974; Eisen 1976).

The objective of the present paper is to compare correlated responses to selection for increased growth rate in two mouse populations of distinctly different genetic origin. The traits assessed are body composition at three ages and feed intake, constituent gains and energetic efficiency during two age intervals. The difference in correlated responses between the selected populations is partitioned into average direct and average maternal genetic effects. Direct heterosis is estimated from crosses of the two selected populations and crosses of the two control populations. The populations are also compared on the basis of the allometric relationship between weight of the major body constituents and empty body weight.

Materials and Methods

The eight mouse populations used in the present experiment have been described by Bakker, Nagai and Eisen (1976) and are briefly reviewed here. The M16 population had undergone 37 generations of selection

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for increased postweaning gain from 3 to 6 weeks of age at the time the study was initiated, while the H_6 population had been selected for 73 generations for large 6-week body weight. Details of the direct responses to selection have been reported for the M16 population (Hanrahan et al. 1973; Eisen 1975) and the H_6 population (Legates 1969). The base population controls for M16 and H_6 were ICR and C_2, respectively. The four reciprocal F_1 crosses formed from these parental populations were M16 × H_6, H_6 × M16, ICR × C_2 and C_2 × ICR, where the male parental population is given first. Since the two base populations differed markedly in body size and genetic origin (ICR was an outbred population and C_2 was derived from crossing two F_1 stocks, CAF_1 and AKD_2F_1, derived from inbred lines), it was deemed essential to include both control populations in the present study to assess differences in correlated responses between the selected lines.

Litters from each population were standardized to eight young at birth. The mice were weaned at 3 weeks of age and randomly designated to be killed at 3, 6 or 9 weeks of age. Only female mice were utilized. All mice were individually caged at weaning and fed Purina Laboratory Chow (gross energy of 4.06 kcal/g) *ad libitum*. The number of mice allotted to each population-age subclass in this cross-sectional design is given in Table 1.

Body weights (BWT) were recorded to the nearest 0.1 g at 3, 6 and 9 weeks of age. Feed intake (FEED), weight gain (GAIN) and feed efficiency (EFF = 100 × GAIN/FEED) were obtained in the 3 to 6 and 6- to 9- week age intervals. The former interval includes the age period when postweaning growth is expected to be maximum (Eisen 1974). Empty body weight of each mouse killed was obtained after removal of the ingesta from the gastro-intestinal tract. The mice were frozen at -18°C and subsequently subjected to whole body composition analysis (Eisen and Leatherwood 1976). After determination of total water (WAT), fat (FAT), protein (PRO) and ash (ASH) weights, each component was calculated as a percentage of empty body weight. Protein and ash were also expressed on a percent fat-free basis. Total body calories (CAL) were determined indirectly as (fat weight × 9.5 kcal/g) + (protein weight × 5.65 kcal/g).

Gain in body constituents (FATG, PROG, ASHG and CALG) between 3 and 6 weeks of age for mice killed at 6 weeks was estimated by the method outlined by Eisen and Leatherwood (1976). Regression equations of the natural logarithm *(ln)* of each body constituent on *ln* body weight were calculated across ages for each population. These regression equations were used to predict body constituent weight at 3 weeks of age for each individual killed at 6 weeks within a population. The difference between the individual's constituent weight at 6 weeks of age and its predicted constituent weight at 3 weeks provided the estimate of constituent gain. The efficiency of constituent gain (FATE, PROE and ASHE) and energetic efficiency (CALE) were estimated by dividing constituent gain by feed intake in the interval. This procedure was repeated for mice killed at 9 weeks to calculate the gain and efficiency of constituents in the 6- to 9-week interval.

Differences among populations in body constituents per unit increase in empty body weight also were evaluated, as outlined by Hayes and McCarthy (1976). The regression coefficients of *ln* body constituent (WAT, FAT, PRO, ASH and CAL) on *ln* empty body weight were used in this analysis.

Table 1. Sample size allocation for each population-age subgroup

Population	Age(wk) 3	6	9	Total
M16	7	6	7	20
H_6	11	12	12	35
M16 × H_6	13	11	12	36
H_6 × M16	11	11	11	33
ICR	12	12	12	36
C_2	12	12	12	36
ICR × C_2	12	12	12	36
C_2 × ICR	12	12	12	36
Total	90	88	90	268

Each trait was analyzed by least squares procedures. The analysis of variance model contained the fixed effects of population, age, population by age interaction and a random error term. Since most traits demonstrated significant population by age interactions and heterogeneous error variances across ages, the data were re-analyzed on a within age basis. Transformation of percentage data to arcsin gave essentially unchanged results, therefore the transformation was not used.

Linear contrasts were developed to determine the correlated response to selection for each trait in each selected population (M16-ICR and H_6-C_2) and the difference between the selected populations in correlated response [(M16-ICR) - (H_6-C_2)]. Differences between selected populations (M16-H_6) and between control populations (ICR-C_2) were partitioned into an average maternal genetic effect [(H_6 × M16) - (M16 × H_6) and (C_2 × ICR) - (ICR × C_2)] and an average direct genetic effect [(M16-H_6) - (H_6 × M16) + (M16 × H_6) and (ICR-C_2) - (C_2 × ICR) + (ICR × C_2)] (Dickerson 1969). The between population difference in correlated response [(M16-ICR) - (H_6-C_2)] was also partitioned into an average maternal genetic effect and an average direct genetic effect in an analogous manner. Direct heterosis in the crosses of both the selected and the control populations was estimated as the difference between the means of the F_1 reciprocal crosses and the parental populations. Further details on these linear contrasts were given by Bakker et al. (1976).

The regression coefficients of *ln* constituent weight on *ln* empty body weight across ages provided an estimate of change in constituent weight per unit change in empty body weight in each population. Linear contrasts, analogous to those obtained among population means on a constant age basis, were calculated for these regression coefficients.

Results

Age trends

Population means plotted against age are given in Fig. 1 for body weight and caloric content and in Figs. 2 and 3 for percent body composition. The means of feed intake, gain and efficiency for the 3- to 6-week and 6- to 9-week age intervals are presented in Table 2.

