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Correlated Responses in Growth and Body Composition of Replicated Single-Trait and Index Selected Lines of Mice*

E.J. Eisen and T. Bandy

Department of Animal Science, North Carolina State University, Raleigh, North Carolina (USA)

Summary. Correlated responses in growth, body composition and efficiency were evaluated in lines of mice selected in the following ways: $W^+T_i^\circ$, increased six-week body weight (WT6); $W^\circ T_i^+$, increased six-week tail length (TL6); $W^+T_i^-$, increased WT6 and decreased TL6; $W^-T_i^+$, decreased WT6 and increased TL6; M16, increased three-to six-week postweaning gain (PWG). Each of the first four selection treatments had two replicate lines (i = 1, 2) selected for 13 generations and the fifth treatment had one line selected for 30 generations. All lines were derived from a randombred ICR albino population which served as a control. Additional traits studied were three-week body weight and tail length, postweaning gain in tail length, percent body composition (ash, fat, moisture and protein) at six weeks of age, and three-to six-week feed consumption (CONS) and efficiency (EFF = PWG/CONS). Efficiency of body constituent gains (ash, fat, protein and caloric value) were determined by dividing each constituent by CONS. Relative to selection treatments, replicate variation in the array of traits was small and was primarily attributable to the effects of genetic drift; more frequent significant replicate differences among traits in W^+T^- were associated with a replicate difference in cumulative selection differentials. Selection for different criteria involving WT6 and TL6 did not change the allometric relationship between tail length and body weight in the three-to six-week age interval. The significant divergence between W^+T° and $W^\circ T^+$ and between W^+T^- and W^-T^+ was as expected for WT6 and TL6. Significant asymmetry of selection response between W^+T^- and W^-T^+ for WT6 and TL6 was attributed to maternal effects. In agreement with theory, antagonistic index selection generally yielded smaller genetic responses than single trait selection. Positive correlated responses in CONS and EFF were found for M16 and W^+T°. Significant correlated changes in CONS (positive in $W^\circ T^+$ and negative in W^-T^+) were not accompanied by a significant change in EFF. In contrast, W^+T^- evinced an increased EFF and no change in CONS. Percent fat increased significantly in W^+T° and M16. For W^+T°, W^+T^- and M16, an increased energetic, fat and ash efficiency was observed, whereas M16 exhibited a positive increment in protein efficiency as well. Among selection treatment means, there were high positive correlations between WT6 and fat weight, protein weight, percent fat, CONS and EFF and a high negative correlation between WT6 and percent protein.

Introduction

Selection for a quantitative character such as body weight is known to result in correlated responses in a variety of growth related traits. Nevertheless, there remains a paucity of information on replicate variability in correlated selection responses and almost no data on correlated responses in lines selected for an index involving body weight and other measures of growth. The objectives of the present paper were to explore the correlated responses in body composition and energetic efficiency and to evaluate the replicate variability in lines of mice which had been selected for six-week body weight, six-week tail length or antagonistic indexes involving body weight and tail length. Ruthledge, Eisen and Legates (1974) have previously reported correlated responses and replicate variability in these lines for several morphological traits.

Materials and Methods

Correlated responses were analyzed for five selection treatments. The first four treatments, each replicated twice, constituted a selection experiment designed to find the realized genetic correlation between six-week body weight and six-week tail length (Rutledge, Eisen and Legates 1973). The lines were selected in the following eay: $W^+T_i^\circ$, increased six-week body weight; $W^\circ T_i^+$, increased six-week tail length; $W^+T_i^-$, increased six-week body weight and decreased six-week tail length; and $W^-T_i^+$, decreased six-week body weight and increased six-week tail length, where i = 1, 2 identifies replicate lines for a particular selection treatment. When describing the average effect of a selection treatment, the subscript will be omitted. Individual selection was practiced in each replicate line through generation nine. Ten males, representing at least eight full-sib families, and 20 females were selected and mated randomly in a hierarchical arrangement of one male with two females. From generations 10 to 13, within full-sib family selection was adopted to reduce the rate of inbreeding; 12 single-pair matings per replicate were

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Table 1. Total number of litters and males and females sampled in each line

Line	Litters	Males	Females	Total
$W^+T_1^0$	10	20	17	37
$W^+T_2^0$	9	19	19	38
$W^0T_1^+$	10	19	19	38
$W^0T_2^+$	9	19	17	36
$W^+T_1^-$	9	19	19	38
$W^+T_2^-$	10	18	18	36
$W^-T_1^+$	13	22	23	45
$W^-T_2^+$	13	25	26	51
M16	10	20	19	39
ICR Control	10	19	19	38
Total	178	200	196	396

Table 2. Summary of the traits and their codes

Trait	Code
Three-week weight (g)	WT3
Six-week weight (g)	WT6
Postweaning gain in body weight (three to six weeks) (g)	PWG
Three-week tail length (cm)	TL3
Six-Week tail length (cm)	TL6
Postweaning gain in tail length (three to six weeks) (cm)	PWT
Feed consumption (g)	CONS
Efficiency = PWG/CONS (%)	EFF
Percent ash	%ASH
Percent fat	%FAT
Percent moisture	%MOIST
Percent protein	%PROT
Percent ash (fat-free)	%A-FF
Percent protein (fat-free)	%P-FF
Ash efficiency (%)	A-EFF
Fat efficiency (%)	F-EFF
Protein efficiency (%)	P-EFF
Energetic efficiency (%)	E-EFF

made in these generations. The fifth selection treatment involved a line (M16) selected within full-sib families for 30 generations for postweaning weight gain from three to six weeks of age (Hanrahan, Eisen and Legates 1973; Eisen 1975). All of the above lines originated from the ICR albino randombred population (Eisen and Hanrahan 1974), which was used as a control in the present experiment.

