CHARACTERIZATION OF FEED EFFICIENCY IN MICE

SELECTED FOR PREWEANING AND POSTWEANING

RATE OF GAIN

By

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CHAPTER I

INTRODUCTION

The livestock industry has become very cognizant of the economic importance of growth rate and the efficiency with which feed is utilized by livestock. Increased interest in production efficiency has been generated on the increased cost of livestock feedstuffs. Experimental studies have presented strong evidence that growth rate can be substantially increased by selection. Consequently, many areas of livestock production have increasingly been practicing selection for increased growth rate as a means to gentically improve livestock for productivity.

There remains, however, a need to study the genetic interrelationships between measures of growth at different stages of the life cycle in livestock. Selection for an economically important trait in one stage of the life cycle might result in a favorable or an unfavorable correlated response in another economically important trait that is expressed during another stage of the life cycle. If such genetic interrelationships exist, knowledge of the kind and relative magnitude of these relationships could be very important in developing breeding programs designed to improve total livestock production efficiency.

Information from selection studies involving farm animals is sometimes limited by the cost of the facilities required to maintain enough animals to obtain meaningful results. Obtaining adequate results from such studies is further hampered by the length of time required to

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obtain information. Interpretation of this data is sometimes made more difficult due to the effects of large environmental influences.

Because of a short generation interval, economy, and more adequate environmental control, mice were chosen as a suitable laboratory organism for a selection experiment. The primary objective of this selection study was to measure direct and correlated selection responses based on selection for increased growth at two different stages of the life cycle, preweaning and postweaning. These selection responses can provide an estimate of the genetic relationship between these two measures of growth and can serve as a genetic model of what to expect when selection is practiced for similar traits in the livestock species.

The purpose of this specific study was to measure postweaning feed efficiency in lines of mice which have been selected for increased preweaning and postweaning growth. The measurement of postweaning feed efficiency would provide an estimate of a correlated response to selection for growth at two different stages of the life cycle. Body composition was measured on samples of mice from these different selection lines in order to compare feed efficiencies on the basis of tissue growth. Some genetic parameters involving feed efficiency and related traits were also estimated.

CHAPTER II

REVIEW OF LITERATURE

Laboratory Animals in Animal Science

Development of the theoretical basis of quantitative genetics was
begun by R. A. Fisher, J. B. S. Haldane, and S. Wright around 1920.
Since its establishment, the development of quantitative genetics has
been largely a matter of clarification and elaboration (Falconer, 1960).
The importance of quantitative genetics to animal breeding was recog-
nized by J. L. Lush. Around 1940, he further developed these theories
into applications for the genetic improvement of livestock species.
Since these were theories, the testing of these experimentally was an
important next step. Ideally, if inference is to be made to farm
animals, these theories should be tested by conducting breeding experi-
ments using large farm animals. However, this is a difficult task to
accomplish due to the large cost per experimental unit and the long
generation intervals in farm animals. Laboratory animals can be more
efficient in testing animal breeding theory because the generation
intervals are much shorter and the costs per animal unit are much lower
in these species (Pirchner, 1969). The use of laboratory animals is
further enhanced by the fact that the measurement of traits are gener-
ally more precise than in farm animals. This is due to the ability to
synthesize the genetically desired strain in laboratory populations and
the less variable environment in laboratories (Staats, 1966). Since

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the laboratory mouse is biologically much closer to farm animals than are other commonly used organisms for genetics studies such as Drosophila or Tribolium, mice have been more often used in experiments related to animal breeding (Falconer, 1953; Pirchner, 1969).

Thus, many of the expectations in animal breeding experiments are known but experimental validations of the expectations have been slow. The role of the laboratory animal in animal breeding research is primarily in learning the extent to which observation from experimentation is in agreement with theoretical expectations and, to some extent, the reason for any non-conformance. If this information was available, we could make more confident generalities to the farm animal species (Chapman, 1951; Falconer, 1953; Robertson, 1955).

It seems reasonable that the measurement of feed efficiency as a correlated response to selection for growth rate in mice would provide valid generalizations and could help in the decisions of selection emphasis in livestock species.

Correlated Response to Selection

The value of a farm animal to the producer or feeder is influenced by many traits. Selection for a trait is very important since it not only affects the trait being selected but also affects any other traits that are genetically correlated with the trait being selected. The direction and extent of correlated responses are determined by the genetic correlation between the traits involved. The genetic basis behind this correlation is the extent to which the same loci are involved in determining two or more traits through pleiotropic gene action (Pirchner, 1969).

Common environment may cause a phenotypic correlation between traits. Since the phenotypic correlation is composed of both the genetic and environmental correlations, measurement of a phenotypic correlation between traits can give neither the magnitude nor direction of genetic or environmental correlations. Thus, for genetic implications of associations between traits, estimates of genetic covariances are imperative (Falconer, 1960).

The components of genetic covariances between traits consist of covariances between additive, dominance, and epistatic effects for these traits. The covariances between additive effects are of more concern since the gene combinations causing dominant and epistatic effects disintegrate at meiosis and are not transmitted from parent to offspring. Thus, the covariance between additive effects constitutes the genetic basis for correlated response over time (Pirchner, 1969).

Feed Efficiency in Mice

Gross efficiency of feed conversion is defined as an unadjusted ratio between the feed consumed on test and the gain on test (Sutherland, et al., 1970). The main expressions found in the literature for mice were: units of feed per units of gain and units of gain per units of feed. There was only one paper (Rahnefeld, et al., 1965) that chose to express feed efficiency in terms of units of feed per units of gain. Sutherland (1965) chose the expression units of feed per units of gain as a measure of "biological efficiency," although the reciprocal was used in a later paper (Sutherland, et al., 1970). Timon and Eisen (1970) discussed the two expressions of gross feed efficiency and concluded that the coefficient of variation was smaller for the expression as units of

gain/units of feed when gross efficiency was measured over a constant age interval.

Many workers have found an increase in gross efficiency in faster growing lines of mice. Fowler (1962) measured gross efficiency from 21 to 42 days of age in lines of mice selected for large six week weight and lines selected for small six week weight. Gross efficiency was reported to be highest in the lines selected for large six week weight, intermediate in the control lines, and lowest in the lines selected for small six week weight. Digestibility was also measured in these lines and there was little evidence found that suggested large differences in digestibility between the lines of mice. It was concluded that the increase in gross efficiency was more a function of appetite than of digestibility.

Rahnefeld, et al. (1965) selected for postweaning rate of gain from 18 to 42 days of age for 18 generations. The gross efficiency from 18 to 42 days of age of the lines selected for 18 to 42-day rate of gain was reported to be increased 40% over the control lines after 18 generations of selection. The genetic correlation between gross efficiency, expressed as the ratio of feed consumed/postweaning gain and postweaning gain was estimated to be -.80.

Lang and Legates (1969) conducted a study with mice selected for 33 generations for large six week weight. Gross efficiency between 21 and 42 days in the lines selected for large six week weight was reported to be improved 6% and males were reported to be 18% more efficient than the females. It was concluded that a favorable genetic relationship between rate of growth and gross efficiency was indicated by the data.

Timon and Eisen (1970) found that mice selected for nine generations

on the basis of 21 to 42-day average daily gain were 0.018 grams (P .05)
of gain per gram of feed more efficient between 21-45 days than the con-
trol lines. The gross efficiency of the males was reported to be 0.021
(P .05) grams of gain per gram of feed larger than the female contempor-
aries. It was concluded that this increased gross efficiency was a
function of increased consumption which, in turn, increased postweaning
gain.

Sutherland, et al., (1970) selected three lines of mice for nine
generations on the basis of high postweaning gain from four to eleven
weeks. After the nine generations of selection, the selection procedures
were altered. One of the lines was thereafter selected on the basis of
high feed consumption, another for high gross efficiency, and in the
third line, selection for postweaning gain was continued. Selection for
growth rate for the first nine generations reportedly resulted in an in-
crease in gross efficiency of 48%, 36%, and 25% higher than the control
line after nine generations of selection. Gross efficiency was reported
to have increased in the next 12 generations of selection with each of
the new selection schemes. After 12 generations of using the modified
selection schemes, the line selected for gross efficiency was 99% more
efficient than the control line, the line selected for feed consumption
was 51% more efficient than the control lines, and the line continued to
be selected for postweaning gain was 39% more efficient than the control
line. The realized heritability of gross efficiency estimated from the
gross efficiency selection line was $0.17 \pm .04$. The realized herit-
ability of feed consumption estimated from the feed consumption line
$0.20 \pm .06$. Genetic correlations were found to be $0.88 \pm .09$ between
growth rate and feed consumption, $0.91 \pm .04$ between growth rate and

feed efficiency and 0.52 ± .33 between feed efficiency and feed consumption. Feed efficiency was expressed as grams of gain per gram of feed and thus positive correlations indicate a favorable relationship. It was concluded that the increased gross efficiencies in the lines were a result of increased rate of gain.

Stanier and Mount (1972), characterized growth rate, food intake, and body composition, preweaning and postweaning, in strains of mice selected for large six week weight and small six week weight. They reported that there was little evidence of any difference in gross efficiency between the large six week weight strain and the control strain. There was only nine mice in the large six week strain and ten mice in the control strain in the comparison. On the other hand, the small six week weight strain was 29% less efficient than the control strain. Digestibility was also measured in these strains and there was no difference reported in digestibility between the three strains. It was concluded that strain differences in gross efficiency could not be attributed to differences in digestibility.

Evidence to date strongly suggests a favorable genetic correlation between postweaning gain and gross feed efficiency in mice. However, there has been little evidence of studies designed to relate preweaning growth and postweaning gross feed efficiency.

One paper that did study the relationship between measures of preweaning growth and gross efficiency in mice from 21 to 42 days was Jara-Almonte and White (1973). The estimates of the heritability for gross efficiency measured as grams of gain per gram of feed was 0.11 ± .10. The genetic correlation between gross efficiency and 21 to 42 day growth rate and between 21 day weight and gross efficiency were

0.75 $\pm$ .28 and - .68 $\pm$ .32, respectively.

Related Work in Farm Animals

Related work in farm animals largely agrees with the hypothesis of a favorable genetic correlation between postweaning growth rate and gross feed efficiency. Previous work in farm animals also suggests that selection for gross efficiency would be successful.

Dickerson and Grimes (1947) reported an estimate of 0.26 $\pm$ .12 for the heritability of feed required per pound of gain in swine. The genetic correlation between feed efficiency and postweaning gain was estimated to be -.78 in this paper.

Rahnefeld, et al., (1965) cited estimates from Fredeen and Jonnson (1957) between feed required per pound of gain and postweaning gain in swine to be -.96 for males and -.87 for females and from Reimer (1959) to be -.68.

Voght, Comstock, and Rempel (1963) estimated the heritability of feed required per pound of gain in swine to be .24 and the genetic correlation between feed efficiency and postweaning gain to be -.22 $\pm$ .23.

Robison and Berruecos (1973a) reported heritability estimates in swine for feed per unit gain to be 0.52 $\pm$ .28 on an age to age basis, 0.77 $\pm$ .25 on a weight to weight basis, and 0.61 $\pm$ .25 on an age to weight basis. When expressed as gain per unit feed, the heritabilities for the respective intervals were 0.00 (negative sire component), 0.08 $\pm$ .21, and 0.55 $\pm$ .26. The difference in the heritabilities was reported to be due to a marked curvilinear relationship between the two expressions of efficiency. The genetic correlations reported by Robison and Berruecos (1973b) between feed per unit gain and gain in these

intervals ranged from -.41 to -1.37 with standard errors between 0.17
and 0.33. The genetic correlations reported between gain per unit feed
and gain in the age to weight interval ranged from 0.86 to 1.16 with
standard errors from 0.20 to 0.29.

In beef cattle, Lindholm and Stonaker (1957) estimated the herit-
ability of feed required per pound of gain to be 1.46. The estimate of
the genetic correlation between feed efficiency and gain reported was
.05, but there were only 118 steers by 19 sires included in this study.

Carter and Kincaid (1959a) estimated the heritability of pounds of
TDN required per 100 pounds of gain in beef cattle to be 0.99 using a
variance-covariance analysis and $0.22 \pm .18$ using the regression of
progeny average on sire. Carter and Kincaid (1959b) reported an esti-
mate of the genetic correlation between pounds TDN required per 100
pounds of gain and gain to be -.32.

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Correlated Changes in Body Composition to

Influence Feed Efficiency

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The efficiency of food utilization is influnced by digestibility,
maintenance, the type of tissue deposited, and the previous nutrition.
If it can be assumed that there is a positive association between growth
rate and feed efficiency, then a review of the literature relative to
the composition of mice selected for growth rate, as well as those
strains in which feed efficiency has been measured and/or selected,
might help elucidate the present status of work.

Morris, Palmer, and Kennedy (1933) found that, in rats selected for
efficiency of food utilization, there was a correlated increase in
growth rate but that this increased growth was largely fat. Dickerson

and Gowen (1947) conducted a study with mice carrying the yellow coat color gene that is associated with hereditary obesity. It was found that the mice with this obesity gained faster and were more efficient past 40 days of age than their litter mates without these gene. This difference was attributed to the increase in fatness and efficiency of gain due to increased appetite and decreased activity. These results agreed with work by Dickerson (1943), cited in the above paper where the genetic causes of increased feed efficiency were also found to be associated with increased fat deposition. Fowler (1958) found that mice selected for large six week weight were fatter at all ages from weaning to 90 days of age. Lassiter, Cullison, and Carmon (1960) showed differences in percent ether extract in mice with different growth rates. Although the author did not comment on it in the paper, there was a tendency for the percentage ether extract to increase with increased growth rate. Hull (1960) found that selection of mice at 21, 32, and 42 days of age in the lines resulted in a decrease in percent fat as selected age increased.