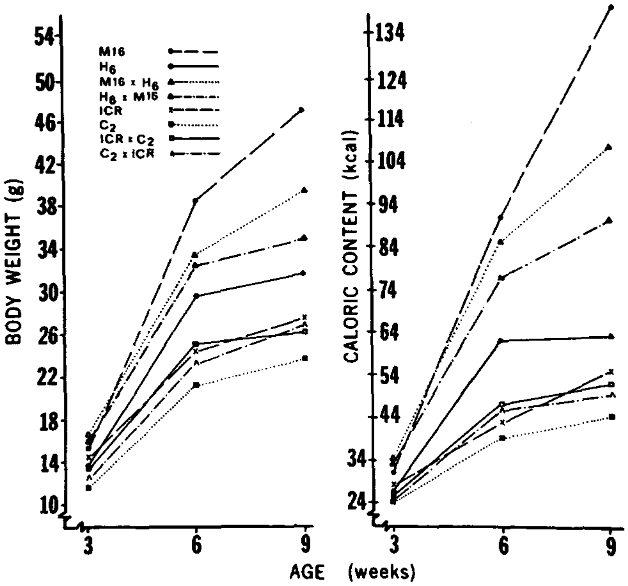

Fig.1. Body weight and caloric content for the eight populations at 3, 6 and 9 weeks of age. Standard errors of the means for N = 12 at the respective ages are 0.47, 0.75 and 1.02g for body weight and 1.50, 3.01 and 5.30kcal for caloric content

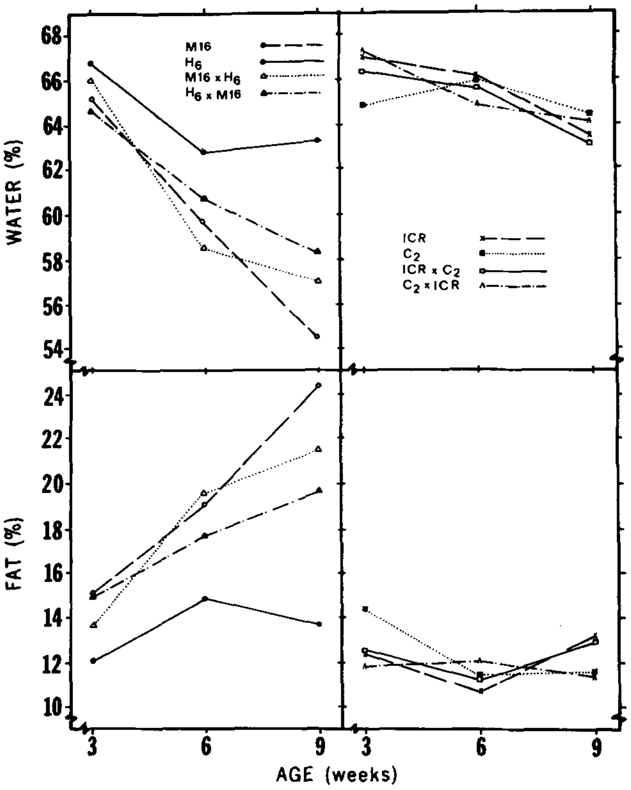

Fig.2. Water and fat percentages for the eight populations at 3, 6 and 9 weeks of age. Standard errors of the means for N = 12 at the respective ages are 0.59, 0.63 and 0.90% for percent water and 0.79, 0.90 and 1.15% for percent fat

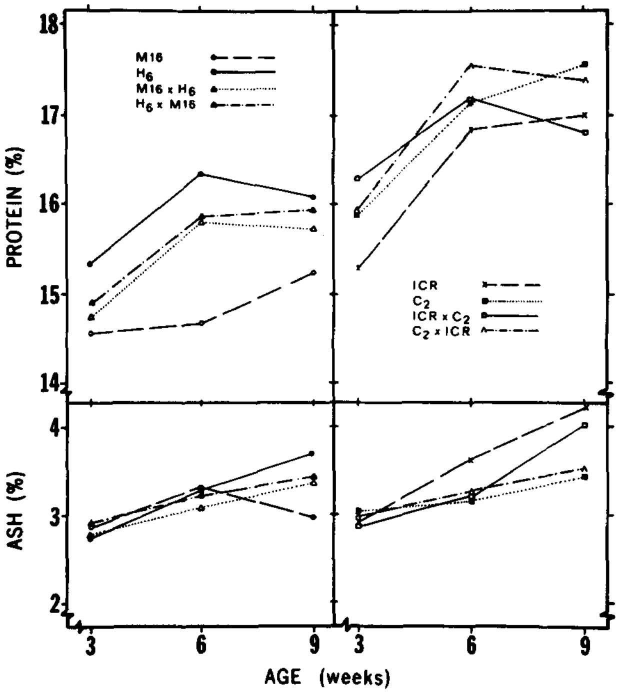

Fig.3. Protein and ash percentages for the eight populations at 3, 6 and 9 weeks of age. Standard errors of the means for N = 12 at the respective ages are 0.25, 0.30 and 0.29% for percent protein and 0.11, 0.13 and 0.13% for percent ash

Significant ($P < .01$) age effects were observed for all traits studied. Feed intake declined slightly in the second age interval for all populations except M16 and C$_2$. The components of gain and the efficiency of each constituent declined sharply ($P < .01$) for all populations in the latter age interval. The M16 population was an exception, showing a relatively high FATG, PROG and CALG from 6 to 9 weeks. Caloric content of the body followed a pattern similar to body weight, increasing to a greater degree from 3 to 6 weeks than from 6 to 9 weeks. Fat percent in the control populations and one of the F$_1$ crosses (ICR × C$_2$) decreased slightly from 3 to 6 weeks and did not change in the reciprocal F$_1$(C$_2$ × ICR). A similar decrease in fat percent in the ICR population, noted by Eisen and Leatherwood (1976), was attributed to standardizing litters to eight mice which minimized competition for milk prior to weaning. In contrast, the selected populations and their F$_1$ crosses increased ($P < .01$) in fat percent from 3 to 6 weeks of age. Fat percent in the M16 population and the F$_1$ crosses of the selected populations increased ($P < .01$) from 6 to 9 weeks but decreased slightly in H$_6$. Water percent was generally inversely related to fat percent. Protein and ash percents in-