Mice were sampled contemporaneously from each of two adjacent generations in each line. Generations 12 and 13 were used for the $W^+T_1^0$, $W^0T_1^+$, $W^+T_1^-$ and $W^-T_1^+$ lines and generations 29 and 30 for M16. From each line, five to eight parental pairs were randomly chosen in each generation to produce second litter progeny, from which two mice of each sex were randomly sampled. The generation effect will henceforth be designated as an experiment effect. The allotment of mice shown in Table 1 indicates that 17 to 26 individuals per line-sex subgroup were analyzed, giving a total of 396 mice.

The management and data collection procedures were identical for all lines over both experiments. A detailed description of environmental control of laboratory conditions and husbandry procedures has been given by Rutledge et al. (1973). Dams were checked for litters daily at 4:30 p.m. Dams and their litters received Purina Mouse Chow *ad libitum*. Within one day after birth, litters were standardized to four randomly chosen mice of each sex. At 12 days of age, mice were individually tow-clipped for identification. Litters were weaned at three weeks of age and the randomly sampled mice were placed in individual cages.

Data collection on live mice commenced at three weeks of age and continued every three days thereafter until six weeks of age. The traits measured in this interval were body weight and feed consumption to the nearest 0.1 g and tail length to the nearest 0.1 cm. These mice were fed Purina Lab Chow *ad libitum*, with a gross energy of 4.06 kcal/g as determined by direct bomb calorimetry. All mice were killed at six weeks of age to estimate body composition. The gastro-intestinal tract was excised, flushed and damp dried. Empty body weight was defined as weight of the body plus the empty tract. The mice were frozen at -18°C until used for analysis. Whole body composition of moisture, fat, ash and protein was determined as in Eisen and Leatherwood (1976).

The traits analyzed in the present study are listed in Table 2. Percent body composition was calculated by dividing constituent weight by empty body weight. Ash and protein were also obtained as a percent of fat-free weight. The efficiencies for the body components during the test period (three to six weeks of age) were estimated in experiment 2 only. A male and female were randomly sampled from each litter of experiment 2 to be killed at weaning. Three-week old mice were pooled into line-sex subgroups and body composition analyses were performed on each subgroup. Postweaning gain of a constituent was estimated by subtracting the appropriate subgroup mean three-week constituent weight from the individual's six-week constituent weight. These constituent gains were not tabulated, but were used to calculate the efficiency of gain in each component. Efficiency of ash, fat and protein gain were computed by dividing the postweaning gain in each constituent during the three-week test period by feed consumption. Energetic efficiency was estimated as

$$\frac{(\text{protein gain} \times 5.65\,\text{kcal/g}) + (\text{fat gain} \times 9.45\,\text{kcal/g})}{\text{feed consumption} \times 4.06\,\text{kcal/g}}.$$

The statistical model for the analyses of variance was as follows:

$$Y_{ijklm} = \mu + E_i + P_j + S_k + L_{l(ij)} + (EP)_{ij} + (ED)_{ik} + (PS)_{jk} + (EPS)_{ijk} + e_{ijklm},$$

where Y_{ijklm} = an observation on the m^th^ mouse of the $(i_{jkl})^{th}$ subgroup, μ = general mean, E_i = fixed effect of the i^th^ experiment, P_j = fixed effect of the j^th^ line, S_k = fixed effect of the k^th^ sex, $L_{l(ij)}$ = random effect of the

l^{th} litter nested within the i^{th} experiment and j^{th} line, $(EP)_{ij}$, $(ES)_{ik}$, $(PS)_{jk}$ and $(EPS)_{ijk}$ were respective interactions and e_{ijklm} = random error effect. Experiment, line and experiment by line mean squares were tested by the litter mean square, whereas all other sources of variation were tested by the error mean square. The model was fitted by the method of least squares for unequal subclass numbers. In addition to conducting a number of mutually orthogonal contrasts involving lines, several non-orthogonal linear contrasts were made. These included comparisons of all lines with the ICR control, using Dunnett's multiple comparison procedure, and Dunn's procedure for specific non-orthogonal contrasts (Kirk 1968).

Results

Age trends

In general, replicates were very similar in their pattern of growth in body weight and in tail length (Figs. 1 and 2, respectively). While sex differences in elevation of the curves are apparent, the line differences in growth were similar for males and females. The M16 line exceeded all others in body weight from three to six weeks, and this difference increased with age. The growth rate of W^-T^+ was the lowest of the six selection treatments. Two distinct trends are apparent in the growth curves. Around 33 days of age, the slopes of the ICR Control, W^0T^+, and W^-T^+ decreased, whereas the slopes of the curves of M16, W^+T^0, and W^+T^- continued unabated. Unlike body weight, distinct line differences in tail length appeared to have been established by weaning, which did not increase substantially by six weeks of age. As might be expected, the W^0T^+ treatment had the longest tails while W^+T^- had the shortest.

