GENETIC ARCHITECTURE OF REPRODUCTIVE AND GROWTH TRAITS IN LABORATORY MICE

by

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INTRODUCTION

Knowledge of genetic architecture for economically important traits in domestic livestock is an important goal for the geneticist. By determining which genetical forces influence the trait investigated, a correct mating scheme can maximize desirable responses. Unfortunately most domestic species possess long generation intervals and the expense involved in animals and facilities become limiting factors. Since many basic quantitative genetic principles transcend species barriers, a pilot organism such as the laboratory mouse with a short generation interval, high fertility rates and easy management of large numbers becomes a useful source of genetical material. Although direct inferences cannot be made to other species, a better understanding of the basic genetic principles involved should be useful for designing and interpreting research in other species.

Reproduction and growth are the most economically important characteristics in domestic livestock. Reproductive traits such as litter size in swine, egg production in poultry, liveability of calves in dairy and beef cattle are the basis for continuance of these species. Growth traits such as gain and live body weight are economic measures of quantity and efficiency of meat production.

No experiment to date has simultaneously investigated all genetic parameters of reproductive and growth traits in mice. Thus, the purposes of this study were (1) to estimate accurately the contribution

additive, dominance and epistatic gene action makes to the phenotypic expression of number of young born per litter, littering time, mortality from birth to 5 days, 12-day litter weight, body weights at 12, 21, 42 and 56 days of age and 12-21, 21-42 and 42-56 day gain, (2) to determine the importance of maternal effects and sex linkage for the above traits and (3) to utilize the mating design proposed by Kearsey and Jinks (1968) in partitioning additive, dominance and epistatic sources of variation.

REVIEW OF LITERATURE

Components of the Genetic Model

The importance of investigation into the genetic structure of quantitative traits can hardly be over-stressed. Genetic improvement of traits in plants and animals is contingent upon knowledge of the relative magnitudes of components which make up heritable variation. Major components of the genetic model are additive, dominance and epistatic effects. Other components also influencing the genotype of an individual are maternal and sex-linked effects. Many studies which will be reviewed have estimated the size of one or more of these components.

Additive and Dominance Effects

Considerable evidence regarding contribution of additive gene action is available for many traits in animals. Relatively few experiments have estimated the contribution dominance makes to genetic expression of traits.

Heritability estimates (in a narrow sense) measure the fraction of phenotypic variance which is additively genetic. Several estimates of heritability have been reported in mice for reproductive and weight traits. A heritability estimate presented by Miller et al. (1963) for litter size in mice shows that .20 of the phenotypic fraction is due to additive gene action. Miller et al. (1963) and Jara-Almonte and White

(1973) obtained heritability estimates of .08 and .24 ± .12, respectively, for 12-day litter weight. As for individual body weight traits at 12-days, a heritability estimate of .05 ± .09 was reported by Jara-Almonte and White (1973). Miller et al. (1963), Vinson et al. (1969) and Jara-Almonte and White (1973) reported values of .16, .24 ± .06 and .33 ± .13, respectively, for heritability of 42-day body weight. For 56-day weight, Vinson et al. (1969) and Jara-Almonte and White (1973) showed a value of .29 ± .07 and .29 ± .13. Heritabilities of postweaning gain traits in mice have also been measured. Miller et al. (1963), Vinson et al. (1969) and Jara-Almonte and White (1973) found heritability estimates for gain in body weight from 21 to 42 days were .12, .27 ± .07 and .22 ± .12, respectively. A realized heritability for 12 generations of selection for increased and decreased gain from 21 to 42 days of age reported by White (1975) was .25 ± .03 for high line and .22 ± .02 for low line. For gain from 42 to 56 days of age, Jara-Almonte and White (1973) reported a heritability of .19 ± .11.

The relative importance of the dominance portion to heritable variance has been studied in only a few cases. Godwin (1972) found dominance was 17% of the phenotypic variance for birth weight and was 0% for all other individual body weight traits in mice. Miller et al. (1963) reported evidence of dominance variance accounting for 28% of total variance for number of mice born in a litter. No dominance effects were found for 12-day litter weight, 21-day and 42-day body weights and 21-42 day gain. Diallel analysis using mice (Jamison et al., 1975) suggests that non-additive gene action was a significant source

of variation for 21-day weight, 12-21 and 42-56 day gain. Using a similar type analysis, Carmon (1963) failed to find any significant variation attributable to dominance effects for 21 and 45 day body weights. In Drosophila melanogaster, Keller and Mitchell (1964) determined that dominance gene action did exist for egg production and was directional. Kearsey and Kojima (1967) found no evidence for directional dominance for female body weight in Drosophila.

Epistasis

Only a few studies have attempted to determine the importance of interactions between additive and dominance effects, or epistasis. An experiment using Drosophila melanogaster (Kearsey and Kojima, 1967) has shown the presence of additive x additive interaction for female body weight and a weak dominance x dominance interaction for hatchability.