Biondini, Sutherland, and Haverland (1969) found that the selection for postweaning growth rate for nine generations resulted in an increase in ether extract in two of the lines proportionately more than the other components but did not note any changes in body composition in a third line selected for postweaning growth rate. The selection criteria in two of the lines was changed to selection for postweaning feed consumption and postweaning feed efficiency, respectively. It was found that the line selected for efficiency of gain did not change in body composition relative to its composition in generation nine. The line further selected for growth rate had a consistent increase in all

components, and the line selected for feed consumption had an increase
in ether extract over the percentage found in the same line for the
generations preceding selection for feed consumption. Lang and Legates
(1969) measured body composition in lines of mice selected for large six
week weight and compared the lines with the control line. Conclusions
inferred that the increased growth was not the result of increased fat
deposition. It was stated, however, that the control line and the line
selected for large six week weight were not contemporary matings and
that the interpretation of the comparisons was conditional. Timon,
Eisen, and Leatherwood (1970) found that selection for increased post-
weaning growth rate resulted in a greater increase in the proportion of
ether extract than of any other component. Stanier and Mount (1972),
however, reported work in agreement with Lang and Legates (1969). No
increase in percent ether extract as a result of selection for large six
week weight was found. McLellan and Frahm (1972) selected for increase
hindleg muscle system weight. In addition to increasing muscle weight,
they obtained a correlated response in growth rate, but the body compo-
sition analysis indicated that the proportion of compositional components
were unchanged after six generations of selection.

Robison and Berruecos (1973b) estimated the genetic correlation be-
tween efficiency and live backfat in swine to be -.27; between effi-
ciency and carcass backfat to be -.45; and between efficiency and per-
centage fat to be 0.81, with efficiency expressed as gain per unit feed.
The estimates of the genetic correlations between growth rate and live
backfat, growth rate and carcass backfat, and growth rate and percent
fat were 0.37, -.45, and 0.02, respectively. All estimates had standard
errors larger than the estimate.

Summary of Review of Literature

The evidence thus far accumulated suggests a favorable genetic correlation between gross feed efficiency and postweaning rate of gain and that selection for efficiency of gain could be successful.

The evidence provided by the literature survey with regards to body composition suggests that there are differences in compositional gain among strains and species. The evidence further suggests that these differences might be associated with feed efficiency differences and that the differences in body composition might influence the interpretation of the results. Carcass composition should therefore be measured concurrently with feed efficiency to characterize this correlated response to selection for both preweaning and postweaning growth rate.

Estimates of some of the genetic parameters in the population being measured might also be of benefit to help elucidate the interpretations of the results obtained in measuring feed efficiency as a correlated response to selection for preweaning and postweaning growth rate.

CHAPTER III

MATERIALS AND METHODS

Base Population and Selection Scheme

Feed efficiency was measured in a population of albino mice that
was synthesized by crossing three highly inbred lines (AKR/J, SLJ/J,
BALB/C) and one non-inbred line (ICR). This four way cross was random
mated for one generation before selection was initiated. The base popu-
lation was divided into eight lines as follows: two random mating con-
trol lines, three lines to be selected for weight at 21 days (preweaning
growth), and three lines to be selected for average daily gain between
21 and 42 days of age (postweaning growth). Thus, there were three dis-
tinct "selection" groups. All eight lines were maintained concurrently
under controlled laboratory conditions and each line consisted of approx-
imately 20 litters each generation.

In each of the control lines one male and one female were randomly
selected from each litter and each selected male was randomly mated to
a non-litter mate, selected female. Selection in each of the preweaning
growth lines was accomplished by selecting the heaviest male and the
heaviest female at 21 days within each litter. Each selected male was
randomly mated to a selected non-litter mate female. Intra-litter se-
lection was practiced in the case of the preweaning growth lines in order
to correct for the differences in maternal effects on 21-day weight
normally expected in different litters. Selection in each of the

14

postweaning growth lines was accomplished by selecting the ten more

rapid gaining males postweaning and the 20 most rapid gaining females

postweaning without regard to what litters they belonged to. Each se-

lected male was randomly mated to two non-litter mate selected females,

thus increasing selection pressure.

General Procedures and Husbandry

The appropriate matings between selected males and females for each

of the lines were made when the youngest mice to be mated reached eight

weeks of age. Most of the mice were approximately 63 days of age at

mating. Males were removed 14 days later and destroyed. The litters

were born when the females were approximately 84 days of age, 19 to 24

days after the males and females were put together. When a litter

reached three days of age it was standardized to eight mice by randomly

removing excess mice or by crossfostering mice born the same day in the

same line into litters of less than eight mice. The foster mice were

identifed at the time by clipping their tails. When selections were

made, fosters were excluded in both the control lines and the preweaning

growth lines because of intralitter selection but were included in the

selections of the postweaning growth lines. At 12 days of age all

litters were weighed and individual mice in the litters were identified

as to line, litter, and individual mouse number by clipping toes. Dur-

ing this process, individual mice were identified as to sex. At 21 days

of age, individual mice were weighed to the nearest tenth of a gram, the

mice were separated into cages of one to four mice and the dams were

destroyed. Only mice of the same sex born on the same day in the same

line were put together. Cages of three and four mice predominated and

generally a cage consisted of littermates although, by necessity, some mice of different litters were mixed. At 42 days of age individual weights were again taken to the nearest tenth of a gram and a 21 to 42-day average daily gain was calculated to the nearest hundredth of a gram for each mouse (42 day weight - 21 day weight $\div$ 21 days). At 56 days of age individual weights were again taken to the nearest tenth of a gram and selections were made for matings as described above.

Mice were kept in 4.53 x 2.95 x 1.97 centimeter polypropylene cages with chromeplated lids that had provisions for holding approximately 300 grams of feed and a 473 milliliter water bottle. All cages were identified as to their contents with a cage identification card. Bedding in the cages was sterilized shredded sugarcane bagasse. All cages were changed weekly and fresh water was provided at that time.

Temperature in the laboratory was held between 20 - 22° Centigrade by an air conditioner-heating unit. Humidity was held at no less than 50% by use of a steam humidifier incorporated into the temperature control unit. Lighting was alternate 12 hours light and dark and controlled by an automatic timer. The cages were maintained on stainless steel racks and the position of each line was randomized every generation with the restriction that the two control lines were not put on the same rack. All mice were allowed to eat _ad_ _libitum_ throughout their life cycle a standard Purina Laboratory Chow.

Measurement of Feed Efficiency

Measurement of feed efficiency was initiated in the 11th generation of selection and continued up to and including the 14th generation of selection. Feed consumption was measured on a cage basis. Individual

measurement would have increased the precision of the estimation of selection group differences but it would also have changed the procedure relative to the primary project. There was also a limited amount of space in the laboratory, thus necessitating that the experimental unit be a cage of mice.

All feed was sifted for dust and fines before being weighed. Feed was weighed to the nearest hundredth of a gram to approximate 150 grams and stored in polyethylene bags until fed. This weight was chosen in an attempt to minimize feed spillage by the mice. At weaning all cages of three or four mice were fed with weighed feed and the feed weight was recorded on the cage identification card. Feed for the cages was checked daily and an additional 150 grams was added and recorded on the cage identification card if the level of feed in the hopper was less than 50 grams. This resulted in a cage having less than 200 grams of feed in the hopper at any given time. In the event a mouse in a cage died between 21 and 42 days, feed measurement on the cage was discontinued and the cage was excluded from the analysis. When a cage of mice reached 42 days of age, all feed remaining in the hopper was weighed and the weight was recorded on the cage identification card.

Feed consumption for a cage was calculated by subtracting the feed weight at 42 days from the total feed weighed into a cage. Gain for a cage was calculated as the sum of 42-day weights for the mice in the cage minus the sum of 21-day weights for the mice in the cage. Feed efficiency was then calculated as the ratio of total gain for the cage to total feed consumption (Timon and Eisen, 1970). Average daily feed consumption for the cage was calculated by dividing the total feed consumption by the quantity: number of mice in the cage times 21 days.

Average daily gain for a cage was calculated by dividing the total gain
for a cage by the quantity: number of mice in the cage times 21 days.
Thus, rounding errors were reduced by these methods of calculation.
Average 21-day weight for a cage was calculated by dividing the sum of
21-day weights by the number of mice in the cage. Average 42-day weight
for a cage was calculated by dividing the sum of 42-day weights by the
number of mice in the cage.

Body Composition Procedures

A chemical determination of body composition was conducted on a
random sample of mice from each of the three groups after 14 generations
of selection. Twenty-four litters per selection group were randomly se-
lected to contribute a random three males to be slaughtered at 21, 42,
and 56 days of age so that full sibs were available for comparison. In
the control group, 12 litters were selected from each line. In the
other two selection lines eight litters were selected from each line.
In this way, numbers were balanced over selection groups. Feed effi-
ciency was also determined for the mice that were slaughtered at 42 and
56 days of age.

Mice were taken off feed for six hours before euthanization at 21
days and for eight hours before euthanization at 42 and 56 days of age
to attempt to correct for variability due to fill. Mice were euthanized
at the prescribed time and placed in polyethylene bages to be stored at
-18° Centigrade until time for grinding. Grinding of mice was in a
completely randomized order within age group. All grinding was done in
a 6° Centigrade cooler. This was accomplished by dipping a mouse in
liquid nitrogen until frozen solid. The mouse was then coarse ground

with a mortar and pestle that had been precooled with dry ice. One half of this sample was then powdered in a high speed cryogenic mill and the other half was powdered immediately thereafter. The powdered sample was then placed in a polyethylene sample bag, identified as to mouse number and age and stored at -18° Centigrade until time for chemical analysis.

The powdered samples were then analyzed for protein, ether extract, and dry matter with ash being estimated by difference. In general, only 11 samples could be analyzed for protein at a time, such that, four samples from two selection groups and 3 from the other were analyzed, with alternate selection groups used for the run of three. The samples were stirred until pasty and duplicate two gram samples were weighed out to the nearest ten-thousandth gram. Nitrogen was estimated by the Kjeldahl procedure (A.O.A.C., 1960) and protein was estimated by multiplying the nitrogen value by 6.25. The samples were then refrozen at -18° Centigrade until ether extract determination.

Ether extraction was accomplished on Goldfisch extractors (A.O.A.C., 1960) by balancing the laboratory runs over selection groups with age completely randomized within selection group. The samples were again stirred until pasty and duplicate two gram samples were weighed out to the nearest ten-thousandth gram and dried at 100° Centigrade. Dry matter was estimated from the loss in weight of the wet sample after 6 hours of drying and the dried sample was extracted with diethyl ether on Goldfisch extractors. Ether extract was then determined as the gain in weight of the clean dry beaker weighed previous to extraction to the nearest ten-thousandth of a gram after at least four hours drying time and one hour cooling. Ash was determined by subtracting the percentage protein, water and ether extract from 100 percent.

Variance-Covariance Analysis for Estimating Genetic

Parameters in the Base Populations

Genetic parameters in the unselected control lines were estimated by analysis of variance and covariance conducted on data obtained from control line mice in generation 15. A hierarchal design was employed in which 62 males were mated to two females each. A total of 432 progeny were available for this analysis. Two males were randomly chosen from each litter and individual feed consumption between 21 and 42 days of age as well as growth performance data were collected. Two females were randomly chosen from each litter for inclusion in the estimation of growth performance, but were not involved in the measurement of feed consumption and efficiency. The female progeny were group fed postweaning and care was taken not to cage full sib or half sib females together. Data collection procedures, other than the exceptions noted, were as given previously in the general procedures and husbandry.

Statistical Analysis

The numbers of cages involved in the measurement of feed efficiency as a correlated response to selection is given in Table I by generation-line-sex subclass and further combined into generation-selection group subclass. Because of unequal subclass numbers, the data were analyzed by general least-squares procedures (Harvey, 1960). The linear model used in this analysis for each performance trait in each generation was:

$$Y_{ijkl} = u + S_i + G_j + (SG)_{ij} + (SL)_{ijk} + e_{ijkl}$$

where:

Y_{ijkl} = observation on the respective traits for l^{th} cage in the

TABLE I

NUMBER OF MALE AND FEMALE CAGES ON WHICH PERFORMANCE
WAS ANALYZED ON EACH LINE EACH GENERATION

| | CONTROL LINES | | | | WEANING WT. LINES | | | | | | 21-42 DAY ADG LINES | | | | | |
| | 1 | | 2 | | 3 | | 4 | | 5 | | 6 | | 7 | | 8 | |
GENERATION	M	F[a]	M	F	M	F	M	F	M	F	M	F	M	F	M	F
11	18	16	21	21	22	18	20	19	25	15	20	17	17	14	22	17
Total		76					119						107			
12	15	13	17	20	23	19	19	19	15	17	18	15	14	12	16	14
Total		65					112						89			
13	16	16	20	16	22	16	21	18	23	18	13	12	20	13	25	16
Total		68					118						99			
14	15	24	17	22	15	12	14	20	12	19	6	9	6	8	13	17
Total		78					92						59			

[a]M = male, F = female.

k^{th} line within the jth selection group and of the ith sex.

u = population mean.

S_i = fixed effect of the ith sex; $i = 1, 2$.

G_j = fixed effect of the jth selection group; $j = 1, 2, 3$.

L_{jk} = fixed nested effect of the kth line in the jth selection

group; $k = 1, 2$ for $j = 1$ and $k = 1, 2, 3$ for $j = 2, 3$.

$(SG)_{ij}$ = interaction effects of the ith sex and the jth group.

$(SL)_{ijk}$ = interaction effects of the ith sex in the jth line within

k^{th} selection group.

e_{ijk} = random residual effects that are normally distributed with a

zero mean and a variance σ^2.

Interaction effects other than $(SG)_{ij}$ and $(SL)_{ijk}$ were assumed to be un-

important and were pooled with the residual effect (e_{ijk}).