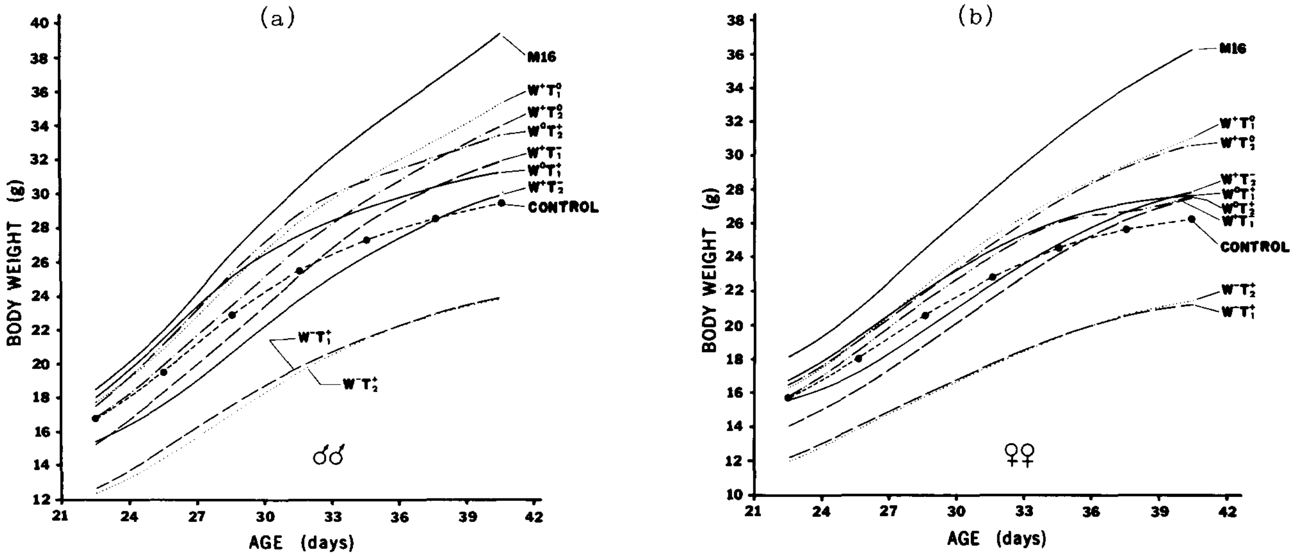

Fig.1. Body weight growth curves for each line, averaged over experiments: a) Males, b) Females

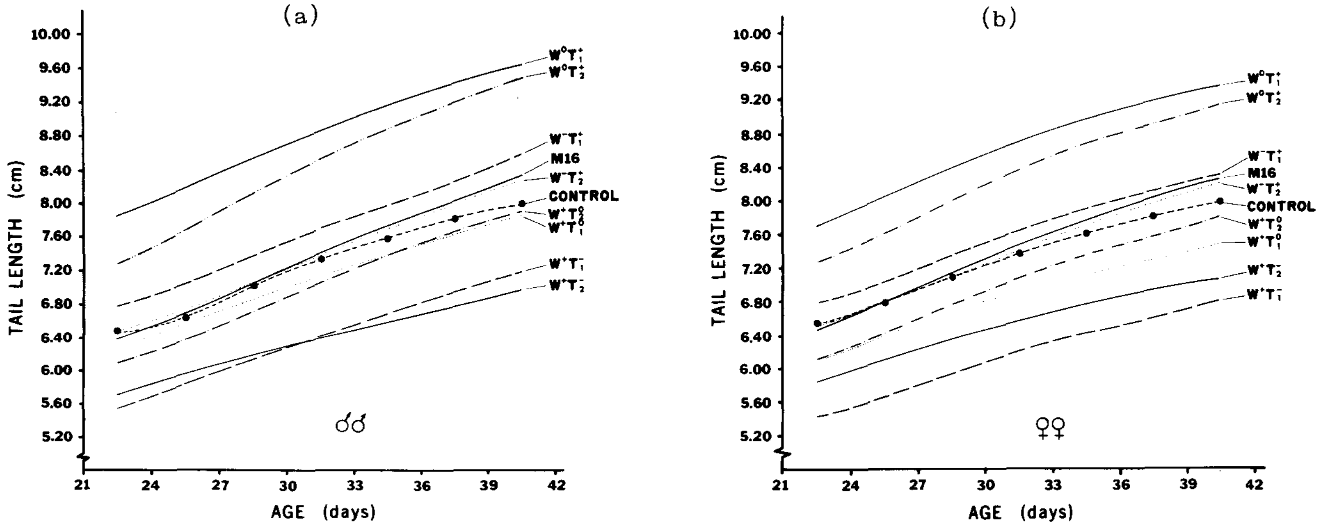

Fig.2. Tail length growth curves for each line, averaged over experiments: a) Males, b) Females

Table 3. Regression coefficients of *ln* tail length on *ln* body weight, adjusted for experiment and sex effects, and line differences in the allometric regression coefficients

Regression		Comparison	
Line	b ± S.E.[a]	Contrast	Difference ± S.E.[b]
$W^+T_1^o$	.291 ± .013	W^+T^o - C	-.009 ± .051
$W^+T_2^o$	.369 ± .008	W^oT^+ - C	.023 ± .050
$W^oT_1^+$	.350 ± .012	W^+T^- - C	-.016 ± .051
$W^oT_2^+$	.374 ± .011	W^-T^+ - C	.016 ± .048
$W^+T_1^-$	.337 ± .009	M16 - C	.029 ± .053
$W^+T_2^-$	.309 ± .012	W^+T^o - W^oT^+	-.032 ± .051
$W^-T_1^+$	.355 ± .010	W^+T^- - W^-T^+	-.032 ± .049
$W^-T_2^+$	.354 ± .007	W^+T^o - W^+T^-	.007 ± .053
M16	.368 ± .010	W^oT^+ - W^-T^+	.008 ± .046
ICR Control	.339 ± .012	W^oT^+ - W^+T^-	.039 ± .052
		W^oT^+ - M16	-.045 ± .054

[a] All regression coefficients (b) are significant at $P < .01$

[b] None of the differences are significant

Since different selection criteria involving growth in tail length and body weight were employed in each selection treatment, it was of interest to determine if the allometric relationship between the two characters within a selection treatment might have changed during the course of selection. Concurrent measurements of tail length and body weight taken every three days from three to six weeks of age were used to calculate the regression of *ln* tail length on *ln* body weight within each line, adjusted for experiment and sex effects (Table 3). No significant differences among regression coefficients were evident for either replicates or selection treatments.

Linear contrasts among line means

Least squares means for each line, averaged over sexes and experiments, are given in Table 4 for live traits and Table 5 for body composition traits. The analyses of variance revealed that line effects were significant ($P < .01$) for all traits investigated except %P-FF. Experiment and sex effects were significant for most traits. Experiment by line interactions were not important. Significant sex by line interactions, where they occurred, appeared to be the result of larger line differences in males than in females.