Table 2. Population means of feed intake, gains and efficiencies

	Trait[a,b]										
Population	FEED(g)	GAIN(g)	FATG(g)	PROG(g)	CALG(kcal)	ASHG(g)	EFF(%)	FATE(%)	PROE(%)	CALE(%)	ASHE(%)
					3 to 6 weeks						
M16	142.7	22.15	4.16	2.61	54.14	0.63	15.36	2.84	1.82	9.16	0.450
H_6	132.2	15.49	2.27	2.18	33.36	0.47	11.73	1.71	1.65	6.21	0.353
M16 x H_6	144.0	17.33	3.92	2.43	50.62	0.49	12.00	2.70	1.68	8.60	0.340
H_6 x M16	138.3	16.02	2.80	2.21	39.39	0.46	11.56	2.00	1.60	6.97	0.337
ICR	112.7	10.33	0.81	1.52	15.48	0.37	9.13	0.70	1.35	3.35	0.328
C_2	98.4	9.55	0.68	1.42	14.01	0.25	9.75	0.71	1.45	3.56	0.258
ICR x C_2	113.8	10.85	0.90	1.66	17.56	0.31	9.56	0.80	1.47	3.82	0.274
C_2 x ICR	109.9	9.98	1.16	1.64	19.91	0.30	9.03	1.04	1.48	4.42	0.275
S.E.[c]	2.5	0.70	0.28	0.12	2.93	0.03	0.46	0.20	0.09	0.51	0.027
					6 to 9 weeks						
M16	155.9	7.30	3.79	1.47	43.42	0.24	4.60	2.36	0.94	6.68	0.158
H_6	125.5	2.76	0.34	0.57	5.66	0.18	2.15	0.29	0.45	1.15	0.142
M16 x H_6	139.2	4.66	1.58	0.60	17.08	0.18	3.29	1.11	0.42	2.93	0.130
H_6 x M16	130.7	2.60	1.03	0.42	12.60	0.15	2.00	0.76	0.33	2.32	0.114
ICR	97.6	1.43	0.58	0.29	5.46	0.15	1.32	0.54	0.27	1.26	0.135
C_2	106.2	2.89	0.29	0.56	4.98	0.13	2.91	0.31	0.57	1.29	0.129
ICR x C_2	108.5	1.01	0.33	0.21	3.49	0.15	0.95	0.34	0.21	0.05	0.159
C_2 x ICR	101.4	1.52	0.02	0.05	0.08	0.05	1.35	0.03	0.04	0.90	0.037
S.E.[c]	3.3	0.58	0.41	0.11	3.87	0.04	0.44	0.29	0.09	0.69	0.032

[a] EFF, FATE, PROE and ASHE are expressed on a g/g basis and CALE is expressed on a kcal/kcal basis. To express FATE on a kcal/kcal basis, multiply by 9.5/4.06, and to express PROE on a kcal/kcal basis, multiply by 5.65/4.06, where 9.5 = kcal fat/g, 5.65 = kcal protein/g and 4.06 = kcal feed/g.

[b] FEED = feed intake; GAIN, FATG, PROG, CALG and ASHG = gain in body weight, fat, protein, calories and ash, respectively; EFF, FATE, PROE, CALE, ASHE = gain of each constituent divided by feed intake.

[c] Standard error of the mean for N = 12.

creased from 3 to 6 weeks in all populations. Ash percent in M16 declined from 6 to 9 weeks but continued to increase in the other populations. The change in percent protein from 6 to 9 weeks was more variable, with most populations changing relatively little after 6 weeks.

The inverse relationship between the percentages of fat and water on a mean basis was also observed on a within population-age basis ($r = -.86$, $P < .01$). A high negative phenotypic correlation between fat percent and water percent has been observed previously (Lang and Legates 1969; Sutherland et al. 1974). The coefficient of variation of water percent was considerably less than fat percent (3.10 vs 20.43, 3.49 vs 21.50, and 5.10 vs 24.93 at 3, 6 and 9 weeks, respectively). Therefore, for a given sample size, a significant difference in fat percent might not be declared, but would be suggested indirectly by a significant difference in water percent.

Correlated responses to selection at a constant age

Correlated responses to selection in M16 and H_6, taken as a deviation from the appropriate control (M16-ICR and H_6-C_2), and the difference between the selected populations in correlated response [(M16-ICR) - (H_6-C_2)] are displayed in Table 3. The M16 population had a higher ($P < .05$) fat percent than ICR at 3 weeks of age, and H_6 had a lower ($P < .05$) fat percent than C_2, resulting a significant ($P < .01$) differential correlated response in fat percent. Water percent showed a typical inverse relationship to percent fat. There was no evidence of correlated responses for total calories and percentages of protein and ash at 3 weeks.

At 6 and 9 weeks of age, M16 had positive ($P < .01$) correlated responses in body weight, caloric content and fat percent and negative correlated responses in water, protein and ash percents. On a fat-

Table 3. Correlated responses to selection in M16 and H_6 and the differential correlated responses [(M16-ICR) - (H_6-C_2)]

	Linear Contrast								
Trait[a]	M16-ICR			H_6-C_2			(M16-ICR)-(H_6-C_2)		
	3 wk	6 wk	9 wk	3 wk	6 wk	9 wk	3 wk	6 wk	9 wk
BWT(g)	0.70	13.98**	19.23**	2.45**	8.64**	8.13**	-1.74	5.34**	11.11**
CAL(kcal)	4.20	47.26**	81.07**	1.79	22.40**	18.22**	2.41	24.86**	62.85**
WAT(%)	-1.58*	-6.26**	-8.97**	1.94*	-3.15**	-1.12	-3.53**	-3.11*	-7.84**
FAT(%)	2.59*	8.37**	11.23**	-2.37*	3.34*	2.09	4.97**	5.02*	9.14**
PRO(%)	-.72	-2.17**	-1.75**	-.53	-.80	-1.47**	-.18	-1.37*	-.28
ASH(%)	-.01	-.32	-1.24*	-.28	0.12	0.24	0.27	-.45	-1.48**
PRO(%ff)	-.32	-.73	0.60	-1.10*	-.16	-1.21	0.31	-.57	1.82*
ASH(%ff)	0.08	0.01	-.93**	-.41*	0.29	0.37	0.78	-.28	-1.30*