In a separate analysis for feed consumption and gross efficiency, in addition to the effects in the described model, a partial regression co-efficient was included using 21-day weight as the covariable. To the extent body maintenance requirements for the 21 to 42-day time period are a function of the 21-day weight (initial weight), this procedure ad-justs for differences in maintenance requirements at the start of the test period. The disadvantage in extra body weight to be maintained after 21 days is then allowed to express itself over the remainder of the test period. This was done to measure the extent to which the added weight in the weaning weight line at 21 days influenced feed efficiency and consumption.

The variance-covariance analysis of the control line population was done by a mixed-model least-squares analysis because of nonorthogonality of the date (Harvey, 1970). Two different analyses of the date were

performed, since feed consumption and feed efficiency were measured only on the males in this generation. Table II gives the distribution of observations for each subclass in these analyses. The linear model used in the analysis of the performance traits, not including feed consumption and efficiency was:

$$Y_{ijkl} = u + S_i + D_{ij} + F_k + e_{ijkl}$$

where:

Y_{ijkl} = observation on the 1th mouse of the kth sex from the jth dam mated to the ith sire.

u = population mean.

S_i = random effect of ith sire; $i = 1, 2, . . ., 62$.

D_{ij} = nested random effect of the jth dam in the ith sire; $j = 1, 2$.

F_k = fixed effect of the kth sex; $k = 1, 2$.

e_{ijkl} = random residual effects that are assumed to be normally distributed with zero mean and variance, σ^2.

The linear model used in the analysis of performance traits including feed consumption and gross efficiency was the same as above with the exception the fixed effect of sex (F_k) was deleted.

Heritabilities were calculated as the ratio of additive genetic variance (σ_A^2) and total phenotypic variance (σ_P^2). The additive genetic variance was estimated as four times the between sire component of variance (σ_S^2). Phenotypic variance was determined by $\sigma_P^2 = \sigma_S^2 + \sigma_{D/S}^2 + \sigma^2$ from the analysis of variance, where $\sigma_{D/S}^2$ is the between dam within sire component of variance and σ^2 is the between progeny within dam within sire component of variance. Genetic correlations were calculated from sire components of variance and covariance as:

TABLE II

NUMBER OF SIRES, DAMS, AND PROGENY IN THE HIERARCHAL VARIANCE-
COVARIANCE ANALYSES TO ESTIMATE GENETIC PARAMETERS OF THE
CONTROL POPULATION

WEIGHT AND GAIN ANALYSIS					WEIGHT, GAIN, FEED CONS., AND FEED EFFIC. ANALYSIS		
SIRES	DAMS	PROGENY			SIRES	DAMS	PROGENY
		M	F				M
62	113	209	214		61	105	203

$$r_g = \frac{Cov\ (i,j)}{\sqrt{V_{A(i)}\ V_{A(j)}}}$$

where:

r_g = the estimate of the genetic correlation between traits i and

j.

Cov (i, j) = the estimate of the additive genetic covariance be-

tween traits i and j and was estimated as four times the be-

tween-sire component of covariance for traits i and j.

$V_{g\ (i\ or\ j)}$ = the estimate of the additive genetic variance for

trait i or j.

The number of males on which body composition was measured is given

in Table III. The design was completely balanced with 24 males from each

selection group were slaughtered at each of the three slaughter ages.

Percentage and grams of protein, ether extract, water, and ash were

analyzed for each age group using the linear model:

$$Y_{ij} = u + G_i + e_{ij}$$

where:

Y_i = observation on the jth male in the ith selection group.

u = population mean.

G_i = fixed effect of ith selection group; j = 1, 2, 3.

e_{ij} = random residual effects that were assumed to be normally dis-

tributed with a zero mean and variance σ^2.

TABLE III

NUMBER OF MALES ON WHICH BODY COMPOSITION WAS ESTIMATED AT
EACH AGE IN EACH LINE

SLAUGHTER AGE	CONTROL LINES		WEANING WT. LINES			21-42 DAY ADG LINES		
	1	2	3	4	5	6	7	8
21 Days	12	12	8	8	8	8	8	8
42 Days	12	12	8	8	8	8	8	8
56 Days	12	12	8	8	8	8	8	8

CHAPTER IV

RESULTS AND DISCUSSION

Growth, Feed Consumption, Feed Efficiency

and Body Composition

Feed consumption was measured in a population of mice consisting of
two unselected control lines (CL), three lines selected for 21-day
weight (WWL), and three lines selected for 21 to 42-day average daily
gain (ADGL). Measurement of feed consumption was initiated after 11
generations of selection and was continued up to and including genera-
tion 14 of selection.

The analyses of variance for 21-day weight, 42-day weight, 21 to
42-day average daily gain, 21 to 42-day daily feed consumption, and 21
to 42-day gross efficiency are presented in the Appendix Tables XIV -
XVII for generations 11, 12, 13, and 14. Analyses of variance for feed
consumption and feed efficiency with 21-day weight included as a co-
variable in the linear model are presented in Appendix Tables XVIII and
XIX.

Since the objective of this study was primarily to compare differ-
ences in feed efficiency as a result of two different selection regimes,
data were pooled over sexes and lines within a selection group. There
was some evidence of a sex by group interaction in some traits in some
generations, but the biase that would result from pooling data from
both sexes would be negligible because of the small magnitude of the

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interaction.

Because the interaction was small and because the objectives of this study did not include the quantification of sex differences, least squares means where the data is adjusted for unequal numbers of groups, lines within groups, and sex were used for making comparisons among the three groups. The use of least squares means in this manner not only gives more precise estimates but also aids in the clarity of the interpretations of the results.

The postweaning feed efficiency of an animal is a function of the postweaning weight gain and feed consumption of that animal. The feed consumption and gain are associated with the weight of an animal at the beginning and end of the test period (Rahnefeld, et al., 1965). Results will be presented in the order: 21-day weight (start of test), 42-day weight (end of test), 21 to 42-day average daily gain (gain on test), 21 to 42-day daily feed consumption, and 21 to 42-day gross feed efficiency. This should aid in the orderly presentation and interpretation of the results.

21-Day Weight

The least squares means for 21-day weight are presented in Tables IV - VII. In generations 11, 12, 13, and 14 the WWL significantly (P<.001) exceeded the CL in 21-day weight by 2.3 grams (23.2%), 2.4 grams (26.7%), 2.1 grams (26.6%) and 2.4 grams (29.6%) respectively. The WWL also significantly (P<.001, P<.001, P<.025, P<.005) exceeded the ADGL in 21-day weight. The ADGL significantly (P<.001) exceeded the CL in 21-day weight by 1.4 grams (14.1%), 1.0 gram (11.1%), 1.7 grams (21.5%), and 1.7 grams (21.0%), respectively.

The response to selection for weight at 21 days has markedly increased the weight to be maintained at the start of the feeding period in the WWL. The ADGL also were required to maintain more weight at the start of the feeding period than were the CL as a result of a correlated increase in 21-day weight when selected for 21 to 42-day average daily gain.

42-Day Weight

The least squares means for 42-day weight are presented in Tables IV - VII. The 42-day weights of the WWL significantly (P<.001) exceeded the 42-day weights of the CL in generations 11, 12, 13, and 14 by 3.6 grams (15.4%), 4.0 grams (18.0%), 4.3 grams (20.4%), and 4.8 grams (21.8%), respectively. The ADGL significantly (P<.001) exceeded the CL in 42-day weight in these generations by 8.0 grams (34.2%), 8.2 grams (36.9%), 9.4 grams (44.6%), and 8.9 grams (40.5%), respectively. The ADGL also significantly (P<.001) exceeded the WWL in 42-day weight in these generations by 4.4 grams (16.3%), 4.2 grams (16.0%), 5.1 grams (20.1%), and 4.1 grams (15.3%), respectively.

The simple average of the weight at the start of the feeding period and the weight at the end of the feeding period gives an indication average weight to be maintained over the test period (Rahnefeld, et al., 1965). The WWL had more weight to maintain, between 21 and 42 days on the average, than the CL in generations 11, 12, 13, and 14 by 3.0 grams (17.7%), 3.2 grams (20.5%), 3.2 grams (22.1%), and 3.6 grams (23.9%), respectively. In the same generations the ADGL had more weight to maintain between 21 and 42 days, than the CL on the average, by 4.7 grams (28.2%), 4.6 grams (29.5%), 5.6 grams (38.3%), and 5.3 grams

(35.2%), respectively. Thus the ADGL were maintaining more weight on the average than the WWL between 21 and 42 days by 1.7 grams (8.9%), 1.4 grams (7.4%), 2.4 grams (13.3%), and 1.7 grams (9.4%) in generations 11, 12, 13, and 14. No formal analyses were done on average weight on test, but the differences noted above are indicative of the differences between the different selection groups in average body weight that had to be maintained between 21 and 42 days.

21 to 42-Day Average Daily Gain

The least squares means for 21 to 42-day average daily gain are presented in Table IV - VII. The 21 to 42-day average daily gains of the WWL and ADGL were significantly (P<.001) higher than the CL in all generations in this study. The differences between the WWL and the CL in generations 11, 12, 13, and 14 in grams per day were of the magnitude 0.07 grams per day (10.9%), 0.07 grams per day (11.0%), 0.10 grams per day (15.9%), and 0.12 grams per day (18.2%). The ADGL had postweaning average daily gains that exceeded the CL in generations 11, 12, 13, and 14 by 0.32 grams per day (50.0%), 0.34 grams per day (54.0%), 0.36 grams per day (57.1%), and 0.35 grams per day (53.0%). The differences between ADGL and WWL lines were significant (P<.001).

There was obviously a difference in 21 to 42-day average daily gain between the different selection groups. Selection for weight at 21 days has resulted in a small but significant correlated increase in average daily gain. Selection for 21 to 42-day average daily gain has resulted in a large response to selection in average daily gain. Any increase in gain is a result of having satisfied the maintenance requirements of an animal and having nutrients remaining that could contribute to growth. This could happen if an animal consumed more feed than was required for

maintenance or if the animal was better able to absorb or utilize the feed it consumed or both of these. Feed consumption was measured for the four generations to quantify differences in consumption.

21 to 42-Day Average Daily Feed Consumption

Least squares means for 21 to 42-day feed consumption are given in Tables IV - VII. The differences in average daily feed consumption follow the same order as did the average daily gains; that is, the CL consumed the least amount of feed, the WWL were intermediate, and the ADGL consumed the most feed. All differences were significant (P<.001). The WWL exceeded the CL by 0.66 grams per day (16.8%), 0.52 grams per day (13.9%), 0.67 grams per day (17.1%), and 0.81 grams per day (20.8%), for each generation, respectively. The differences in daily feed consumption between the ADGL and the CL were of the magnitude of 1.13 (28.8%), 0.88 (23.6%), 0.97 (24.8%), and 1.14 (29.3%) grams per day, for generations 11, 12, 13, and 14.

When 21-day weight was included in the model as a covariable, the mean daily feed consumption was significantly (P<.05) changed in both the CL and the WWL, for all generations but the inclusion of 21-day weight as a covariable did not significantly change the mean daily feed consumption of the ADGL for any generation. Thus, the ADGL were the intermediate 21-day weight adjusted to. This adjustment resulted in the mean daily feed consumptions of the WWL to be larger than the CL but to a lesser extent than the unadjusted means in each generation. The differences between the WWL and the CL adjusted mean feed consumption for each generation were 0.28 (6.7%), 0.08 (2.0%), 0.26 (6.2%), and 0.33 (7.9%) grams per day. The differences were significant (P<.001) with the exception of generation 12. The ADGL was still significantly

(P<.001) higher than either the WWL or the CL in adjusted mean daily feed consumption. It exceeded the CL for each of the generations by 0.90 (21.6%), 0.69 (17.3%), 0.65 (15.5%), and 0.82 (19.7%) grams per day.

Selection for weight at 21 days has resulted in a significant increase in feed consumption even when the data were adjusted for 21-day weight. Part of this consumption contributes to the increased maintenance requirements accured through the increase in 21-day weight. The other part of the feed consumption contributes to growth. The difference between the WWL and the CL in feed consumption could not be accounted for by increased weight at 21 days. Since there was a proportional increase over the CL in average daily gain, this might be attributed to the increase in feed consumption.

Selection for 21 to 42-day average daily gain has resulted in a significant increase in feed consumption over both the WWL and the CL even when the data were adjusted for 21-day weight.

21 to 42-Day Gross Efficiency

The ratio of body weight gain to feed consumed was determined to measure feed efficiency. Least squares means for 21 to 42-day feed efficiency can be found in Tables IV - VII. The WWL was consistently less efficient than the CL, although this was not always statistically significant. The mean differences between the WWL means and the CL means were -.009 (-5.4%),(P<.025); -.001 (-.6%), (P>.50); -.002 (-1.1%), (P>.50); and -.005 (-3.1%),(P<.05) grams of gain per gram of feed for generations 11, 12, 13, and 14, respectively. The ADGL were significantly more efficient than either the CL or the WWL (P<.001) in any generation. The differences found between the ADGL and the CL were

.026 (16.0%), 0.047 (27.5%), 0.44 (27.3%), and .030 (17.6%) gram of gain

per gram of feed for generations 11, 12, 13, and 14, respectively. The

differences noted between the ADGL and the WWL in efficiency were 0.035

(22.6%), 0.048 (28.3%), 0.046 (28.7%), and 0.035 (21.3%) for generations

11, 12, 13, and 14, respectively.

Inclusion of 21 day weight as a covariable significantly (P<.05)

altered the mean efficiencies on the CL and the WWL for all generations

but did not significantly change the mean efficiency of the ADGL again

showing the ADGL to be intermediate in 21-day weight. Adjustment of the

data for 21-day weight resulted in the WWL being significantly (P<.05)

for generation 11 and (P<.001) for the other generations) more efficient

than the CL in each generation by 0.0070 (4.5%), 0.0180 (11.4%), 0.0150

(10.0%), and 0.0160 (10.1%) grams of gain per gram of feed. The ad-

justed mean efficiency of the ADGL significantly (P<.05) exceeded both

the CL and the WWL in all generations. The differences between the ADGL

and the CL for the four generations were 0.0360 (23.1%), 0.0550 (34.4%),

0.0580 (38.3%), and 0.0440 (28.1%).