Tables 6 and 7 list the orthogonal contrasts for live and body composition measurements, respectively. Males significantly exceeded females for most traits. Contrasts 3 to 6 tested replicate differences. No significant replicate effects were observed for six-week body weight and six-week tail length, the primary traits involved in selection. Significant replicate differences were found in W^OT^+ and W^+T^- for PWG and PWT. The W^+T^- treatment also had replicate differences in seven traits associated with body composition or efficiency. The remaining selection treatments did not demonstrate significant replicate effects for body composition or efficiency-related traits; notably, replicate differences in %FAT were absent for all four selection treatments. Of the 72 replicate comparisons, 13 were significant, but nine of these were associated with W^+T^-.

For all live traits measured, the two antagonistic index treatments diverged (contrast 7), and usually

Table 4. Least-squares means for lines: live traits

Line	Trait							
	WT3	WT6	PWG	TL3	TL6	PWT	CONS	EFF
$W^+T_1^o$	16.08	34.14	18.06	6.08	7.80	1.72	136.67	13.26
$W^+T_2^o$	15.63	33.10	17.48	6.00	8.02	2.03	135.90	12.87
$W^oT_1^+$	16.13	29.96	13.88	7.61	9.54	1.93	127.47	10.90
$W^oT_2^+$	15.38	31.28	15.90	7.11	9.45	2.34	133.31	11.86
$W^+T_1^-$	13.74	30.41	16.67	5.39	7.11	1.72	123.34	13.55
$W^+T_2^-$	14.79	29.45	14.65	5.70	7.13	1.44	122.21	12.16
$W^-T_1^+$	11.74	22.54	10.79	6.72	8.53	1.81	108.19	9.96
$W^-T_2^+$	11.31	22.81	11.50	6.47	8.39	1.92	111.62	10.33
M16	17.15	38.99	21.84	6.32	8.42	2.10	145.71	15.06
ICR Control	15.22	28.47	13.25	6.40	8.08	1.68	122.71	10.80
Range of S.E.M.[a]	.35-.42	.43-.51	.38-.46	.10-.12	.10-.12	.07-.08	2.04-2.43	.30-.40

[a] Standard error of mean

Table 5. Least-squares means for lines: body composition and constituent efficiencies

Line	Trait									
	%ASH	%FAT	%MOIST	%PROT	%A-FF	%P-FF	A-EFF	F-EFF	P-EFF	E-EFF
$W^+T_1^o$	2.68	7.48	68.57	17.74	3.01	19.94	0.39	0.72	2.41	5.02
$W^+T_2^o$	2.94	7.10	68.95	18.02	3.27	20.04	0.41	0.41	2.37	4.24
$W^oT_1^+$	3.11	6.97	68.91	18.40	3.44	20.34	0.38	0.13	2.23	3.39
$W^oT_2^+$	2.96	6.38	69.42	18.20	3.27	20.10	0.41	0.38	2.43	4.27
$W^+T_1^-$	2.31	6.36	68.21	18.25	2.60	20.56	0.39	0.87	2.51	5.51
$W^+T_2^-$	2.76	6.87	69.38	17.72	3.06	19.73	0.40	0.57	2.20	4.39
$W^-T_1^+$	2.86	4.61	71.11	18.57	3.09	20.06	0.34	0.28	2.00	3.43
$W^-T_2^+$	2.83	4.82	70.66	18.75	3.07	20.34	0.32	0.24	2.03	3.39
M16	2.32	10.64	65.47	17.17	2.74	20.22	0.39	1.76	2.58	7.69
ICR Control	2.86	5.76	69.77	18.39	3.14	20.21	0.32	0.16	2.15	3.37
Range of S.E.M.[a]	.10-.12	.46-.55	.38-.46	.14-.17	.11-.13	.18-.21	0.01	.08-.10	.05-.06	.23-.27

[a] Standard error of mean

Table 6. Orthogonal contrasts: live traits

Comparison	Trait WT3	WT6	PWG	TL3	TL6	PWT	CONS	EFF
1. Expl - Exp2	-.43	-1.65**	-1.23**	-.10	-.14	-.04**	-19.38**	0.85**
2. Males - Females	-.42**	3.86**	3.45**	-.01	0.18**	0.18**	9.09**	1.91**
3. $W^+T_1^o - W^+T_2^o$	0.45	1.04	0.59	0.08	-.22	-.31*	0.76	0.39
4. $W^oT_1^+ - W^oT_2^+$	0.75	-1.32	-2.02**	0.50**	0.09	-.41**	-5.83	-.96
5. $W^+T_1^- - W^+T_2^-$	-1.05	0.96	2.02**	-.31	-.02	0.28*	1.13	1.39**
6. $W^-T_1^+ - W^-T_2^+$	0.43	-.27	-.70	0.25	0.14	-.11	-3.43	-.37
7. $W^+T^- - W^-T^+$	2.74**	7.26**	4.52**	-1.05**	-1.34**	-.28**	12.87**	2.71**
8. $\frac{1}{2}(W^-T^+ + W^+T^-)$ - ICR	-2.32**	-2.14**	0.16	-.33*	-.29*	0.04	-6.37*	0.70
9. $W^+T^o - W^oT^+$	0.10	3.00**	2.88**	-1.32**	-1.58**	-.26**	5.90*	1.68**