	M16-ICR		H_6-C_2		(M16-ICR)-(H_6-C_2)	
	3-6 wk	6-9 wk	3-6 wk	6-9 wk	3-6 wk	6-9 wk
FEED(g)	29.98**	49.68**	33.73**	27.88**	-3.76	21.79**
GAIN(g)	11.83**	5.87**	5.94**	-.13	5.88**	5.99**
FATG(g)	3.36**	3.22**	1.59**	0.05	1.77**	3.16**
PROG(g)	1.08**	1.18**	0.76**	0.01	0.33	1.18**
CALG(g)	38.66**	37.97**	19.34**	0.68	19.32**	37.28**
ASHG(g)	0.26**	0.10	0.21**	0.06	0.05	0.04
EFF(%)	6.23**	3.27**	1.99**	-.75	4.25**	4.04**
FATE(%)	2.14**	1.82**	1.00**	-.02	1.14*	1.84**
PROE(%)	0.47**	0.67**	0.20	-.12	0.27	0.79**
CALE(%)	5.81**	5.42**	2.64**	-.14	3.16**	5.56**
ASHE(%)	0.12*	0.02	0.09*	0.01	0.03	0.01

*P < .05 , **P < .01.

[a] BWT = body weight; CAL = calories; WAT, FAT, PRO and ASH = percentages of total body water, fat, protein and ash, respectively (%ff = percentage on a fat-free basis); FEED = feed intake; GAIN, FATG, PROG, CALG and ASHG = gain in body weight, fat, protein, calories and ash, respectively; EFF, FATE, PROE, CALE, ASHE = gain of each constituent divided by feed intake.

free basis, H_6 and M16 did not exhibit significant correlated responses in protein and ash percents except for a decrease in ash percent at 9 weeks in M16. Feed intake, weight gain and efficiency in the 3 to 6 and 6- to 9-week intervals were significantly ($P < .01$) greater in M16 than ICR. This was reflected in the increased gains and efficiencies of fat, protein, caloric content and ash in M16. These correlated responses in constituent gains and efficiencies were similar at 6 to 9 weeks, except for ash which was not significant.

The H_6 population exhibited positive ($P < .01$) correlated responses in body weight (direct response at 6 weeks) and caloric content at 6 and 9 weeks. The significant ($P < .05$) increase in fat percent at 6 weeks was not present at 9 weeks. As was the case for M16, the H_6 population showed positive correlated responses from 3 to 6 weeks of age in feed intake, gain efficiency and constituent gains and efficiencies. However, from 6 to 9 weeks, only feed intake was significantly increased in H_6, whereas no significant correlated responses in constituent gains or efficiencies were noted.

The differential correlated responses between M16 and H_6 are reflected in the contrast, (M16-ICR) - (H_6-C_2), presented in Table 3. For body weight, caloric content and fat percent at 6 and 9 weeks of age, this comparison showed significant positive values. Thus, fat percent definitely exhibited a greater positive correlated response to selection in M16 compared to H_6. In general, the correlated responses in constituent gains and efficiencies were markedly larger in M16 than in H_6. The comparisons were particularly striking in the 6- to 9-week interval since, except for feed intake, none of these traits revealed significant responses in H_6.

While the present design does not permit a partitioning of the correlated response to selection for M16 or H_6 into average direct and average maternal genetic effects, the differential correlated response [(M16-ICR) - (H_6-C_2)] can be so partitioned (Table 4). The results indicate that the major cause of the

Table 4. Partitioning of the differential correlated response [(M16-ICR) - (H_6-C_2)] into average direct and average maternal genetic effects

Trait[a]	Average Direct Genetic Effect (M16-ICR)-(H_6-C_2)			Average Maternal Genetic Effect (M16-ICR)-(H_6-C_2)		
	3 wk	6 wk	9 wk	3 wk	6 wk	9 wk
BWT(g)	-2.13	4.48*	16.13**	0.39	0.86	-5.02*
CAL(kcal)	-.84	32.81**	78.83**	3.25	-7.95	-15.97
WAT(%)	-1.45	-6.03**	-8.03**	-2.07	2.92*	0.19
FAT(%)	3.10	7.69**	9.45**	1.86	-2.66	-.31
PRO(%)	-.74	-1.04	0.09	0.56	-.32	-.38
ASH(%)	0.18	-.54	-2.11**	0.09	0.10	0.63*
PRO(%ff)	-.26	0.42	2.35*	1.03	-.99	-.54
ASH(%ff)	0.33	-.29	-2.00	0.17	0.01	0.71
	3-6 wk	6-9 wk		3-6 wk	6-9 wk	
FEED(g)	-1.97	37.40**		-1.79	-15.61*	
GAIN(g)	6.31**	8.56**		-.43	-2.57*	
FATG(g)	3.15**	3.40**		-1.38*	-.24	
PROG(g)	0.52	1.20**		-.20	-.03	
CALG(g)	32.89**	38.35**		-13.57*	-1.06	
ASHG(g)	0.07	-.03		-.02	0.08	
EFF(%)	4.15**	5.73**		0.10	-1.69	
FATE(%)	2.08**	1.88*		-.94*	-.04	
PROE(%)	0.37	0.70*		-.10	0.07	
CALE(%)	5.39**	5.34*		-2.22*	0.22	
ASHE(%)	0.03	0.00		0.00	0.11	

*P < .05 , **P < .01.

[a] BWT = body weight; CAL = calories; WAT, FAT, PRO and ASH = percentages of total body water, fat, protein and ash, respectively (%ff = percentage on a fat-free basis): FEED = feed intake; GAIN, FATG, PROG, CALG and ASHG = gain in body weight, fat, protein, calories and ash, respectively; EFF, FATE, PROE, CALE, ASHE = gain of each constituent divided by feed intake.

differential response between the selected populations was due to average direct genetic effects. Significant average maternal genetic effects for the differential response favored H_6, being most frequent at 3 to 6 weeks, e.g., fat and caloric gain and fat and energetic efficiency. Nagai, Bakker and Eisen (1976) found similar results for postweaning body weights in these populations.