Thus, selection for 21-day weight has not largely altered the gross

efficiency of the WWL. The extra weight at 21-days, however, required a

larger magnitude of feed consumption relative to gain between 21 and 42

days such that the correlated response in gain served only to keep the

gross efficiency about the same as the CL. This is shown by the adjust-

ment for 21-day weight resulting in the WWL being significantly more ef-

ficient than the CL.

Selection for 21 to 42 day average daily gain has resulted in a

markedly increased efficiency. Adjustment for 21-day weight did not

markedly alter the efficiencies in the ADGL in any generation.

Discussion of Growth Performance, Feed Consumption,

and Feed Efficiency Comparisons

In the WWL, selection for 21 day weight has resulted in a significantly larger amount of weight to be maintained at the start of the feeding period and a larger average weight to be maintained between 21 and 42 days as compared to the CL. These increases were the result of a direct selection response and a correlated response in 21 to 42 day-average daily gain to selection for 21 day weight. Frahm and Brown (1973) estimated the genetic correlation between 21 day weight and 21 to 42 day-average daily gain in this population to be 0.33. The increase in weight in the WWL was accompanied by an increase in feed consumption from 21 to 42 days. Consequently, the ratio of gain to feed consumed was decreased slightly as compared to the CL but not to a large extent. This data, therefore, indicates that selection for 21 day weight increased weights and feed consumption at a proportional rate so that feed efficiency was not markedly altered due to the associated increase in gain.

In the ADGL, selection for 21 to 42-day average daily gain has resulted in a significant increase in weight to be maintained at the start of the feeding period as compared to the CL and an increase over both the CL and the WWL in average weight to be maintained over the test period. As in the WWL, these increases were due to both a direct and a correlated response to selection. Feed consumption was also increased from 21 to 42 days, but the magnitude of the increased gain was such that the resultant gross efficiency was markedly increased.

These data indicated that an increase in average daily gain over the CL in both the WWL and the ADGL was accompanied by an increase in

feed consumption. Part of this feed consumption was required for main-
tenance and the remainder contributed to growth. However, differences
between the WWL and the ADGL in average daily gain and feed efficiency
do not seem explainable on the basis of differences in feed consumption.
In generation 11, the ADGL had an average of 1.75 grams (8.9%) more
weight to maintain on test than the WWL, consumed 0.47 more grams of
feed per day (10.2%), but gained 0.25 grams (35.2%) more per day than
the WWL. The same general pattern occurred in the other three genera-
tions, with the differences between the ADGL and the WWL in average
weight on test, daily feed consumption, and average daily gain being:
1.4 grams (7.4%), 0.36 grams of feed per day (8.5%), 0.27 grams of gain
per day (38.6%) in generation 12; 2.4 grams (13.3%), 0.30 grams of feed
per day (6.6%), 0.26 grams of gain per day (35.6%) in generation 13; and
1.7 grams (9.4%), 0.33 grams of feed per day (7.0%), 0.23 grams of gain
per day (29.5%) in generation 14. Thus, even though the ADGL consumed
more feed, part of this feed would be used in maintaining the extra
weight on test such that the increased gain would be associated with a
small amount of extra feed consumed. Part of this could be explained if
there were differences in digestibility between the selection groups.
Fowler (1962) and Stanier and Mount (1972) found no large differences in
digestibility between control mice and mice selected for growth. Dif-
ferences in tissue deposition could also influence differences between
the WWL and the ADGL in average daily gain, thus influencing gross ef-
ficiency. Two situations could possibly exist in this respect. If the
WWL were gaining largely fat tissue and the ADGL were increasing in all
body components, then the WWL could be less efficient on a gross basis.
If both the WWL and the ADGL were depositing largely fat tissue but the

TABLE IV

LEAST SQUARES MEANS BY TYPE OF SELECTION LINE
AFTER 11 GENERATIONS OF SELECTION

	CONTROL LINES $\pm$ S.E.	WEANING WT. LINES $\pm$ S.E.	21-42 DAY ADG LINES $\pm$ S.E.
No. Cages	76	119	117.
21-Day Weight (g)	9.9 ± 0.12^a	12.2 ± 0.10^b	$11.3 \pm .10^c$
42-Day Weight (g)	23.4 ± 0.18^a	27.0 ± 0.14^b	31.4 ± 0.15^c
21-42 Day ADG (g/day)	0.64 ± 0.006^a	0.71 ± 0.005^b	0.96 ± 0.005^c
21-42 Day Daily[e] Feed Consumption (g/day)	3.93 ± 0.052^a 4.17 ± 0.058^a	4.59 ± 0.042^b 4.45 ± 0.043^b	5.06 ± 0.044^c 5.07 ± 0.040^c
21-42 Day Feed[e] Efficiency (g gain/g feed)	0.1639 ± 0.0027^a 0.1542 ± 0.0031^a	0.1551 ± 0.0022^d 0.1611 ± 0.0023^d	0.1901 ± 0.0023^c 0.1898 ± 0.0022^c

a, b, c Means on same line with different superscripts differ significantly
    (P<.01).

d Significantly different from CL (P<.05) and from ADGL (P<.01).

e Second row adjusted for 21 day weight.

TABLE V

LEAST SQUARES MEANS BY TYPE OF SELECTION LINE
AFTER 12 GENERATIONS OF SELECTION

	CONTROL LINES $\pm$ S.E.	WEANING WT. LINES $\pm$ S. E.	21-42 DAY ADG LINES $\pm$ S.E.
No. Cages	65	112	89
21-Day Weight (g)	9.0 ± 0.19^a	11.4 ± 0.15^b	10.0 ± 0.16^c
42-Day Weight (g)	22.2 ± 0.26^a	26.2 ± 0.20^b	30.4 ± 0.22^c
21-42 Day ADG (g/day)	0.63 ± 0.008^a	0.70 ± 0.006^b	0.97 ± 0.007^c
21-42 Day Daily[d] Feed Consumption	3.73 ± 0.074^a 3.98 ± 0.072^a	4.25 ± 0.057^b 4.06 ± 0.055^a	4.61 ± 0.063^c 4.67 ± 0.056^b
21-42 Day Feed[d] Efficiency (g gain/g feed)	0.1702 ± 0.0038^a 0.1594 ± 0.0038^a	0.1692 ± 0.0029^a 0.1775 ± 0.0029^b	0.2170 ± 0.0032^b 0.2142 ± 0.0030^c

a, b, c Means on the same line with different superscripts differ
    significantly (P<.01).

d Second row adjusted for 21 day weight.

TABLE VI

LEAST SQUARES MEANS BY TYPE OF SELECTION LINE
AFTER 13 GENERATIONS OF SELECTION

	CONTROL LINES ± S. E.	WEANING WT. LINES ± S. E.	21-42 DAY ADG LINES ± S.E.
No. Cages	68	118	99
21-Day Weight (g)	7.9 ± 0.14^a	10.0 ± 0.11^b	9.6 ± 0.12^d
42-Day Weight (g)	21.1 ± 0.21^a	25.4 ± 0.16^b	30.5 ± 0.18^c
21-42 Day ADG (g/day)	0.63 ± 0.008^a	0.73 ± 0.006^b	0.99 ± 0.007^c
21-42 Day Daily[e] Feed Consumption	3.91 ± 0.057^a 4.20 ± 0.060^a	4.58 ± 0.043^b 4.46 ± 0.041^b	4.88 ± 0.049^c 4.85 ± 0.043^c
21-42 Day Feed[e] Efficiency (g gain/g feed)	0.1620 ± 0.0025^a 0.1502 ± 0.0027^a	0.1602 ± 0.0019^a 0.1652 ± 0.0018^b	0.2062 ± 0.0021^b 0.2077 ± 0.0019^c

[a,b,c] Means on the same line with different superscripts differ significantly (P<.01).

[d] Significantly different from CL (P<.01) and WWL (P<.05).

[e] Second line adjusted for 21 day weight.

TABLE VII

LEAST SQUARES MEANS BY TYPE OF SELECTION LINE
AFTER 14 GENERATIONS OF SELECTION

	CONTROL LINES ± S.E.	WEANING WT. LINES ± S.E.	21-42 DAY ADG LINES ± S.E.
No. Cages	78	92	59
21-Day Weight (g)	8.1 ± 0.16^a	10.5 ± 0.15^b	9.8 ± 0.20^c
42-Day Weight (g)	22.0 ± 0.20^a	26.8 ± 0.19^b	30.9 ± 0.24^c
21-42 Day ADG (g/day)	0.66 ± 0.006^a	0.78 ± 0.006^b	1.01 ± 0.008^c
21-42 Day Daily[e] Feed Consumption (g/day)	3.89 ± 0.042^a 4.17 ± 0.031^a	4.70 ± 0.039^b 4.50 ± 0.027^b	5.03 ± 0.051^c 4.99 ± 0.032^c
21-42 Day Feed[e] Efficiency (g gain/g feed)	0.1707 ± 0.0019^a 0.1581 ± 0.0014^a	0.1654 ± 0.0017^d 0.1741 ± 0.0012^b	0.2007 ± 0.0022^c 0.2026 ± 0.0014^c

[a,b,c] Means on the same line with different superscripts differ
significantly (P<.05).

[d] Significantly different from the CL (P<.05) and the ADGL (P<.01).

[e] Second line adjusted for 21 day weight.

WWL were depositing more fat tissue than the ADGL, a difference in gross efficiency might exist.

The data for the four generations of measurement of the performance and consumption traits is plotted over generations in Figures 1-4. The graph for weight at 21 days over all generations is shown in Figure 1. Weight at 21 days shows a slight decline through generation 13 in all lines and then stabilizes to generation 14. Since 21-day weight is largely influenced by environment, some small environmental deviations could explain this segment of the overall graph of weight plotted against generation.

The graph for weight at 42 days over all generations is presented in Figure 1. Weight at 42 days reflects the weight at 21 days in the WWL and the CL in that a decline in 42-day weight is observed through generation 13 and then 42-day weight stabilized at generation 14. In the ADGL, however, the effect of 21-day weight is compensated for by the continued response in average daily gain.

The graph for 21 to 42-day average daily gain over all generations is presented in Figure 2. In the ADGL, 21 to 42-day average daily gain increases over all generations shown. The WWL shows a slight decline from generation 11 to generation 12, and an increase thereafter. The CL remains relatively stable throughout all four generations. In this graph, the magnitude of difference in average daily gain between the selection groups can be easily seen. As mentioned earlier, the ADGL had a much higher average daily gain than either CL or the WWL. The magnitude of correlated response in average daily gain to selection for 21-day weight in the WWL can also be seen in this graph.

The graph for average daily feed consumption from 21 to 42 days is

shown in Figure 3. When the data was left unadjusted for 21-day weight, the CL feed consumption was markedly lower than the other two selection groups and the WWL had a lower feed consumption than did the ADGL. When the data was adjusted for 21-day weight, it is easily visualized that the mean feed consumption of the CL shifted upward and the mean feed consumption of the WWL shifted downward to a lesser extent. The differences between the selection groups are fairly consistent from generation to generation. This is reassuring in that measurement of feed consumption can be affected by wastage error and, if this error was present, it was consistent over all generations.

The graph for 21 to 42-day feed efficiency over all generations is shown in Figure 4. Since feed efficiency is affected by both feed consumption and gain, this trait is slightly more variable from generation to generation. The differences between selection groups, however, are fairly consistent from generation to generation. The effect of adjustment for 21-day weight on the differences between selection groups can be easily visualized in this graph for the four generations.

Body Composition

Body composition was measured after 14 generations of selection on 24 male mice from each selection group at each of three ages, 21 days, 42 days, and 56 days. Full sibs were used such that a mouse at one age was represented by full sibs at the other ages. Means and standard errors for protein, ether extract, moisture, and ash for each age and each selection group are presented in Tables VIII - X, expressed both as actual weight and as percentage of body weight.