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

Table 7. Orthogonal contrasts: body composition traits

Comparison	Trait %ASH	%FAT	%MOIST	%PROT	%A-FF	%P-FF	A-EFF	F-EFF	P-EFF	E-EFF
1. Expl - Exp2	-.50**	-1.85**	0.66*	-.14	-.56**	-.16	—	—	—	—
2. Males - Females	-.17**	-.78**	0.37*	0.68**	-.22**	0.56**	0.01	-.21**	0.48**	0.18
3. $W^+T_1^o - W^+T_2^o$	-.26	0.37	-.38	-.28	-.26	-.10	-.02	0.31	0.04	0.78
4. $W^oT_1^+ - W^oT_2^+$	0.14	0.59	-.51	0.19	0.17	0.24	-.03	-.25	-.20	-.88
5. $W^+T_1^- - W^+T_2^-$	-.44*	-.51	-1.17	0.53*	-.46*	0.83**	-.01	0.30	0.31*	1.11*
6. $W^-T_1^+ - W^-T_2^+$	0.03	-.21	0.45	-.18	0.02	-.28	0.02	0.04	-.03	0.04
7. $W^+T^- - W^-T^+$	-.31*	1.90**	-2.09**	-.68**	-.25	-.05	0.06**	0.46**	0.34**	1.54**
8. $\frac{1}{2}(W^-T^+ + W^+T^-)$ - ICR	-.17	-.10	0.06	-.07	-.18	-.04	0.04*	0.33*	0.04	0.81
9. $W^+T^o - W^oT^+$	-.22	0.62	-.41	-.42*	-.22	-.23	0.01	0.31*	0.06	0.80

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

the divergence was asymmetric about the control (contrast 8). The W^+T^- treatment was greater ($P < .01$) than W^-T^+ for %FAT, A-EFF, F-EFF, P-EFF and E-EFF, but less for %ASH, %MOIST and %PROT. On a fat-free percentage basis, the W^+T^- and W^-T^+ lines did not differ appreciably. Comparisons of the single-trait selected lines (contrast 9) indicated that W^+T^0 was significantly greater than W^0T^+ for WT6, PWG, CONS, EFF, A-EFF and F-EFF but was less for TL3, TL6, PWT and %PROT. Several sex by line interaction contrasts reached statistical significance, but these were due primarily to larger male than female differences.

The five linear contrasts of each selection treatment with the ICR control are listed in Table 8. The W^+T^0 lines, selected for increased WT6, showed

Table 8. Comparisons with ICR Control

	Comparison[a]				
Trait	W^+T^o	W^oT^+	W^+T^-	W^-T^+	M16
WT3	0.64	0.54	-.96	-3.69**	1.93**
WT6	5.15**	2.15**	1.18[b]	-5.80**	10.52**
PWG	4.52**	1.64*	2.41**	-2.10**	8.60**
TL3	-.36	0.96**	-.86**	0.20	-.08
TL6	-.17	1.42**	-.96**	0.38[b]	0.34
PWT	0.20	0.46**	-.10	0.20	0.42**
CONS	13.58**	7.68*	0.06	-12.80**	23.00**
EFF	2.27**	0.58	2.06**	-.66	4.26**
%ASH	-.05	0.18	-.32	-.02	-.53**
%FAT	1.54[b]	0.92	0.86	-1.04	4.88**
%MOIST	-1.01	-.60	-.98	1.12	-4.30**
%PROT	-.51	-.09	-.40	0.27	-1.22**
%A-FF	0.01	0.22	-.30	-.05	-.40
%P-FF	-.22	0.01	-.06	-.01	0.01
A-EFF	0.08**	0.08**	0.08**	0.01	0.07**
F-EFF	0.40	0.10	0.56**	0.10	1.60**
P-EFF	0.24	0.18	0.20	-.14	0.43**
E-EFF	1.26*	0.46	1.54**	0.04	4.32**

[a] Contrasted with ICR Control in each case

[b] These traits were significant at $P < .05$ by the t-test

*$P < .05$ **$P < .01$

significant positive correlated responses in PWG, EFF, CONS, A-EFF and E-EFF. None of the tail length traits exhibited correlated responses in W^+T^0. The failure of the correlated response in %FAT (1.54%) to reach statistical significance was likely a result of the conservative nature of the test of all lines relative to the control. A direct t-test indicated that W^+T^0 showed a positive ($P < .05$) correlated response in %FAT.

Positive correlated responses to selection for increased TL6 in W^0T^+ were evident for WT6, PWG, TL3, PWT and CONS, but not for EFF. Partitioning of EFF into several components revealed that W^0T^+ was greater than the ICR control for A-EFF only. Correlated responses in body composition were not detected in W^0T^+.

The absolute value of the differences in correlated responses between W^+T^- and W^-T^+ are a reflection, in part, of the asymmetry noted previously. The absence of a significant increase for WT6 in W^+T^- and for TL6 in W^-T^+ was probably due to the conservative test procedure. Direct t-tests, ignoring the other contrasts, indicated significant ($P < .05$) changes in the expected direction, based on the intended selec-

Table 9. Non-orthogonal comparisons

	Comparison			
Trait	M16 - W^+T^o	M16 - W^+T^-	$W^+T^o - W^+T^-$	$W^oT^+ - W^-T^+$
WT3	1.30*	2.88**	1.59**	4.22**
WT6	5.37**	9.06**	3.69**	7.69**
PWG	4.07**	6.18**	2.11**	3.74**
TL3	0.28	0.78**	0.50**	0.76**
TL6	0.51**	1.30**	0.79**	1.04**
PWT	0.22	0.52**	0.30**	0.27**
CONS	9.42**	22.94**	13.51**	20.49**
EFF	2.00**	2.20**	0.21	1.24**
%ASH	-.49**	-.22	0.28	0.19
%FAT	3.35**	4.02**	0.68	1.96**
%MOIST	-3.28**	-3.32**	-.04	-1.72**
%PROT	-.71**	-.82**	-.10	-.36
%A-FF	-.40	-.09	0.31	0.28
%P-FF	0.23	0.08	-.16	0.02
A-EFF	-.01	-.01	0.01	0.06**
F-EFF	1.20**	1.04**	-.16	-.01
P-EFF	0.19*	0.22*	0.04	0.32**
E-EFF	3.06**	2.74**	-.32	0.42

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

tion criteria. W^-T^+ declined ($P < .01$) in WT3, WT6, PWG and CONS, whereas EFF and all of its components remained unchanged. As expected, TL3 and TL6 decreased ($P < .01$) in W^+T^-. Note that there was a positive ($P < .01$) correlated response in EFF of W^+T^- whereas CONS showed no significant response. The increased total efficiency was due to A-EFF, F-EFF and E-EFF. Percentage body composition remained unaltered in the index selected lines.