Differences between growth selected and between control populations at a constant age

Direct comparisons between the high growth selected populations (M16-H_6) and between the control populations (ICR-C_2) are given in Table 5. The M16 population was larger than H_6 in body weight, caloric content and fat percent at all three ages, and the magnitude of these differences tended to increase with age. From 3 to 6 weeks of age, the M16 population consumed more feed and had larger gains and efficiencies than H_6. This trend continued from 6 to 9 weeks. The ICR population had a significantly higher body weight than C_2 at all ages. The ICR population also exhibited a higher feed intake and ash percent from 3 to 6 weeks and lower total efficiency and protein efficiency from 6 to 9 weeks.

Partitioning the difference between the selected populations (M16-H_6) into average direct and average maternal genetic effects (Tables 6 and 7) revealed no significant effects at 3 weeks. At 6 and 9 weeks of age and in the two age intervals, average direct genetic effects were generally larger in absolute value than average maternal genetic effects. Differences in average direct genetic effects followed a pattern similar to the overall differences between the selected populations. For example, the M16 population exceeded H_6 for average direct genetic effects in fat, protein and caloric gain and efficiency. A similar pattern was reported for body weights in these populations (Nagai et al. 1976). Average ma-

Table 5. Differences between selected populations and between control populations

Trait[a]	Linear Contrast					
	$M16-H_6$			$ICR-C_2$		
	3 wk	6 wk	9 wk	3 wk	6 wk	9 wk
BWT(g)	1.35	8.62**	15.32**	3.10**	3.28**	4.21*
CAL(kcal)	5.68*	28.74**	74.14**	3.28	3.87	11.29
WAT(%)	-1.72*	-3.15**	-8.75**	1.80*	-.04	-.89
FAT(%)	2.99*	4.25**	10.71**	-1.98	-.77	1.57
PRO(%)	-.77	-1.69**	-.84	-.59	-.32	-.55
ASH(%)	0.14	0.03	-.72**	-.13	0.47*	0.76**
PRO(%ff)	-.31	-1.08	1.55**	-1.09*	-.51	-.27
ASH(%ff)	0.27	0.22	-.34	-.22	0.50*	0.96*
	3-6 wk	6-9 wk		3-6 wk	6-9 wk	
FEED(g)	10.48*	30.38**		14.24**	8.59	
GAIN(g)	6.66**	4.53**		0.78	-1.45	
FATG(g)	1.89**	3.46**		0.12	0.29	
PROG(g)	0.43*	0.91**		0.11	-.27	
CALG(g)	20.78**	37.77**		1.47	0.49	
ASH(g)	0.17**	0.06		0.12*	0.01	
EFF(%)	3.63**	2.45**		-.61	-.40*	
FATE(%)	1.13**	2.07**		-.01	0.22	
PROE(%)	0.16	0.49**		-.10	-.30*	
CALE(%)	2.95**	5.53**		-.22	-.02	
ASH(%)	0.10*	0.02		0.07	0.01	

$^{*}P < .05$, $^{**}P < .01$.

[a] BWT = body weight; CAL = calories; WAT, FAT, PRO and ASH = percentages of total body water, fat, protein and ash, respectively (%ff = percentage on a fat-free basis); FEED = feed intake; GAIN, FATG, PROG, CALG and ASHG = gain in body weight, fat, protein, calories and ash, respectively; EFF, FATE, PROE, CALE, ASHE = gain of each constituent divided by feed intake.

ternal genetic effects tended to favor H_6 for body weight, caloric content, fat and caloric gain and efficiency from 3 to 6 weeks. Few significant differences between the control populations were observed for average direct and average maternal genetic effects. The ICR population had significantly greater average direct genetic effects than C_2 for body weight at 3 and 6 weeks, ash percent at 9 weeks and 3- to 6-week feed intake. The only significant average maternal genetic effect showed ICR to have a lower ash percent than C_2.

Direct heterosis at a constant age

Estimates of direct heterosis in the selected crosses and in the control crosses are listed in Table 8 for the various traits. Percent direct heterosis (difference as a percent of midparent values) for fat percent in the selected crosses was 6.0, 10.1 and 8.2% at 3, 6 and 9 weeks, respectively, but statistical significance was not reached. Water percent showed significant heterosis at 6 weeks of age. Significant levels of direct heterosis were absent, for the most part, for the other traits. The absence of consistent positive heterosis for body weight or gain contrasts with previous reports indicating significant heterosis in these crosses (Bakker et al. 1976; Nagai et al. 1976).

Differences in body constituents per unit change in empty body weight

Regression coefficients of *ln* body constituents on *ln* empty body weight across ages are presented in Table 9. All regression coefficients were highly significant ($P < .01$), and no significant deviations from linearity were observed. Preliminary tests of differences among the within age regression coefficients for each population revealed no significant heterogeneity. The

Table 6. Partitioning the difference between M16 and H_6 and between ICR and C_2 into average direct and average maternal genetic effects for body weight, caloric content and percent body composition

Trait[a]	M16-H_6			ICR-C_2		
	3 wk	6 wk	9 wk	3 wk	6 wk	9 wk
			Average Direct Genetic Effect			
BWT(g)	1.83	9.55**	19.74**	3.96**	5.08**	3.61
CAL(kcal)	4.43	37.31**	92.15**	5.27	4.49	13.32
WAT(%)	-.39	-5.36**	-9.94**	1.06	0.67	-1.90
FAT(%)	1.69	6.22**	12.51**	-1.41	-1.47	3.05
PRO(%)	-.94	-1.70*	-1.06	-.18	-.65	-1.15
ASH(%)	-.02	-.12	-.80**	-.21	0.43	1.31*
PRO(%ff)	-.77	-.62	1.75*	-.51	-1.04	-.61
ASH(%ff)	0.03	0.11	-.35	-.29	0.41	1.65**
			Average Maternal Genetic Effect			
BWT(g)	-.47	-.93	-4.42**	-.86	-1.79	0.60
CAL(kcal)	1.26	-8.57	-18.01*	-1.99	-.62	-2.03
WAT(%)	-1.33	2.21*	1.20	0.74	-.71	1.00
FAT(%)	1.30	-1.97	-1.79	-.57	0.69	-1.49
PRO(%)	0.16	0.01	0.21	-.41	0.33	0.59
ASH(%)	0.16	0.14	0.08	0.08	0.04	-.54**
PRO(%ff)	0.46	-.46	-.20	0.37	-.53	0.34
ASH(%ff)	0.24	0.10	0.01	-.58	0.09	-.69**

*P < .05 , **P < .01.