Within all age groups, differences in proportional composition were
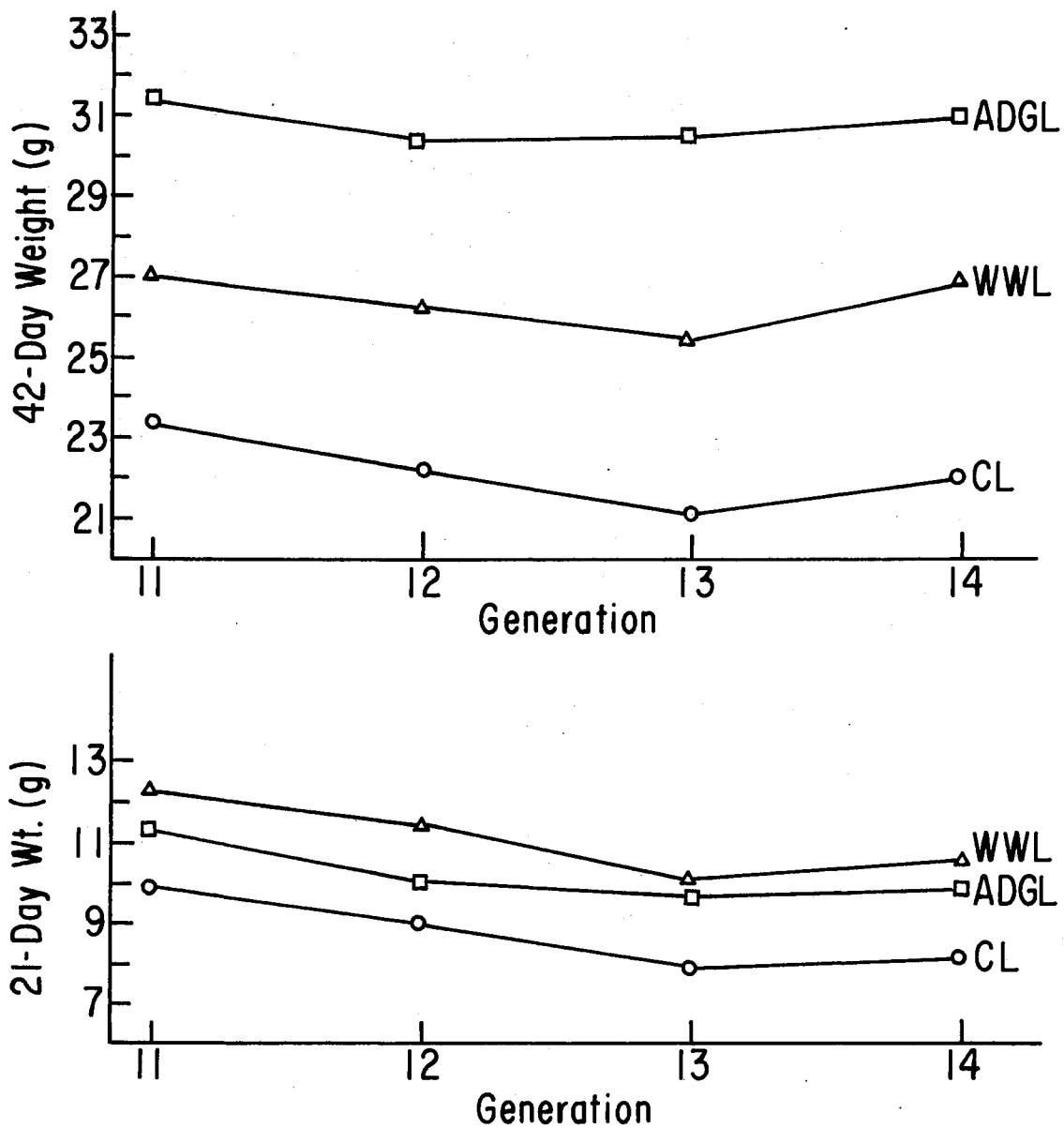
Figure 1. Weights at 21 and 42 Days Plotted on Generation.
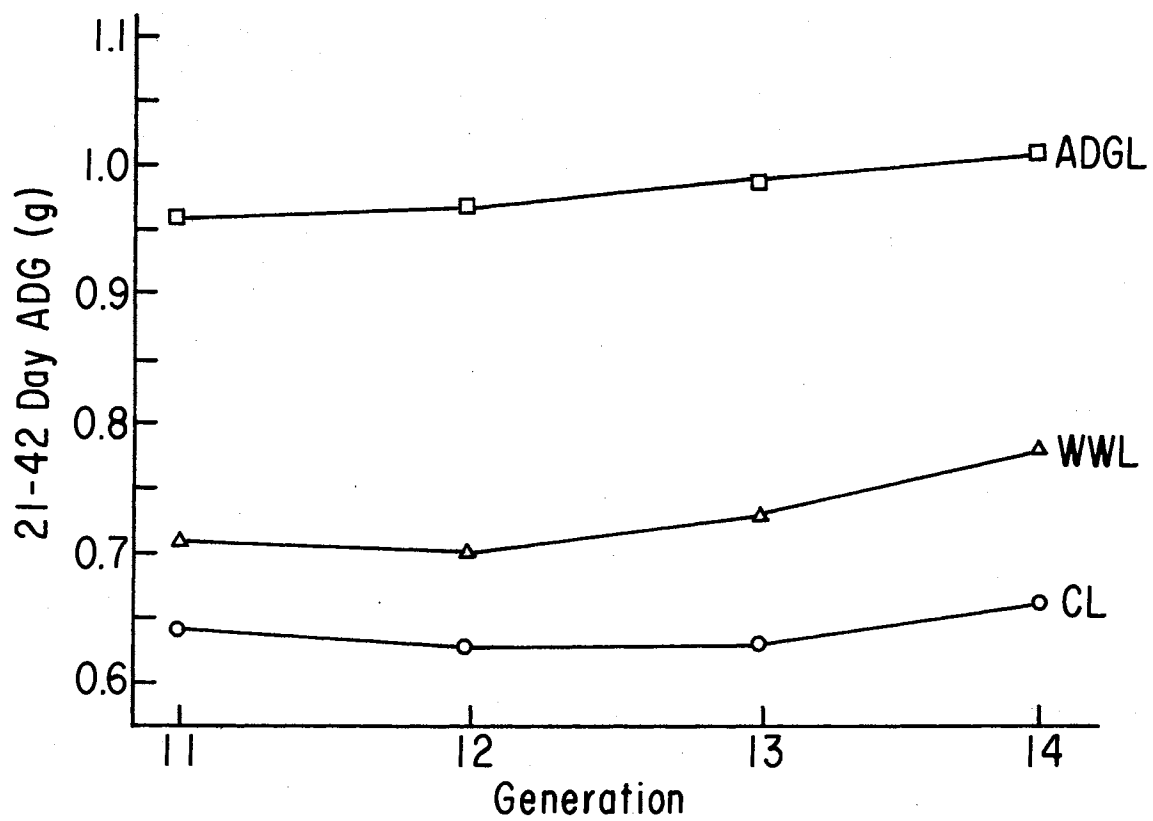
Figure 2. Average Daily Gain from 21 to 42 Days
Plotted on Generation.
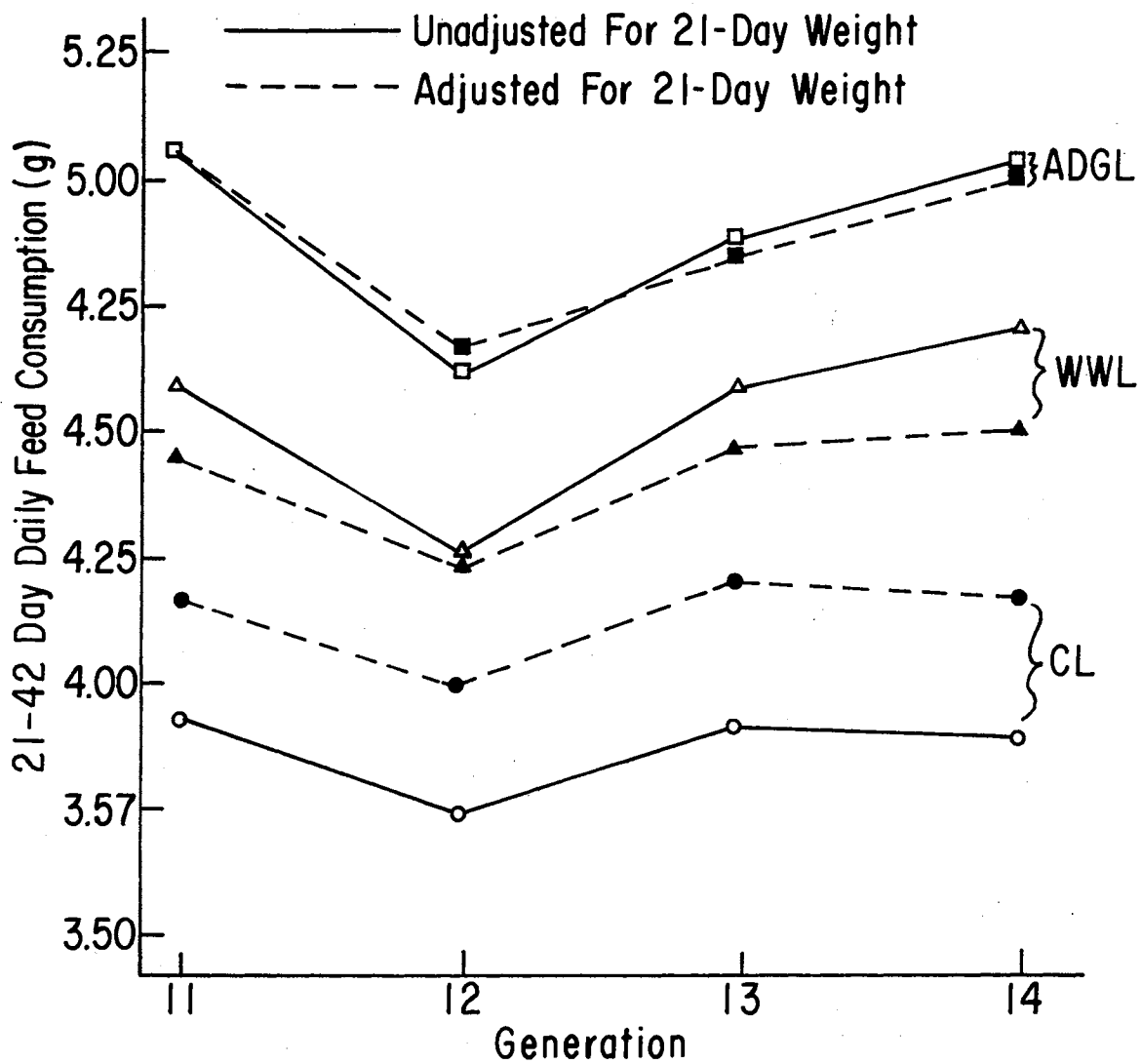
Figure 3. Daily Feed Consumption from 21 to 42 Days
Plotted on Generation.
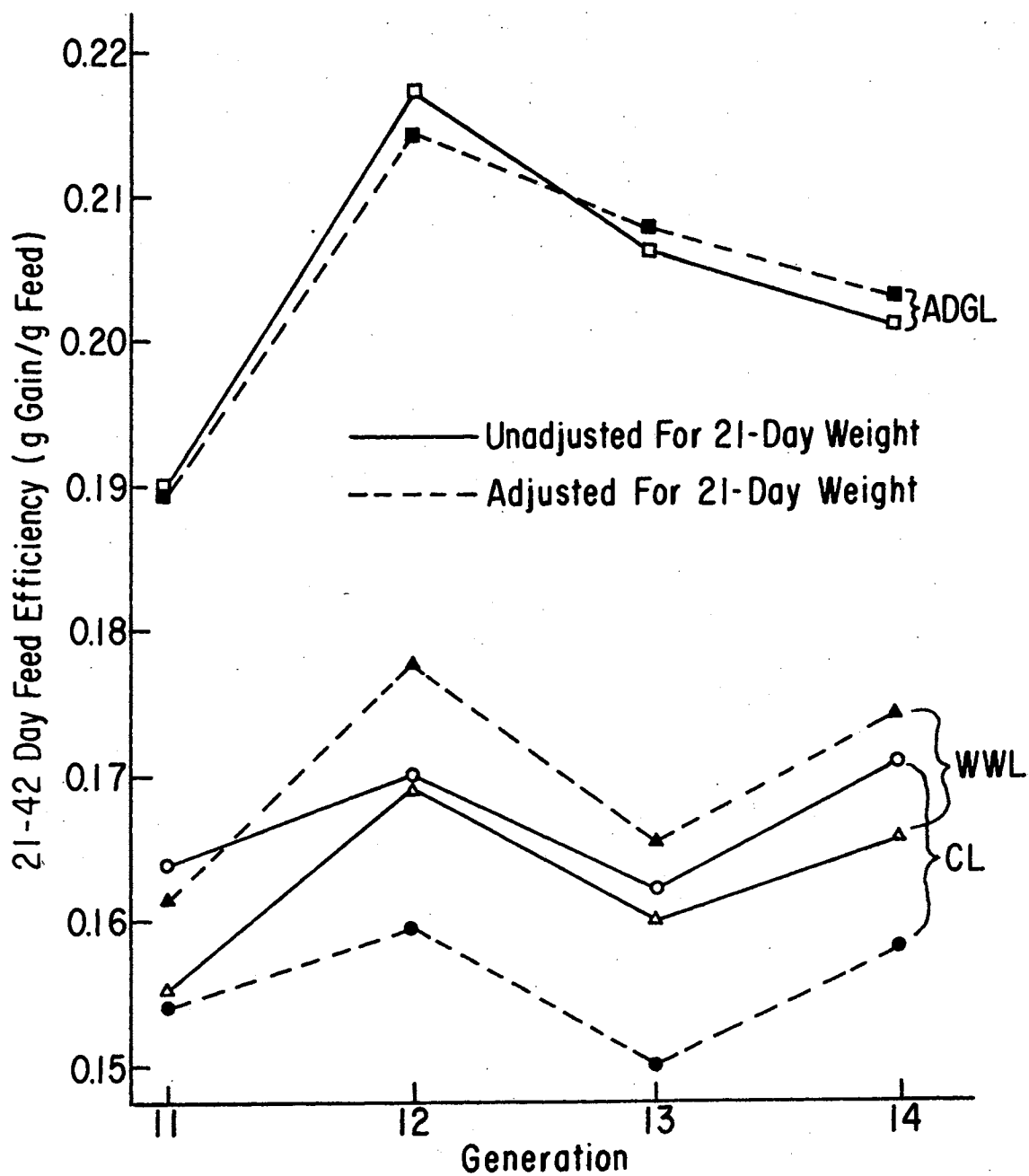
Figure 4. Feed Efficiency from 21 to 42 Days
Plotted on Generation.