The M16 population had positive ($P < .01$) correlated responses in all live traits except TL3 and PWT. Regarding body composition, %FAT increased ($P < .01$) and %PROT, %MOIST and %ASH decreased ($P < .01$), whereas the percentages of ash and protein on a fat-free basis were not changed. The efficiency of all components and energetic efficiency were increased ($P < .01$) due to the long-term selection for postweaning gain in M16.

Some of the most meaningful non-orthogonal comparisons are presented in Table 9. For all live traits, M16 was greater than W^+T^0 and W^+T^-. When each single-trait selection treatment, W^+T^0 and W^0T^+, was compared with its antagonistic index counterpart, W^+T^- and W^-T^+, respectively, it was found that single-trait selection generally resulted in higher means for the live traits. It was found that M16 exceeded W^+T^0 and W^+T^- for %FAT, F-EFF, P-EFF and A-EFF. Unlike the live measurements, body composition and constituent efficiency contrasts for W^+T^0 and W^+T^- showed no significant differences.

Relative to W^0T^+, W^-T^+ had less %FAT and decreased A-EFF and P-EFF.

Among selection treatment correlations

The existence of distinct lines, each selected for some aspect of growth, affords the opportunity to compare correlated selection responses for two traits simultaneously over the several treatments. The among selection treatment correlations (r), adjusted for sex, replicates and experiments, were calculated from an analysis of covariance which also removed correlations among individuals within lines. Standard errors of these among selection treatment correlations were calculated by the method of Tallis (1959).

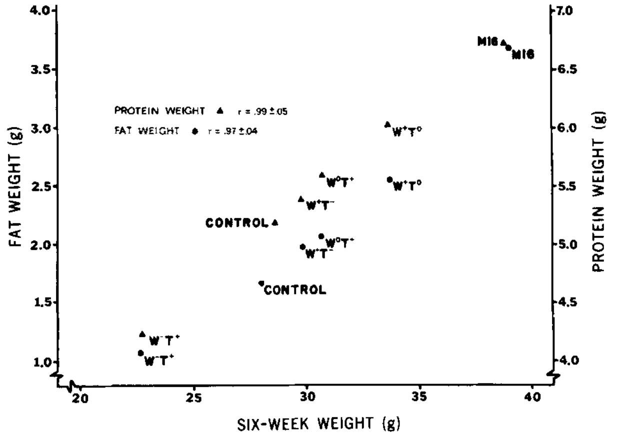

Fig.3. Selection treatment means of fat weight and protein weight plotted against six-week body weight, averaged over replicates, sexes and experiments

Fat weight and protein weight means were highly correlated (r = 0.97 ± .03), and both were positvely correlated with WT6 (Fig.3). Figure 4 illustrates the high positive relationship between the selection treatment means of WT6 and CONS, %FAT and EFF. Replacing WT6 with fat weight or protein weight essentially yielded the same trends. Fat percent was positively related with EFF and CONS (Fig.5). The realtionship between protein percent and the variables considered are approximately the inverse of those involving fat percent, since the correlation between the percentages of fat and protein were highly negative (r = -.96 ± .05), as expected.