[a] BWT = body weight; CAL = calories; WAT, FAT, PRO and ASH = percentages of total body water, fat, protein and ash, respectively (%ff = percentage on a fat-free basis).

Table 7. Partitioning the difference between M16 and H_6 and between ICR and C_2 into average direct and average maternal genetic effects for feed intake, gains and efficiencies

	Average Direct Genetic Effect				Average Maternal Genetic Effect			
Trait[a]	M16-H_6		ICR-C_2		M16-H_6		ICR-C_2	
	3-6 wk	6-9 wk	3-6 wk	6-9 wk	3-6 wk	6-9 wk	3-6 wk	6-9 wk
FEED(g)	16.17**	38.86**	18.14**	1.46	-5.69	-8.47	-3.90	7.13
GAIN(g)	7.95**	6.59**	1.65	-1.97	-1.30	-2.06*	-.88	0.51
FATG(g)	3.01**	4.00**	-.14	0.60	-1.12*	-.55	0.26	-.31
PROG(g)	0.66*	1.09**	0.13	-.11	-.22	-.18	-.03	-.16
CALG(g)	32.01**	42.24**	-.88	3.90	-11.23*	-4.48	2.34	-3.41
ASHG(g)	0.19*	0.09	0.12	0.12	-.03	-.03	-.01	-.11
EFF(%)	4.06**	3.75**	-.08	-1.98*	-.43	-1.30*	-.53	0.39
FATE(%)	1.82**	2.41**	-.26	0.54	-.69*	-.34	0.24	-.31
PROE(%)	0.25	0.58**	-.12	-.13	-.08	-.09	0.02	-.17
CALE(%)	4.57**	6.15**	-.81	0.81	-1.63*	-.61	0.60	-.84
ASHE(%)	0.10	0.03	0.06	0.13	0.00	-.02	0.00	-.10

*P < .05 , **P < .01.

[a] FEED = feed intake; GAIN, FATG, PROG, CALG and ASHG = gain in body weight, fat, protein, calories and ash, respectively; EFF, FATE, PROE, CALE, ASHE = gain of each constituent divided by feed intake.

Table 8. Direct heterosis in the selected crosses and in the control crosses

	Selected Crosses			Control Crosses		
Trait[a]	3 wk	6 wk	9 wk	3 wk	6 wk	9 wk
BWT(g)	1.75**	-1.12	-2.18	0.13	1.68*	0.92
CAL(kcal)	4.62**	4.45	-1.17	-.56	5.65	1.15
WAT(%)	-.67	-1.66*	-1.23	0.90	-.72	-.27
FAT(%)	0.82	1.72	1.56	-1.27	0.63	0.16
PRO(%)	-.13	0.37	0.17	0.53*	0.40	-.20
ASH(%)	0.03	-.11	0.09	-.01	-.15	-.06
PRO(%ff)	-.05	0.85*	0.55	0.33	0.60	-.28
ASH(%ff)	0.01	-.04	0.20	-.07	-.14	-.08

	3-6 wk	6-9 wk	3-6 wk	6-9 wk
FEED(g)	3.75	-5.75	6.27*	2.99
GAIN(g)	-2.14*	-1.40*	0.49	-.90
FATG(g)	0.14	-1.53	0.28	-.53
PROG(g)	-.08	-1.02**	0.18	-.60*
CALG(g)	1.25	-19.41*	3.98	-6.86
ASHG(g)	-.08	-.10	0.00	-.07
EFF(%)	-1.75**	-.74	-.14	-.96*
FATE(%)	0.07	-.79	0.21	-.48
PROE(%)	-.09	-.64**	0.07	-.59**
CALE(%)	0.19	2.57	0.67	-1.59
ASHE(%)	-.06	-.01	-.02	-.01

*P < .05 , **P < .01.

[a] BWT = body weight; CAL = calories; WAT, FAT, PRO and ASH = percentages of total body water, fat, protein and ash, respectively (%ff = percentage on a fat-free basis); FEED = feed intake; GAIN, FATG, PROG, CALG and ASHG = gain in body weight, fat, protein, calories and ash, respectively; EFF, FATE, PROE, CALE, ASHE = gain of each constituent divided by feed intake.

Table 9. Regression coefficients (b) of *ln* body constituent weight on *ln* empty body weight and coefficients of determination (r^2) calculated for each population[a]

	Trait[b]									
	ℓn WAT		ℓn FAT		ℓn PRO		ℓn CAL		ℓn ASH	
Population	b	r^2	b	r^2	b	r^2	b	r^2	b	r^2
M16	0.85	0.99	1.38	0.93	1.02	0.99	1.28	0.95	1.03	0.92
H_6	0.92	0.98	1.26	0.84	1.04	0.98	1.16	0.93	1.30	0.97
M16 x H_6	0.81	0.98	1.59	0.90	1.07	0.96	1.41	0.96	1.18	0.94
H_6 x M16	0.86	0.98	1.33	0.85	1.07	0.97	1.24	0.93	1.14	0.86
ICR	0.93	0.98	1.07	0.61	1.16	0.97	1.12	0.85	1.51	0.90
C_2	0.99	0.99	0.71	0.43	1.12	0.98	0.90	0.84	1.15	0.90
ICR x C_2	0.95	0.99	0.99	0.69	1.04	0.96	1.02	0.90	1.29	0.87
C_2 x ICR	0.94	0.99	1.10	0.63	1.11	0.97	1.09	0.88	1.18	0.90

[a] All regression coefficients are significant at P < .01.

[b] ℓn WAT, ℓn FAT, ℓn PRO, ℓn ASH = natural logarithm of water, fat, protein and ash weights, respectively; ℓn CAL = natural logarithm of calories.