TABLE VIII

BODY COMPOSITION AT 21 DAYS BY TYPE OF SELECTION LINE
AFTER 14 GENERATIONS OF SELECTION

	CONTROL LINES	WEANING WT. LINES	21 to 42-DAY ADG LINES	POOLED S.E.
Protein				
Percentage	18.49^a	18.19^b	18.52^a	0.109
Grams	1.36^a	1.81^b	1.65^c	0.049
Ether Extract				
Percentage	3.88	3.84	3.49	0.157
Grams	0.29^a	0.39^b	0.32^a	0.020
Moisture				
Percentage	76.57^a	76.87^a	77.49^b	0.224
Grams	5.65^a	7.62^b	6.94^c	0.220
Ash				
Percentage	1.04	1.14	1.04	0.182
Grams	.08	0.13	0.11	0.020

[a, b, c] Means on the same line with different superscripts differ
significantly (P<0.05).

small. At 21 days of age the WWL had significantly (P < .05) less per-
centage protein than did the CL by 0.30 percent of body weight. The
ADGL were not significantly different in percentage protein from the CL,
but had a significantly (P<.05) higher percentage protein than did the
WWL by 0.33 percent of body weight. No significant (P>.05) differences
in percentage ether extract were found between the three selection
groups. The percentage moisture of the ADGL was 0.92% of body weight
more than the CL, representing a significant (P<.01) increase in per-
centage moisture. The ADGL also were significantly higher (P<.05) than
the WWL in percentage moisture by 0.62% of body weight at 21 days. When
ash was expressed as a percentage of body weight at 21 days, no signifi-
cant differences between the selection groups were found. Both the WWL
and ADGL significantly (P<.01) exceeded the CL in total grams of protein
by 0.45 grams (33.1%) and 0.29 grams (21.3%). The WWL significantly
(P<.05) exceeded the ADGL by 0.16 grams of protein. The WWL also signif-
icantly (P < .01) exceeded the CL in grams of ether extract by 0.10 grams
(34.5%). The ADGL was not significantly different from the CL but did
have significantly less grams of fat (P<.05) than the WWL by 0.07 grams
(-17.5%). Both the WWL and the ADGL significantly (P<.01) exceeded the
CL in grams of moisture by 1.97 grams (34.9%) and 1.29 grams (22.8%),
respectively. No significant differences in total grams of ash were
found between the selection groups at 21 days of age.

Thus, the main differences between the selection groups at 21 days
of age were differences in total grams of compositional components. The
differences noted in percentage of compositional components were of
small magnitude and would not have a great deal of influence on the
postweaning feed efficiencies.

At 42 days of age the WWL were not significantly different from
the CL in percentage protein, but the ADGL had 0.57 (-3.0%) and 0.85
(-4.5%) percent of body weight less protein than the CL and the WWL,
respectively. Both differences were significant (P<0.01). Differences
in percentage ether extract, percentage moisture, and percentage ash be-
tween the selection groups at 42 days were all nonsignificant. In terms
of total grams of protein, all differences between selection groups
were significant (P<.01). The WWL and the ADGL exceeded the CL in
grams of protein by 1.01 grams (25.3%) and 1.65 grams (41.4%), re-
spectively. The ADGL exceeded the WWL by 0.64 grams (12.8%). The WWL
significantly (P<.05) exceeded the CL in total grams of ether extract
by 0.35 grams (27.8%). The ADGL had significantly more grams of ether
extract than the CL (P<.01) and the WWL (P<.05) by 0.66 grams (52.4%)
and 0.31 grams (19.3%), respectively. All differences between se-
lection groups in total grams of moisture at 42 days were significant
(P<.01). The WWL and the ADGL had 3.43 (22.2%) and 6.33 grams (41.0%)
more moisture than the CL. The ADGL were 2.90 grams (15.4%) in excess
of the CL in moisture at 42 days of age. The WWL had significantly
(P<.05) more grams of ash than the CL by 0.20 grams (29.9%) and the
ADGL had significantly (P<.01) more grams of ash than the CL by 0.34
grams (50.7%). The difference between the ADGL and the WWL was small
and nonsignificant.

Although the ADGL had significantly less protein at 42 days than
either the WWL or the CL on a percentage basis, the effect of this
difference on feed efficiency is unclear. Since it is a very small
difference, this should not effect feed efficiency to any large extent.
All other percentage components were not significantly different

TABLE IX

BODY COMPOSITION AT 42 DAYS BY TYPE OF SELECTION LINE
AFTER 14 GENERATIONS OF SELECTION

	CONTROL LINES	WEANING WT. LINES	21 to 42-DAY ADG LINES	POOLED S.E.
Protein				
Percentage	18.70^a	18.98^a	18.13^b	0.134
Grams	3.99^a	5.00^b	5.64^c	0.089
Ether Extract				
Percentage	5.87	6.06	6.10	0.330
Grams	1.26^a	1.61^b	1.92^c	0.107
Moisture				
Percentage	72.34	71.61	72.49	0.377
Grams	15.43^a	18.86^b	21.76^c	0.331
Ash				
Percentage	3.13	3.32	3.28	0.243
Grams	0.67^a	0.87^b	1.01^b	0.067

[a, b, c] Means on the same line with differing superscripts differ significantly (P<.05).

between the selection groups and, thus, should not be associated with the difference in feed efficiencies between the selection groups. The total grams of compositional components were different between all selection groups, as might be expected, since body weights were different.

The same pattern held for body composition at 56 days of age as it did for 42 days of age. The WWL were not significantly different in protein percentage from the CL at 56 days of age but the ADGL had significantly (P<.05, P<.01) less protein as a percentage of body weight than the CL and the WWL by 0.42 percent and 0.58 percent, respectively. Again, all other components when expressed as a percentage of body weight were not significantly different between any of the selection groups. The total grams of body components also followed the same pattern as did those at 42 days of age. The differences between groups in total grams of protein were all significant (P<.01). The WWL and the ADGL exceeded the CL in grams of protein by 0.92 grams (20.1%) and 2.18 grams (47.7%), respectively. The ADGL exceeded the WWL by 1.26 grams (23.0%). The difference in grams of ether extract between the WWL and the CL was significant (P<.05) and amounted to 0.37 grams (23.6%). The ADGL had significantly (P<.01) more grams of ether extract than CL or the WWL by 1.00 grams (63.7%) and 0.63 grams (32.5%), respectively. The total grams of moisture were significantly (P<.01) different between all selection groups. The WWL had 3.23 grams (18.5%) more moisture than the CL and the ADGL exceeded both the CL and WWL by 8.83 grams (50.6%) and 5.60 grams (27.1%), respectively. No significant difference was noted between the WWL and the CL in grams of ash. The ADGL did, however, significantly (P<.01) exceed the CL and the WWL by 0.48 grams (53.9%) and 0.32 grams (30.5%), for each group respectively.

TABLE X

BODY COMPOSITION AT 56 DAYS BY TYPE OF SELECTION LINE
AFTER 14 GENERATIONS OF SELECTION

	CONTROL LINES	WEANING WT. LINES	21 to 42-DAY ADG LINES	POOLED S.E.
Protein				
Percentage	18.69[a]	18.85[a]	18.27[b]	0.149
Grams	4.57[a]	5.49[b]	6.75[c]	0.087
Ether Extract				
Percentage	6.42	6.55	6.93	0.337
Grams	1.57[a]	1.94[b]	2.57[c]	0.119
Moisture				
Percentage	71.27	71.00	71.17	0.395
Grams	17.45[a]	20.68[b]	26.28[c]	0.297
Ash				
Percentage	3.62	3.59	3.75	0.260
Grams	0.89[a]	1.05[a]	1.37[b]	0.085

[a, b, c] Means on the same line with differing superscripts differ
significantly (P<.05).

Measurement of compositional components at 56 days of age in the three selection groups also failed to account for the differences in feed efficiency noted between the selection groups. The ADGL has slightly less protein on a percentage basis than did the WWL on the CL but this could scarcely account for the large differences in feed efficiency. The total grams of components followed the same pattern at 56 days of age as at 42 days of age. The ADGL had the highest total grams of body tissue, the WWL were intermediate, and the CL had the lowest total grams of body components.

Weights at 21 days were taken for all ages at sacrifice. Weights at 42 days, 21 to 42-day feed consumption, 21 to 42-day gross efficiency, and 21 to 42-day average daily gain were determined for those mice sacrificed at 42 days of age and 56 days of age. Weights at 56 days were taken on those mice slaughtered at 56 days. Means and standard errors for these are presented in Table XI. The same patterns of differences between selection groups in weights, performance, consumption, and efficiency that were noted in the measurements of generations 11, 12, 13, and 14 were noted in this subpopulation of generation 14. Thus, the mice involved in these body composition analyses were a very typical sample of the three selection group populations involved in the feed efficiency comparisons.

The différences in percentage body composition between the WWL and the CL at 21 days suggest that the WWL had slightly less protein (P<.05) on a percentage basis, slightly more water (P>.05), and slightly less percentage of ether extract (P>.05). At 42 and 56 days of age, the trend seemed reversed, that is, the WWL had a slightly greater percentage protein than did the CL (P>.05), a slightly higher percentage ether

TABLE XI

LIVE PERFORMANCE DATE BY TYPE OF SELECTION
LINE FOR EACH SLAUGHTER GROUP

TRAIT	CONTROL LINES	WEANING WT. LINES	21 to 42 DAY ADG LINES	POOLED S.E.
21-Day Wt. (g)				
21-Day Slaughter	7.4^a	9.9^b	9.0^c	0.29
42-Day Slaughter	7.8^a	10.5^b	10.0^b	0.33
56-Day Slaughter	8.0^a	10.5^b	9.9^b	0.33
42-Day Wt. (g)				
42-Day Slaughter	23.5^a	28.5^b	33.3^c	0.48
56-Day Slaughter	23.7^a	27.8^b	33.1^c	0.46
21 to 42-Day ADG (g/day)				
42-Day Slaughter	0.75^a	0.86^b	1.11^c	0.016
56-Day Slaughter	0.75^a	0.82^b	1.10^c	0.016
21 to 42-Day Feed Cons. (g/day)				
42-Day Slaughter	4.18^a	5.10^b	5.39^c	0.108
56-Day Slaughter	4.35^a	5.06^b	5.56^c	0.102
21 to 42-Day Feed Effic. (g/g)				
42-Day Slaughter	0.1793^a	0.1690^a	0.2087^b	0.0046
56-Day Slaughter	0.1731^a	0.1643^a	0.2003^b	0.0041
56-Day Wt. (g)				
56-Day Slaughter	26.2^a	30.8^b	39.0^c	0.46

a, b, c Means on the same line with differing superscripts differ
significantly (P<.05).

extract (P>.05), and a slightly lower percentage moisture (P>.05).

The differences in percentage body composition between the ADGL and the CL at 21 days showed trends suggesting that the ADGL had about the same percentage protein, slightly less percentage ether extract (P>.05), and slightly more percentage moisture (P<.05). At 42 and 56 days of age the ADGL tended to have a smaller percentage protein (P<.05), larger percentage ether extract (P>.05), and about the same percentage moisture as compared to the CL.

The ADGL tended to exceed the WWL in percentage protein at 21 days (P<.05), had slightly less percentage ether extract than the WWL at 21 days (P>.05), and slightly more moisture (P<.05). At 42 days of age, the ADGL had less percentage protein than did the WWL (P<.05), about the same percentage fat, and slightly higher percentage moisture (P>.05). At 56 days of age, the ADGL had less percentage protein than the WWL (P<.05), tended to have slightly more percentage ether extract (P>.05), but about the same percentage moisture.

These results imply that differences in percentage body composition are not of large magnitude. The total grams of compositional components, however, were significantly different (P<.05) between all the selection groups at all ages with the exception of ash at all ages and ether extract at 21 days. The WWL had significantly more total grams of compositional components at 21 days than the other two selection groups, with the exception of ash (P>.05). The ADGL exceeded the CL in grams of protein and moisture, but was not significantly higher in grams of ether extract or ash. At 42 and 56 days of age the ADGL significantly exceeded the WWL and the CL in total grams of protein, ether extract, and moisture and had significantly more ash than the CL.

It would appear that selection for weight at 21 days has increased the total grams of compositional components, but has not markedly altered the percentage of compositional components. Selection for 21 to 42-day average daily gain has resulted in the same pattern as the WWL in total compositional components but to a larger extent. Again, body composition as a percentage basis has not been markedly altered.

It would be hard to explain the differences in gross efficiency between the selection groups in terms of differences in percentage body composition. There were no statistically significant differences in proportionate ether extract deposition between the selection groups at any of the ages although a trend existed suggesting the ADGL went from proportionately less ether extract at 21 days to proportionately more at 42 and 56 days. McLellan (1972) reported results from a selection study in a population that was extracted from the foundation population of this study. When mice were selected for large and small hind-leg muscle weight, no difference in percentage compositional components was found between the controls, large line, or small line, even though there were differences in 21 to 42-day average daily gain. The small differences found in percent composition in this study are also in agreement with work by Lang and Legates (1969) that found no differences in percent ether extract between mice selected for large six week weight and control line mice. These results further agree with work Stanier and Mount (1972), where no significant differences in percent ether extract were found between mice selected for large six week weight and control line mice.

Differences were noted in the percentage protein between the WWL and the other two groups at 21 days and the ADGL and the other two groups

at 42 and 56 days. These differences were relatively small proportions of their comparative mean. The statistical significances found were more a function of experimental precision than of large differences between selection groups. Also, the literature to date does not suggest that percentage protein can be markedly altered by selection.

At any rate, there is little evidence that suggests that the CL and the WWL were depositing a grossly larger proportion of tissue than required more feed energy to deposit. Many workers have noted that increased efficiency is associated with increased proportionate fat deposition (Dickerson and Grimes, 1947; Fowler, 1958; Biondini, et al., 1969; Timon, et al., 1970). This is in opposition to what might be expected, but nevertheless, has been supported by evidence from several studies. Since feed efficiency is a function of the amount of gain relative to the feed consumed, any proportionate increase in gain (fat or lean or both) would contribute to increased efficiency. The evidence from this data suggest that the proportionate increase in gain in this population was in terms of all components and not any one component.