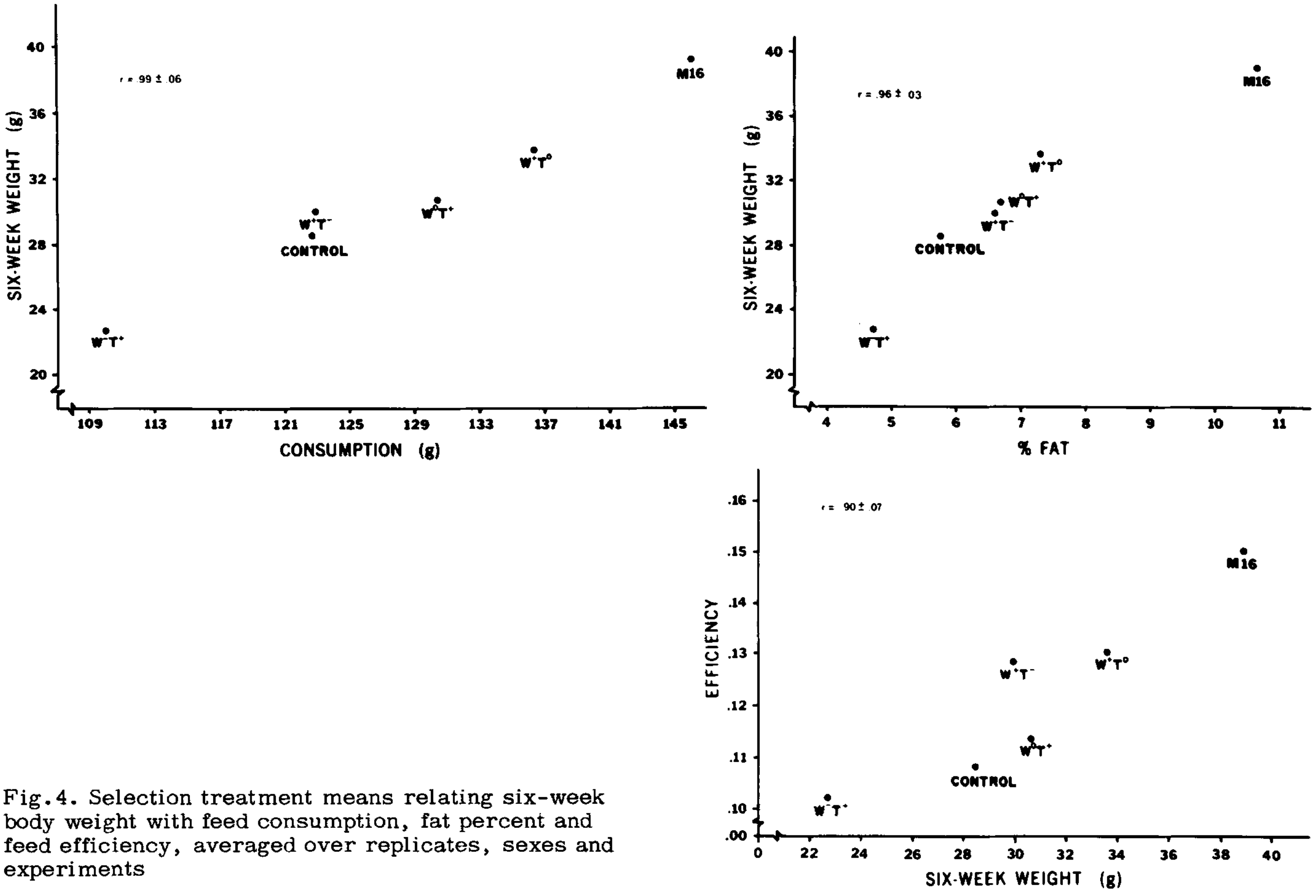

Fig.4. Selection treatment means relating six-week body weight with feed consumption, fat percent and feed efficiency, averaged over replicates, sexes and experiments

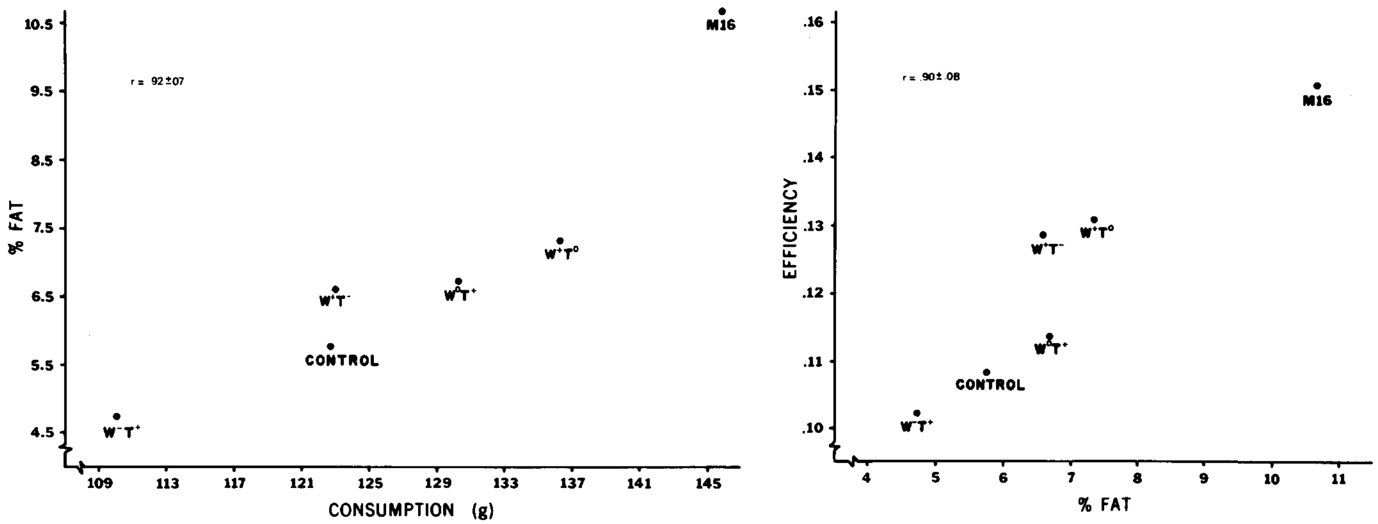

Fig.5. Selection treatment means relating fat percent with feed efficiency and feed consumption, averaged over replicates, sexes and experiments

Discussion

After analyzing replicate variation in W^+T^0, W^0T^+ W^+T^- and W^-T^+ for body weight, tail length, femur weight and length, and caudal vertebrae number and length using a generalized distance analysis, Rutledge et al. (1974) concluded that there was relatively little variation between replicates compared to variation among lines having different selection criteria. Relatively few of the replicate contrasts were significant for the traits analyzed in the present study, which supports the findings of Rutledge et al. (1974). The large number of replicate differences in W^+T^- was probably due to the marked difference between replicates in their cumulative selection differentials (Rutledge et al. 1973). Additional replicate differences that were found may be attributable, in part, to genetic drift or the interaction of drift with selection. Falconer (1973) also reported replicate variation among lines selected for body weight and indicated that identical selection at the phenotypic level may not lead to fixation of the same alleles because of genetic drift.

Selection for different criteria involving six-week body weight and six-week tail length has had remarkably little influence on the increase in tail length per unit increase in body weight from three to six weeks of age within each line. However, examination of the growth curves for body weight and tail length suggests that a difference in tail growth relative to body weight may have already occurred by three weeks of age. Body weight differences among lines were relatively small at three weeks and increased markedly from three to six weeks. This is a typical finding for growth curves following selection for body weight (Fowler 1958; Timon and Eisen 1969). Unlike body weight, the line differences in tail length appeared to be established by three weeks and, for the most part, did not change appreciably thereafter.

Contrasts 7 through 16 (Table 6) were also made by Rutledge et al. (1974) for WT6 and TL6 at generation eight. The contrasts in WT6 and TL6 between the single-trait selected lines were similar to those found in the earlier study. Both analyses confirm that the antagonistic index lines also diverged with respect to WT6 and TL6.

At generation 8, as in the present generation, TL6 had decreased more in W^+T^- than it had increased in W^-T^+. In addition, in the current generation, antagonistic index selection was more successful in decreasing WT6 in W^-T^+ than in increasing WT6 in W^+T^-. Developmentally, this asymmetry of response in both WT6 and TL6 occurred prior to weaning since the correlated responses in WT3 and TL3 were asymmetric, while responses in PWG and PWT were symmetric. This asymmetry may be due to maternal differences between W^+T^- and W^-T^+ which have resulted from divergent selection for body weight in the index lines. White, Legates and Eisen (1968) showed that a line selected for high body weight was maternally superior to a line selected for small body weight. Rutledge, Robison, Eisen and Legates (1972) reported that tail length as well as body weight was influenced by maternal effects. Another possible reason for the asymmetrical responses is genetic drift, as observed by Falconer (1973) in replicated divergent selection for body weight.