Table 10. Linear contrasts among the regressions of *ln* body constituent weight on *ln* empty body weight

	Trait[a]				
Linear Contrast	ℓn WAT	ℓn FAT	ℓn PRO	ℓn CAL	ℓn ASH
M16-ICR	-.07*	0.31*	-.14**	0.16	-.47**
H_6-C_2	-.07*	0.55**	-.07	0.26**	0.16
(M16-ICR)-(H_6-C_2)	0.00	-.24	-.07	-.10	-.63**
M16-H_6	-.07*	0.12	-.02	0.11	-.26**
ICR-C_2	-.07*	0.36*	0.04	0.22*	0.36**
Average direct genetic (M16-H_6)	-.01	-.14	-.02	-.05	-.30*
Average direct genetic (ICR-C_2)	-.08	0.47	0.10	0.29*	0.24
Average direct genetic (sel.-con.)	0.07	-.61	-.12	-.34	-.54*
Average maternal genetic (M16-H_6)	-.06*	0.26	0.00	0.16	0.04
Average maternal genetic (ICR-C_2)	0.01	-.11	-.06	-.07	0.12
Average maternal genetic (sel.-con.)	-.07	0.37	0.06	0.23	-.08
Direct heterosis (selected)	-.05*	0.14	0.03	0.11	-.01
Direct heterosis (control)	-.02	0.15	-.06	0.05	-.09
Direct heterosis (sel.-con.)	-.03	-.01	0.09	0.06	0.08

$^{*}P < .05$, $^{**}P < .01$.

[a] ℓn WAT, ℓn FAT, ℓn PRO, ℓn ASH = natural logarithm of water, fat, protein and ash weights, respectively; ℓn CAL = natural logarithm of calories.

linearity of the regression coefficients across ages and the homogeneity of the regression coefficients within ages are essential assumptions for further significance tests.

Selected linear contrasts among the regression coefficients across ages are shown in Table 10. Both M16 and H_6 exhibited significant positive correlated responses in rate of fat increase relative to empty body weight. The M16 population responded negatively in water, protein and ash deposition per unit increase in empty body weight, while caloric content was not altered significantly. The H_6 population evinced a positive correlated response in caloric value per unit increase in empty body weight. There was no differential correlated response except for the difference in ash.

Direct comparisons of M16 and H_6 revealed that M16 had a significantly lower increase in water and ash relative to empty body weight. The ICR population had a significantly smaller regression coefficient for water than C_2, but larger regressions for ash, fat and caloric content. The latter contrasts were greatly affected by the extremely small regression of *ln* fat weight on *ln* empty body weight in the C_2 population. Partitioning the regression contrasts into average direct and average maternal genetic effects for the selected populations did not reveal any consistent pattern. In general, direct heterosis contrasts in the regressions did not exhibit significance.

Discussion

Selection for rapid growth rate in two populations of mice (M16, selected for increased postweaning gain and H_6, selected for large 6-week body weight) has led to distinctly different growth patterns in the components of body weight. The findings may be summarized as follows. Fat percent at 3 weeks of age showed a positive correlated response in M16 and a negative correlated response in H_6. When compared to their respective controls at constant ages of 6 and 9 weeks, body weight increased much more dramatically in M16 (57 % and 69 %) than in H_6 (40 % and 34 %). This was reflected in considerably higher increases for M16 in body fat, protein and ash weight and caloric content. The correlated responses in fat percent were about 2.7 and 4.7 times greater in M16 than in H_6 at 6 and 9 weeks, respectively. In contrast, differential correlated responses in protein and ash percents were relatively small.

Another approach to evaluating correlated responses in body fat involves measuring the accumulation of total body fat relative to overall body growth (Hayes and McCarthy 1976). When *ln* fat weight was regressed on *ln* empty body weight across ages, both M16 and H_6 evinced positive correlated responses in rate of fat deposition relative to empty body weight. However, the between population difference in the correlated response [(M16-ICR) - (H_6-C_2)] was not significant for this trait, nor was the direct contrast between M16 and H_6. Thus it would appear that selection has changed degree of fatness relative to body weight to the same extent in both selected populations.

The M16 population actually decreased in *ln* protein and *ln* ash weight per unit increase in *ln* empty body weight, when compared to the ICR control. This may be a manifestation of the disproportionately large contribution of fat to empty body weight in M16. In contrast, no such correlated responses were found in H_6.

The differential pattern in correlated responses between the selected populations also was apparent from a comparison of gains and efficiencies in the components of growth over a fixed age interval. From 3 to 6 weeks, fat and caloric gain and efficiency exhibited a higher correlated response in M16 than in H_6. Protein and ash gain were also higher in M16, although not significantly. The results from 6 to 9 weeks distinguished the growth pattern of the lines more definitively. In the H_6 population, feed intake remained about the same as in the 3- to 6-week period and gains of body constituents were negligible. The M16 population continued to demonstrate positive correlated responses in gains and efficiencies of fat, protein and caloric value. The absence of continued gain in ash may reflect a diminution of skeletal growth beyond 6 weeks of age. The greater feed intake in M16 than in H_6 during this interval may indicate differences in appetite as well as a higher maintenance requirement for the larger body size of M16.

Reports from earlier selection generations had noted an increased fat percent in M16 (Timon, Eisen and Leatherwood 1970) and no appreciable change in fat percent in H_6 (Lang and Legates 1969). Romsos and Leveille (1974) reported similar results for these populations. The positive correlated response observed in H_6 for fat percent at 6 weeks of age in the present study may have been the result of continued selection. However, a recent experiment showed no significant fat percent increase in H_6 (Eisen, unpublished), suggesting that if there has been any increase in fat percent, it is probably relatively small.

There are several reports in the literature of selection for increased body weight or postweaning gain in mice, where correlated responses in body composition have been measured (see reviews by Sutherland et al. 1974; Eisen 1974, 1976). Fowler (1958) compared the fat percentages of two lines of mice selected for increased rate of growth. There was a clear difference in fat percentage between the two lines. Biondini, Sutherland and Haverland (1968) reported that of three strains of mice selected for increased growth rate, two showed a positive change in fat percent while a third did not. Robinson and Bradford (1969) found an increased percent fat due to selection for rapid postweaning gain. Selection for high body weight in more recent studies has also demonstrated increased fat percentages (Bakker 1974; Hayes and McCarthy 1976).