The question of the causal effect in the increased efficiency of the ADGL in this population is still a matter of speculation. The larger proportionate increase in gain cannot be accounted for solely in increased feed consumption, nor can the differences in fat deposition account for the differences in gain. This might suggest, then that differences in digestibility might exist or that there might be differences in the utilization of feed energy in the metabolic pathways. This is not saying that increased feed consumption cannot cause differences in efficiency. It is saying, however, that increased consumption may not be the sole causative factor in differences in efficiency. There is

need to further investigate genetic differences in digestibility and body metabolism.

Estimates of Heritabilities, Genetic Correlations
and Phenotypic Correlations

Heritabilities, genetic correlations, and phenotypic correlations were estimated from variance-covariance analysis using 203 male progeny and 220 female progeny from the control line population. A hierarchal design was employed as described in the materials and methods. The analyses of variance and covariance for both males and females are presented in Appendix Tables XX and XXI. The general forms of the analyses can be found in Table XII. The estimates of the population parameters can be found in Table XIII. The estimates of the genetic correlations were taken from half sib estimates from the analysis of the 203 males since the majority of these correlations were unavilable in the combined analysis due to negative sire components and since feed consumption and efficiency was measured only on the male progeny. The estimates of the heritabilities of the growth traits were taken from the combined analysis of males and females as were the phenotypic correlations involving only growth traits. The estimates of the heritabilities of consumption and efficiency were taken from the analysis involving the male progeny as were the phenotypic correlations.

The negative heritability of 21-day weight was the result of a negative sire component in the combined analysis of males and females and is suggestive of large maternal effects as might be expected with this trait. The positive genetic correlation between 21-day weight and 42 day weight of 0.44 agrees with the increased 42-day weight noted in

TABLE XII

GENERAL FORM OF ANALYSES OF VARIANCE AND COVARIANCE FOR
ESTIMATING GENETIC PARAMETERS IN CONTROL
LINE POPULATION

Source	df	Expected Mean Squares	Expected Mean Products[c]
Males and Females[a]			
Total	422		
Sires	61	$\sigma^2 + 3.793\sigma_{D_2}^2 + 6.815\sigma_S^2$	$(\sigma_1\sigma_2) + 3.793\ (\sigma_1\sigma_2)_D + 6.815\ (\sigma_1\sigma_2)_S$
Dams/Sires	51	$\sigma^2 + 3.681\sigma_D^2$	$(\sigma_1\sigma_2) + 3.681\ (\sigma_1\sigma_2)_D$
Sex	1		
Progeny/ Dams/Sires	309	σ^2	$(\sigma_1\sigma_2)$
203 Males[b]			
Total	202		
Sires	60	$\sigma^2 + 1.951\sigma_D^2 + 3.324\sigma_S^2$	$(\sigma_1\sigma_2) + 1.951\ (\sigma_1\sigma_2) + 3.324\ (\sigma_1\sigma_2)$
Dams/Sires	44	$\sigma^2 + 1.909\sigma_D^2$	$(\sigma_1\sigma_2) + 1.909\ (\sigma_1\sigma_2)$
Progeny/ Dams/Sires	98	σ^2	$(\sigma_1\sigma_2)$

[a] Values for analysis of 209 males and 213 females.

[b] Values for analysis of 206 males on which feed consumption and feed efficiency was measured.

[c] $\sigma_1\sigma_2$ = Covariance between trait 1 and trait 2.

the WWL. The negative genetic correlation between 21-day weight and 21

to 42-day average daily gain of -.12 is not in agreement with the corre-

lated increase in gain noted in the WWL or the correlated increase in

21-day weight in the ADGL, but the standard error is of such a magnitude

($\pm$.27) that not too much confidence can be placed on the sign of this

estimate. The positive genetic correlation between 21-day weight and

feed consumption of 0.37 is in agreement with the increased feed con-

sumption in the WWL. The negative genetic correlation between 21-day

weight and efficiency of -.48 agrees in sign with the slight decrease

in efficiency noted in the WWL but the results of selection and the

standard error on this estimate ($\pm$.38) tend to make the magnitude of the

estimate questionable.

Weight at 42 days seems to be moderately heritable (0.35) and shows

a large positive genetic correlation to average daily gain (0.85). This

agrees with the increased 42-day weights in the ADGL. Weight at 42 days

had a positive genetic correlation to both feed consumption and feed

efficiency of 0.69 and 0.31, respectively.

Average daily gain from 21 to 42 days showed a high heritability

(0.88) and moderately high positive genetic correlations to feed con-

sumption and efficiency of 0.55 and 0.63, respectively. This agrees well

with the response to selection noted in the ADGL and with the increased

consumption and efficiency of the lines noted in the four generations

measured.

Weight at 56 days had a negative sire component in both analyses

and no genetic correlations between this trait and other traits were

available. A maternal effect was not expected in 56-day weight such

that this result was inexplicable.

Daily feed consumption from 21 to 42 days had a high heritability of 0.73. The genetic correlation of feed consumption and efficiency was -.31 but the standard error of $\pm.32$ tended to make this estimate questionable in value.

Feed efficiency showed a high heritability of greater than one (1.09) and suggested that satisfactory selection progress might be made if direct selection were practiced for this trait.

The phenotypic correlations were of the same sign and approximate magnitude of the genetic correlations with the exception of the phenotypic correlation between 42-day weight and feed efficiency. The genetic correlation between these traits was 0.31, whereas the phenotypic correlation was -.08. Neither were significantly different from zero.

Conclusions

Selection for weight at 21 days has resulted in an increase of weight at all ages, including average weight between 21 and 42 days of age. Selection for this trait has also significantly increased feed consumption between 21 and 42 days, but a correlated increase in average daily gain during this period of time offset the increased feed consumption. Thus, the feed efficiency between 21 and 42 days was not markedly altered, although it was slightly decreased. Body composition analysis of mice selected for 21-day weight did not yield evidence that selection had resulted in a large proportional change of any of the compositional components at 21, 42, or 56 days. Estimates of genetic correlations between the performance traits largely substantiated the results of measurement of the performance, consumption, and efficiency in this selection group. It might be surmised that selection for weight at 21 days has

TABLE XIII

ESTIMATES OF HERITABILITIES, GENETIC CORRELATIONS[b]
AND PHENOTYPIC CORRELATIONS FROM VARIANCE-
COVARIANCE ANALYSIS OF CONTROL LINE
MALES AND FEMALES[a]

	21-Day Weight	42-Day Weight	ADG 21-42	56-Day Weight	Daily Feed Cons. (21-42)	Feed Effic. (21-42)
21-Day Weight	-.03 ± .12[c]	0.44 ± .23	-.12 ± .27	--	0.37 ± .26	-.48 ± .38
42-Day Weight	0.66[c]	0.35 ± .17[c]	0.85 ± .08	--	0.69 ± .14	0.31 ± .26
ADG 21-42 Days	-.01[c]	0.74[c]	0.88 ± .22[c]	--	0.55 ± .18	0.63 ± .16
56-Day Weight	0.55[c]	0.86[c]	0.66[c]	-.04 ± .12[c]	--	--
Daily Feed Cons. (21-42)	0.61[b]	0.80[b]	0.57[b]	0.69[b]	0.73 ± .37[b]	-0.31 ± .32
Feed Effic. (21-42)	-.59[b]	-.08[b]	0.39[b]	-.12[b]	-.51[b]	1.09 ± .38[b]

[a] Estimates of heritability are on the diagonal, estimates of genetic correlations are above the diagonal, and phenotypic correlations are below the diagonal. SE are given for h^2 and r_g.

[b] Estimates are from the analysis of the 203 males on which feed consumption and efficiency was measured.

[c] Estimates are from the analysis of the 423 males and females.

resulted in a larger animal with larger maintenance requirements, but with larger feed consumption over maintenance. However, the increase in gain derived from the increase in consumption was not of such magnitude that the efficiency of gain was increased.

Selection for average daily gain between 21 to 42 days has resulted in increased weight at all ages. Selection for average daily gain has also resulted in increased feed consumption, but the magnitude of increased gain is such that the efficiency of gain has been markedly increased. Body composition analysis of mice selected for 21 to 42-day average daily gain presented evidence of decreased percentage protein at 42 and 56 days. The difference detected was more a function of experimental precision than of large differences. A trend for the percentage ether extract to be higher was noticed, but the differences were relatively small and nonsignificant. The estimates of heritability and genetic correlations between the performance, consumption, and efficiency traits largely substantiated the results obtained in the measurement of these traits.

If the data were unavailable from the group selected for 21-day weight, then it might be reasonable to assume that the increase in average daily gain in the group selected for 21 to 42 day average daily gain was due to the increase in feed consumption. However, the difference in feed consumption between the group selected for 21-day weight and the group selected for 21 to 42-day average daily gain was proportionally much smaller than was the difference in average daily gain. It would be difficult to attribute the large difference in gain to the small differences in consumption. Efficiency could be due to something more than differences in feed consumption. At 42 days of age there was

no difference in percent ether extract between the two selection groups
which further suggests that the group selected for 21-day weight was not
depositing proportionally more fat. Therefore, this data presents evidence
that there may be genetic differences in either digestibility or
the metabolism of nutrients after absorption. Further work on these two
aspects of efficiency might more fully elucidate the problem of feed efficiency
in animals.

In terms of generalities applicable to farm animals, these date
and results from the literature strongly suggest that selection for post-
weaning average daily gain would be accompanied by an increase in gross
efficiency postweaning. Thus, selection directly for feed efficiency
may not be necessary. The results of this study, compared with similar
studies, imply differences in gain of body components between these
strains of mice and other strains besides differences in gain relative
to the feed consumption. This implies that close attention should be
paid, during the course of a selection experiment, to the composition
of gains. This study would imply that increased feed consumption is not
necessarily indicative of increased efficiency of gain.

CHAPTER V

SUMMARY

Feed consumption from 21 to 42 days and feed efficiency from 21 to 42 days (expressed as gain/feed) was measured in a population of mice that had been selected for 11, 12, 13, and 14 generations. The selection criterion in three of the lines was weight at 21 days (WWL) and the selection criterion in another three lines was 21 to 42-day average daily gain (ADGL). Two unselected control lines (CL) were maintained for each generation of selection. In the 14th generation of selection 24 litters from each selection group were randomly chosen to contribute three males for body composition analysis at 21, 42, and 56 days of age. In addition, genetic parameters were estimated from variance-covariance analyses of the control lines.

The WWL significantly exceeded the CL in 21-day weight in all four generations with the differences ranging from 2.1 grams (26.6%) to 2.4 grams (29.6%). The WWL was significantly heavier than the CL at 42 days of age in all four generations with these differences ranging from 3.6 grams (15.4%) to 4.8 grams (21.8%). The 21 to 42-day average daily gains of the WWL were also higher than the CL in all four generations with the differences ranging from 0.07 grams (10.9%) to 0.12 grams (18.2%). Feed consumption between 21 to 42 days was significantly higher in the WWL as compared to the CL in all four generations. The differences between these two groups ranged from 0.52 grams (13.9%) to 0.81

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(20.8%). The feed efficiency of the WWL was less than the feed efficiency of the CL in all four generations but the differences were significant in only two of the four generations and were small in all generations. These differences had values ranging from -.001 grams/gram (-.6%) to -.009 grams/gram (-5.4%).

Body composition analyses of the WWL at three different ages did not present evidence of large differences in percentage compositional components between the WWL and the CL. The estimates of genetic correlations between 21-day weight and other traits largely supported the observations from measurement. The genetic correlations between 21-day weight and feed consumption or feed efficiency were estimated to be $0.37 \pm .26$ and $-.48 \pm .38$, respectively.

Selection for 21-day weight has resulted in an animal that was heavier at all ages and, thus, required more feed for maintenance. Consumption in the WWL was sufficiently greater than the CL to cause a difference in average daily gain. The resultant ratio of the gain to the feed consumed was very nearly the same as the CL. The percentage composition of growth in the WWL was essentially the same as in the CL.

The ADGL were also significantly heavier at 21 days than were the CL in all four generations. The differences in 21-day weight had values ranging from 1.0 gram (11.1%) to 1.7 grams (21.5%). The ADGL were also significantly heavier at 42 days of age than the CL in these generations with differences ranging from 8.0 grams (34.2%) to 9.4 grams (44,5%). The 21 to 42-day average daily gains of the ADGL significantly exceeded those of the CL with differences in the four generations ranging from 0.32 grams (50.0%) to 0.36 grams (57.1%). The differences in feed consumption between the ADGL and the CL were significant for all four

generations with values ranging from 0.88 grams (23.6%) to 1.14 grams (29.3%). The feed efficiency of the ADGL were significantly higher than the CL in all four generations. These differences had values ranging from 0.026 grams/gram (16.0%) to 0.047 grams/gram (27.5%).

Body composition analyses of the ADGL at three different ages did not present strong evidence of any large differences between the ADGL and the CL in percentage components at any age. Estimations of genetic correlations between traits again largely supported the results of the measurement of the performance and consumption traits. The genetic correlation between 21 to 42-day average daily gain and feed consumption or feed efficiency were estimated to be $0.55 \pm .18$ and $0.63 \pm .16$, respectively.

Selection for 21 to 42-day average daily gain has resulted in a heavier animal at all ages with corresponding increased weight to maintain. The feed consumption of the ADGL also increased as a result of selection but the increased gain resulting from selection was of sufficient magnitude to result in a higher ratio of gain to feed. Body composition analyses indicated that selection for 21 to 42-day average daily gain has not largely altered percentage composition.