The absence of a correlated response in TL6 in W^+T^0 does not agree with earlier positive findings (Rutledge et al. 1973). In a line of mice selected for six-week body weight, Falconer (1953) found that the correlated response in six-week tail length ceased to increase after five generations and subsequently became erratic, and he suggested that the positive genetic correlation between the two traits was starting to disintegrate.

A comparison of M16 and W^+T^0 is of particular interest. Having originated from the same base, they differ primarily in their cumulative selection differentials. M16 was selected for PWG for 17 more generations than W^+T^0, which had been selected for WT6; WT6 and PWG are genetically highly correlated (Rutledge et al. 1973). The positive correlated response in %FAT (1.54%) for W^+T^0 is remarkably similar to the value (1.42%) obtained for M16 at generation nine of selection (Timon, Eisen and Leatherwood, 1970). Thus, the additional 17 generations of selection for positive growth rate have likely led to the greater correlated responses in M16 than in W^+T^0 for CONS, EFF, percent body composition and efficiency of constituent gains.

Correlated responses in CONS and EFF are the general rule in populations selected for increased body weight or gain. Sutherland, Biondini and Ward (1974) stated that this resultant ability to consume more feed has led to automatic increases in efficiency since proportionately more of the consumed energy is available, above maintenance, for growth. This phenomenon was observed in M16 and W^+T^0 but W^0T^+, W^+T^- and W^-T^+ did not exhibit simultaneous correlated responses in CONS and EFF. In W^0T^+ and W^-T^+, significant changes in CONS were not accompanied by noticeable correlated changes in EFF, whereas EFF increased and CONS did not change in W^+T^-. Thus, correlated changes in CONS were detected only in those lines whose peak gain in the postweaning growth period was altered (M16, W^+T^0, W^0T^+ and W^-T^+), and improved EFF resulted only in lines whole postweaning growth gradient was extended (M16, W^+T^0 and W^+T^-) (Fig.1). The extended type of growth curves postulated might be expected in lines in which the proportion of gain due to one or more components changed significantly. Thus, the percentage of postweaning gain due to fat gain was significantly ($P < .01$) increased in M16 (9.06%) and W^+T^- (3.92%) and approached significance in W^+T^0 (2.67%).

A-EFF, F-EFF, P-EFF and E-EFF are key components of EFF, so that changes in EFF are traceable to one or more of these components, Fowler's (1958) statement that energetic efficiency should reflect changes in gain due to fat deposition appears to be verified in the present study. For W^+T^0 and W^+T^-, increased E-EFF, F-EFF and A-EFF were noted, although F-EFF was not statistically significant in W^+T^0. M16 displayed positive genetic changes in P-EFF as well as E-EFF, F-EFF and A-EFF. The improved P-EFF may be related to the findings by Martin (1974) that enzymes involved in deamination and conversion of amino acids to glucose exhibited depressed activities. Based on standard biochemical pathways, the energy required to synthesize a gram of fat or protein is constant. Thus, any differences in efficiency of fat or protein deposition might be explained largely by differences in turnover rates (Priestley and Robertson 1973).

The contrasts between each single-trait selection treatment and the index treatment in which positive selection pressure was applied to the same trait illustrate the effects of index selection on reducing responses. Indeed, W^+T^0 had a heavier mean WT6 than W^+T^-, and W^0T^+ had a longer mean TL6 than W^-T^+, as selection theory predicts. Prediction of correlated responses in other traits are, of course, less reliable. Antagonistic selection generally resulted in smaller correlated responses in live traits than did single-trait selection; this, in itself, may not always be unfavorable. For example, the antagonistic index, W^+T^-, consumed less feed than W^+T^0, but W^+T^0 gained more weight. Nevertheless, the contrast with the ICR control indicated that W^+T^- realized a genetic improvement in PWG. The notable exception to the absence of differences in live trait means was EFF between W^+T^0 and W^+T^-. Hence, a difference in final weight did not lead to a difference in EFF. In contrast to the live trait measurements, antagonistic selection and single-trait selection resulted in similar body composition characteristics.

This result indicates that at a lighter weight, W^+T^- achieved a %FAT equal to that of W^+T^0. This relationship did not hold true in the comparison between W^0T^+ and W^-T^+. It is concluded that antagonistic index selection has resulted in proportionately less genetic change than the respective singe-trait lines in most components of growth.

The correlations among selection treatment means for the various traits are of interest in predicting average genetic correlated responses in an array of traits when direct or indirect selection pressure is placed on body weight. These are not true genetic correlations as they are influenced by the particular selection history of the lines involved and may include non-additive and maternal effects. On the average, genetic increases in body weight under *ad libitum* feeding resulted in linear increases in fat and protein weight, %FAT, CONS and EFF and a decreased %PROT. Timon and Eisen (1970) showed that appetite was a primary factor leading to the increased growth, fat deposition and energetic efficiency of the M16 line. These results agree with Blaxter (1968) who noted that the growth rate of an animal is dependent upon its level of feed intake.

Based on these results, it is possible to make some conjectures about selection procedures that could be applied to change the components of growth differentially. If it were desirable to alter one component of body growth, say protein, while minimizing change in a second component, say fat, specific restrictions on other traits in a selection index would be essential to realize these goals. Alternative approaches would be to select for growth rate in a fixed age interval, using a constant feed intake based on an average or percent of average *ad libitum* feed intake, or to select directly for gain or efficiency of protein deposition.

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Dr. E.J. Eisen
Department of Animal Science
North Carolina State University
Raleigh, North Carolina 27607 (USA)