The positive correlated response in total body fat deposition per unit increase in empty body weight agrees with a study by Clarke (1969). Hayes and McCarthy (1976) found that a line selected for increased 10-week body weight showed a positive correlated response in this trait, whereas there was no significant increase in fat in a line selected for increased 5-week body weight.

Clearly, the majority of populations selected for increased body size have exhibited positive correlated responses in fat percent at a constant age. In the present experiment substantial differences in the correlated response for fat percent were found between M16 and H_6. Undoubtedly the presence of different alleles in the base population could have caused this effect (Fowler 1958). At 6 weeks of age, the only major differences observed between the controls were for body weight, feed intake and percent ash. Differences in physiological age at the time of selection may account for some of the differences in fat deposition (Eisen 1974). Genetic drift might also be a factor (Falconer 1973; Eisen 1976), particularly if genes with divergent effects on fat deposition at a constant age were at a very low frequency. Investigating genetic drift as a possible factor would require the examination of several replicate selected lines, which were not available in the present study. Although replicate differences in fat percent due to drift are feasible, they have not been investigated extensively. Eisen and Bandy (1976) reported no replicate differences in fat percent in four selection treatments involving direct or correlated responses in body weight. Genotype by diet interaction could conceivably result in a differential response in fat percent (Eisen 1976). Since H_6 and M16 were both selected in the same laboratory using an identical postweaning diet, this would not appear to be a likely factor, although it obviously cannot be eliminated entirely. Fowler (1958) speculated that selection for postweaning gain and 6-week weight might yield different correlated responses in fat or that populations differing in fat may be at different stages of selection. The latter factor seems improbable for the present study since both lines have undergone long-term selection and have essentially plateaued. The validity of the former suggestion depends, in part, on the genetic correlation between 6-week body weight and 3- to 6-week postweaning gain, which is high in these populations [estimates of 0.75 and 1.10 in the ICR (Hanrahan and Eisen 1973; Rutledge, Eisen and Legates 1973) and 0.90 in the C_2 (Young and Legates 1965)]. Assuming a genetic correlation of 0.9, less than 20 percent of the variation in the two traits would be operating independently of each other. Although this amount of independence could explain a difference in correlated responses, inspection of the reports in the literature does not reveal any trend as to differential fat percent response in weight-selected compared with postweaning gain-selected lines.

Regardless of the factor(s) which have led to the genetic differences between the selected populations in fat deposition and growth pattern, these populations are of value as models in growth studies from two standpoints: 1) to determine differences in physiolo-

Table 11. Comparison of means of the selected populations (M16, H_6) and their reciprocal crosses ($\bar{F}_1$) for measures of total body fat

	FAT (%)			
Population	3 wk	6 wk	9 wk	b[a]
M16	15.0 ± 1.0	19.3 ± 1.3	24.3 ± 1.5	1.40 ± .12
$\bar{F}_1$[b]	14.3 ± .6	18.6 ± .7	20.5 ± .8	1.46 ± .07
H_6	12.0 ± .8	14.8 ± .9	13.6 ± 1.2	1.26 ± .10
% Heterosis[c]	6.0	10.1	8.2	9.8
	FAT (g)			ℓn fat wt at constant ℓn body wt[d]
M16	2.14 ± .17	6.60 ± .41	10.55 ± .55	1.50 ± .05(4.48)
$\bar{F}_1$[b]	2.22 ± .10	5.67 ± .21	7.17 ± .34	1.46 ± .03(4.31)
H_6	1.61 ± .14	3.95 ± .28	3.87 ± .41	1.21 ± .04(3.35)
% Heterosis[c]	18.4	7.5	-.6	7.7

[a] Regression of ℓn fat weight on ℓn empty body weight.

[b] Mean of M16 x H_6 and H_6 x M16.

[c] $\bar{F}_1$ minus midparent mean as a percent of midparent mean.

[d] Constant ℓn body weight = ℓn 25 g; means in parentheses are in grams.

gical and metabolic patterns, particularly in fat development and protein synthesis and 2) to ultimately evaluate the regulatory and/or structural genes that may be responsible for these differences.

The M16 population exhibited hyperglycemia and an increased rate of fatty acid synthesis in the liver when compared with ICR, whereas the H_6 and C_2 populations did not differ in these characteristics (Romsos and Leveille 1974). Our yet unpublised findings indicate considerable differences in adipose tissue cellularity between the selected populations. Whereas M16 had developed greater fat cell volume and cell number in gonadal fat pad tissue relative to ICR, correlated responses in H_6 were apparent for fat cell number only. In addition, the differential correlated responses were greater in M16 for both of these traits. Thus, preliminary data suggest that M16 and H_6 differ in lipogenic activity and adipose cellularity.

The partitioning of correlated response differences between M16 and H_6 into average direct and average maternal genetic effects for body composition and energetic efficiency traits agrees with previous findings regarding body weights and weight gains (Bakker et al. 1976; Nagai et al. 1976); i.e., that average direct genetic effects favoring M16 provided the major difference between the selected populations and that average maternal genetic effects were of relatively minor importance.

The absence of significant direct heterotic effects for most postweaning traits is difficult to explain. It almost certainly is related to the lack of heterosis for body weight and a slight negative heterosis for weight gain. However, there was a tendency, although nonsignificant, for total body fat content to exhibit heterosis. This trend is summarized in Table 11 for several measures of total body fat. At 3 and 6 weeks of age, mean fat weight and fat percent of the reciprocal crosses of the selected populations were much closer to M16, the population with the higher fat content. Fat deposition per unit increase in *ln* body weight and *ln* fat weight at a constant *ln* body weight (*ln* 25g) provided a similar result. Although more definitive data are needed, these results suggest that rate of fat deposition was partially controlled by genes showing directional dominance. It is well documented that body weight exhibits directional dominance in the mouse (Roberts 1965), so that the existence of directional dominance in fat content, a component of body weight, is not surprising.

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