Comparisons of the WWL and the ADGL showed that the WWL was significantly heavier at 21 days than the ADGL but the ADGL were significantly higher in average daily gain, 42-day weight, feed consumption, and feed efficiency. Comparisons showed, however, that while the ADGL and WWL had differences in the four generations ranging from 1.4 grams (7.4%) to 2.35 grams (13.3%), average weight on test, with the ADGL the higher of the two, the ADGL consumed only slightly more feed than the WWL in the four generations, with the differences ranging 0.30 (6.6%)

grams to 0.47 (10.2%) grams. This increase in feed consumption in the ADGL was accompanied by increased average daily gain as compared to the WWL, with differences between the two groups in the four generations ranging from 0.23 (29.5%) grams per day to 0.27 (38.6%) grams per day. If this increase in feed consumption was the causative factor in increased gain then the increased feed consumption of the WWL should have resulted in more gain than it did, even with the increased maintenance requirements of the WWL over the CL. On this basis, it was concluded that the increase in 21 to 42-day gain and efficiency in the ADGL was not solely a function of increased consumption.

Since there were no large differences in percentage body components between the selection groups, it was further concluded that part of the increase in gain and efficiency in the ADGL might be a function of increased digestibility or differences in metabolism once the nutrients are absorbed.

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APPENDIX

TABLE XIV

ANALYSIS OF VARIANCE FOR GENERATION 11

SOURCE	D.F.	MEAN SQUARES				
		21-DAY WT.	42-DAY WT.	21-42 DAY ADG.	21-42 DAY FEED CONS.	21-42 DAY FEED EFFIC.
Group	2	119.81**	1428.73**	2.6676**	28.1795**	0.03546**
Sex	1	3.03	1452.63**	3.0009**	12.2285**	0.06692**
Line/Group 1	1	8.33**	5.75	0.0005	0.2108	0.00086
Line/Group 2	2	3.12	15.20**	0.0110*	0.9734**	0.00207*
Line/Group 3	2	7.30**	2.06	0.0279**	0.4766	0.00297
Sex X Group	2	0.39	6.15	0.0168**	0.0398	0.00028
Sex X Line/Group 1	1	0.83	0.46	0.0053	0.1045	0.00113
Sex X Line/Group 2	2	0.21	8.56*	0.0156**	0.7676*	0.00121
Sex X Line/Group 3	2	0.57	0.27	0.0031	0.0682	0.00014
Residual	286	1.08	2.33	0.0030	0.2022	0.00054

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

TABLE XV

ANALYSIS OF VARIANCE FOR GENERATION 12

SOURCE	D.F.	MEAN SQUARES				
		21-DAY WT.	42-DAY WT.	21-42 DAY ADG.	21-42 DAY FEED CONS.	21-42 DAY FEED EFFIC.
Group	2	122.09**	1247.43**	2.6273**	14.0657**	0.06544**
Sex	1	5.65	961.35**	1.8604**	7.1016**	0.04722**
Line/Group 1	1	0.00	0.68	0.0012	0.0226	0.00012
Line/Group 2	2	4.80	4.53	0.0019	5.2994**	0.01243**
Line/Group 3	2	52.71**	30.71**	0.0220**	7.4006**	0.02250**
Sex X Group	2	1.61	12.83	0.0214**	0.0205	0.00096
Sex X Line/Group 1	1	1.06	8.10	0.0076	0.2838	0.00001
Sex X Line/Group 2	2	1.20	9.18	0.0111	0.7331	0.00055
Sex X Line/Group 3	2	4.17	32.69**	0.0340**	0.3235	0.00127
Residual	250	2.32	4.41	0.0044	0.3522	0.00092

*P<.05   **P<.01

TABLE XVI

ANALYSIS OF VARIANCE FOR GENERATION 13

SOURCE	D.F.	MEAN SQUARES				
		21-DAY WT.	42-DAY WT.	21-42 DAY ADG.	21-42 DAY FEED CONS.	21-42 DAY FEED EFFIC.
Group	2	100.30**	1749.53**	2.9901**	18.9733**	0.06318**
Sex	1	3.90	948.05**	1.8786**	15.9949**	0.01892**
Line/Group 1	1	0.62	24.66**	0.0416**	1.0856**	0.00854**
Line/Group 2	2	8.09**	3.94	0.0027	0.1460	0.00007
Line/Group 3	2	14.37**	5.08	0.0069	1.3103**	0.00449**
Sex X Group	2	2.32	14.65**	0.0169*	0.3123	0.00072
Sex X Line/Group 1	1	0.01	2.83	0.0054	0.0016	0.00046
Sex X Line/Group 2	2	0.39	4.16	0.0080	0.1040	0.00038
Sex X Line/Group 3	2	0.32	1.01	0.0004	0.0044	0.00005
Residual	269	1.34	3.05	0.0042	0.2180	0.00042

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

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TABLE XVII

ANALYSIS OF VARIANCE FOR GENERATION 14

SOURCE	D.F.	MEAN SQUARES				
		21-DAY WT.	42-DAY WT.	21-42 DAY ADG.	21-42 DAY FEED CONS.	21-42 DAY FEED EFFIC.
Group	2	121.21**	1238.70**	1.8238**	23.1121**	0.02154**
Sex	1	7.42*	579.89**	1.0367**	8.9802**	0.01112**
Line/Group 1	1	0.01	12.22*	0.0297**	0.0009	0.00205**
Line/Group 2	2	9.78**	6.44	0.0058	0.1240	0.00020
Line/Group 3	2	9.60**	4.09	0.0173**	0.1442	0.00157**
Sex X Group	2	0.85	6.06	0.0145*	0.0198	0.00014
Sex X Line/Group 1	1	2.63	0.02	0.0073	0.0393	0.00015
Sex X Line/Group 2	2	1.64	2.39	0.0109*	0.2222	0.00049
Sex X Line/Group 3	2	1.62	1.52	0.0010	0.0074	0.00008
Residual	213	2.01	3.05	0.0032	0.1331	0.00026

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

TABLE XVIII

ANALYSIS OF VARIANCE FOR POSTWEANING DAILY FEED CONSUMPTION ADJUSTED
FOR 21-DAY WEIGHT IN GENERATIONS 11, 12, 13 AND 14

SOURCE				MEAN SQUARES				
	d.f.	GEN. 11	d.f.	GEN. 12	d.f.	GEN. 13	d.f.	GEN. 14
Group	2	0.03403**	2	0.06112**	2	0.07057**	2	0.02709**
Sex	1	0.07249**	1	0.05533**	1	0.02317**	1	0.01646**
Line/Group 1	1	0.00009	1	0.00013	1	0.00970**	1	0.00197**
Line/Group 2	2	0.00228**	2	0.01322**	2	0.00030	2	0.00120**
Line/Group 3	2	0.00206*	2	0.00712**	2	0.00128*	2	0.00034*
Sex X Group	2	0.00027	2	0.00082	2	0.00022	2	0.00028
Sex X Line/Group 1	1	0.00075	1	0.00012	1	0.00050	1	0.00000
Sex X Line/Group 2	2	0.00106	2	0.00022	2	0.00031	2	0.00012
Sex X Line/Group 3	2	0.00009	2	0.00184	2	0.00012	2	0.00013
21-Day Wt. B Linear	1	0.01439**	1	0.03732**	1	0.02218**	1	0.03315**
Residual	285	0.00049	249	0.00078	268	0.00034	212	0.00010

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

TABLE XIX

ANALYSIS OF VARIANCE FOR POSTWEANING FEED EFFICIENCY ADJUSTED
FOR 21-DAY WEIGHT IN GENERATIONS 11, 12, 13 AND 14

SOURCE				MEAN SQUARES				
	d.f.	GEN. 11	d.f.	GEN. 12	d.f.	GEN. 13	d.f.	GEN. 14
Group	2	19.0674**	2	11.9379**	2	7.6875**	2	8.8951**
Sex	1	10.0824**	1	4.9178**	1	12.9609**	1	5.9224**
Line/Group 1	1	0.0023	1	0.0199	1	1.4214**	1	0.0001
Line/Group 2	2	0.8876**	2	5.6139**	2	0.5826*	2	0.9064**
Line/Group 3	2	0.5429*	2	1.6946**	2	0.1973	2	0.0548
Sex X Group	2	0.0127	2	0.0475	2	0.1082	2	0.0724
Sex X Line/Group 1	1	0.0266	1	0.1178	1	0.0041	1	0.2700*
Sex X Line/Group 2	2	0.6308*	2	0.4490	2	0.0412	2	0.1913*
Sex X Line/Group 3	2	0.1514	2	0.1502	2	0.0020	2	0.0439
21-Day Wt. B Linear	1	9.5615**	1	19.5694**	1	13.2861**	1	16.9402**
Residual	285	0.1694	249	0.2750	268	0.1692	212	0.0538

*P<.05   **P<.01

TABLE XX

ANALYSIS OF VARIANCE AND COVARIANCE FOR ESTIMATING GENETIC PARAMETERS USING CONTROL LINE MALES AND FEMALES

SOURCE	D.F.	MEANS SQUARES AND COMPONENTS						K_1^a	K_2^b
		21-Day Wt.		42-Day Wt.		21 to 42 Day ADG			
		M.S.	COMP.	M.S.	COMP.	M.S.	COMP.		
Sires	61	5.3719	-.0128	10.9216	0.3304	0.0149**	0.0011	3.7932	6.8147
Dams/Sires	51	5.3084**	1.3395	8.4608**	1.8551	0.0070**	0.0011	3.6805	-
Sex	1	1.3938**	-	985.6487**	-	2.0039**	-	-	-
Progeny/Dam/ Sire	309	0.3784	-	1.6331	-	0.0029	-	-	-

SOURCE	D.F.	MEAN CROSSPRODUCTS AND COMPONENTS						K_1^a	K_2^b
		21-Day Wt. and 42-Day Wt.		21-Day Wt. and 21 to 42 Day ADG		42-Day Wt. and 21 to 42 Day ADG			
		M.P.	COMP.	M.P.	COMP.	M.P.	COMP.		
Sires	61	4.9932	-.0859	-.0188	-.0049	0.2857	0.0188	3.7932	6.8147
Dams/Sire	51	5.4246	1.3672	0.0140	.0036	0.1545	0.0261	3.6805	-
Progeny/Dams/ Sires		0.3926	-	0.0008	-	0.0584	-	-	-

[a]Coefficient for dam within sire component.

[b]Coefficient for sire component.

*P<.05   **P<.01

TABLE XXI

ANALYSIS OF VARIANCE AND COVARIANCE FOR ESTIMATING GENETIC PARAMETERS USING CONTROL LINE MALES

SOURCE	D.F.	MEAN SQUARES AND COMPONENTS							
		21-Day Wt.		42-Day Wt.		21 to 42 Day ADG		K_1^a	K_2^b
		M.S.	COMP.	M.S.	COMP.	M.S.	COMP.		
Sires	60	3.5774	0.2796	8.7283*	0.9719	.0107**	.0017	1.9506	3.3236
Dams/Sires	44	2.5978**	1.4159	1.9766**	0.0050	0.0050*	0.0010	1.9091	—
Progeny/Dams/Sires	98	0.2864	—	1.6423	—	0.0030	—		

SOURCE	D.F.	MEAN SQUARES AND COMPONENTS					
		21 to 42 Day Feed Comp.		21 to 42 Day Feed Effic.		K_1^a	K_2^b
		M.S.	COMP.	M.S.	COMP.		
Sires	60	0.4197**	0.0418	0.0005**	0.0001	1.9506	3.3236
Dams/Sires	44	0.2767**	0.0989	0.0002**	0.0001	1.9091	—
Progeny/Dams/Sires	98	0.0879	—	0.0001	—		

TABLE XXI (Continued)

SOURCE	D.F.	MEAN CROSS PRODUCTS AND COMPONENTS						$K_1{}^a$	$K_2{}^b$
		21 Day Wt. and 42 Day Wt.		21 Day Wt. and 21 to 42 Day ADG		21-Day Wt. and 21 to 42 Day Feed Cons.			
		M.P.	COMP.	M.P.	COMP.	M.P.	COMP.		
Sires	60	3.8327	0.2287	0.0123	-.0026	0.7516	0.0404	1.9506	3.3236
Dams/Sire	44	3.0144	1.4061	0.0207	0.0096	0.6054	0.2844	1.9091	-
Progeny/Dams/ Sires	98	1.7361	-	0.0119	-	0.3469	-	-	-

SOURCE	D.F.	MEAN CROSSPRODUCTS AND COMPONENTS						$K_1{}^a$	$K_2{}^b$
		21 Day Wt. and 21 Day to 42 Day Effic.		42 Day Wt. and 21 to 42 Day ADG		42-Day Wt. and 21 to 42 Day Feed Cons.			
		M.P.	COMP.	M.P.	COMP.	M.P.	COMP.		
Sires	60	-.0250	-.0021	0.2341	0.0346	1.5322	0.1385	1.9506	3.3236
Dams/Sires	44	-.0178	-.0084	0.1179	0.0289	1.0550	0.4087	1.9091	-
Progeny/Dams/ Sires	98	-.0102	-	0.0916	-	0.6834	-	-	-

TABLE XXI (Continued)

SOURCE	D.F.	42 Day Wt. and 21 to 42 Day Effic.		21 to 42 Day ADG and 21 to 42 Day Feed Cons.		21 to 42 Day ADG and 21 to 42 Day Effic.		K_1^a	K_2^b
		M.P.	COMP.	M.P.	COMP.	M.P.	COMP.		
Sires	60	−.0055	0.0025	0.0375	0.0046	0.0009	0.0002	1.9506	3.3236
Dams/Sires	44	−.0133	−.0083	0.0219	0.0063	0.0002	−	1.9091	−
Progeny/Dams/ Sires	98	−.0051	−	0.0162	−	0.0002	−	−	−

SOURCE	D.F.	21 to 42 Day Feed Cons. and 21 to 42 Day Effic.						K_1^a	K_2^b
		M.P.	COMP.						
Sires	60	−.0072	−.0005					1.9506	3.3236
Dams/Sires	44	−.0054	−.0023					1.9091	−
Progeny/Dams/ Sires	98	−.0032	−						

[a]Coefficient for dam within sire component.
[b]Coefficient for sire component.
*P<.05   **P<.01

VITA λ

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