Maternal and Sex-linked Effects

When reciprocal crosses are not identical, maternal and sex-linked effects must be important influences affecting the phenotype of the offspring. Genetic maternal effects which cause the genotype of the offspring to be influenced by the dam's genotype for maternal ability can be broken down into additive, dominance and epistatic genetic components. Presence of sex-linked genes becomes evident when differences between reciprocal crosses are confined to one sex. Sex-linkage effects can also be partitioned into additive, dominance and interaction components attributable to those genes.

Various experiments have been conducted to show the importance

of maternal effects. Bateman (1954) found that maternal effects (genetic and environmental) accounted for 73% of the variance for individual 12-day body weights in laboratory mice. Carmon and Golley (1964) using field mice obtained similar results; 72% of total variance for 21-day weight was due to maternal effects. Rutledge et al. (1972), Miller et al. (1963) and Jamison et al. (1975) found that maternal influences, in mice, have an insignificant effect on total phenotypic variance for body weight at birth but rise sharply through weaning and decline rapidly as the animal matures. Jamison et al. (1975) further showed that maternal effects were not an important source of variation for gain from 12 to 21 and 21 to 42 days of age, but are for gain from 42 to 56 days.

Generally most experiments estimating maternal effects divide the maternal variance into genetic and environmental maternal variances. A few studies have further partitioned the genetic maternal variance into additive and dominance components. Eisen et al. (1970) found 6% of phenotypic variation for 12-day litter weight in mice was attributal to additive maternal and 50% to maternal environmental variation. Robinson et al. (1974) showed that maternal additive genetic variance made up 16% of the variance for 12-day body weight. For postweaning individual weight traits, Godwin (1972) found additive maternal accounted for 25%, 0% and 0%; dominance maternal 6%, 26% and 19%; and maternal environmental 20%, 11% and 16% of total phenotypic variation for 21, 42 and 60 day weights, respectively. In Drosophila, Barnes (1968) found that for yield of progeny the maternal genotype showed directional dominance.

Presence of sex-linked effects in mice has been reported. Carmon (1963) found a highly significant sex-linked effect for weight of mice at 21 and 45 days. White et al. (1970) crossing selected and control lines of mice indicated that sex-linked genes probably have little effect on body weight and gain traits. Utilizing crosses between inbred lines of mice, White et al. (1975) did find some sex-linkage affecting the same weight and gain traits. Tests for sex-linkage, especially in diallel analyses, are confounded with non-additive maternal effects as shown by Eisen et al. (1966).

Mating Designs Used to Estimate Genetic Components

Estimates of genetic components can arise only through carefully planned mating designs; designs which allow us to equate computed phenotypic variances or covariances to expected genetic components and obtain efficient estimates of these components. The most common types of designs used to measure genetic parameters are matings within a random mating population, selection experiments and crossing between lines.

Mating designs within a random mating population use sets of relatives to estimate desired genetic components. The most common sets of relatives used are parent-offspring and half- or full-sibs. Generally, these relatives give us estimates of additive effects only. By utilizing many sets of relatives at a time as indicated by Eisen (1967), more genetic information, including maternal effects, can be obtained.

Selection for a particular characteristic can be carried out in

many ways: mass selection, family selection, sib selection, progeny testing, etc. (Falconer, 1960). Amount of genetic gain measured from response to selection for increased or decreased performance can be used to estimate the realized heritability of the selected trait which is another way to calculate the contribution of additive genetic variation to the total phenotypic variation. Some idea as to significance of non-additive gene action can be achieved by measuring heterosis originating from crossing extreme selection lines.

Many mating designs which cross different lines are used to estimate genetic parameters. The distinct advantage of these designs is that only one generation of data is needed. The two discussed here are diallel crossing among inbred lines and the triple test cross. The diallel model presented by Henderson (1948) allows one to indicate the importance of autosomal, maternal and sex-linked genetic variance through estimation of general, specific and maternal combining abilities. The triple test cross devised by Kearsey and Jinks (1968) can provide a test for epistasis as well as estimates of additive and dominance effects. The triple test cross will be the mating design described in this study.

MATERIAL AND METHODS

Experimental Design and Laboratory Procedure

Two lines of mice selected for increased and decreased gain from 21 to 42 days of age were the genetic material. These lines originated from a large random bred ICR population. The high line (H), completed 24 generations of selection for increased postweaning gain while the low line (L), completed 21 generations for decreased gain. Figure 1 shows a plot of the generation means for high and low lines. The mating design of this experiment, referenced by Kearsey and Jinks (1968), was the triple test cross, but two preceding generations were needed to generate F_1 and F_2 lines. In total five generations were needed to complete the study--generation 0 was used to expand the high and low lines, generation 1 generated H, L and F_1 lines, generation 2 generated H, L, F_1 and F_2 lines, generations 3 and 4 (a replicate of generation 3) were the actual backcross of F_2 males to H, L and F_1 females. Since parentals are maintained through generation 2, any changes in genotype or environment could be easily noted. Figure 2 shows the triple test mating design for generation 1 through 4. Due to the complexity of alphabetic notation, high line was designated 1, low line 2, F_1 cross HL 3, F_1 cross LH 4 and combinations of F_2 crosses HL x HL, HL x LH, LH x HL, LH x LH were 5, 6, 7, 8, respectively. Assignment of males to respective females was done randomly with sib and cousin restrictions.

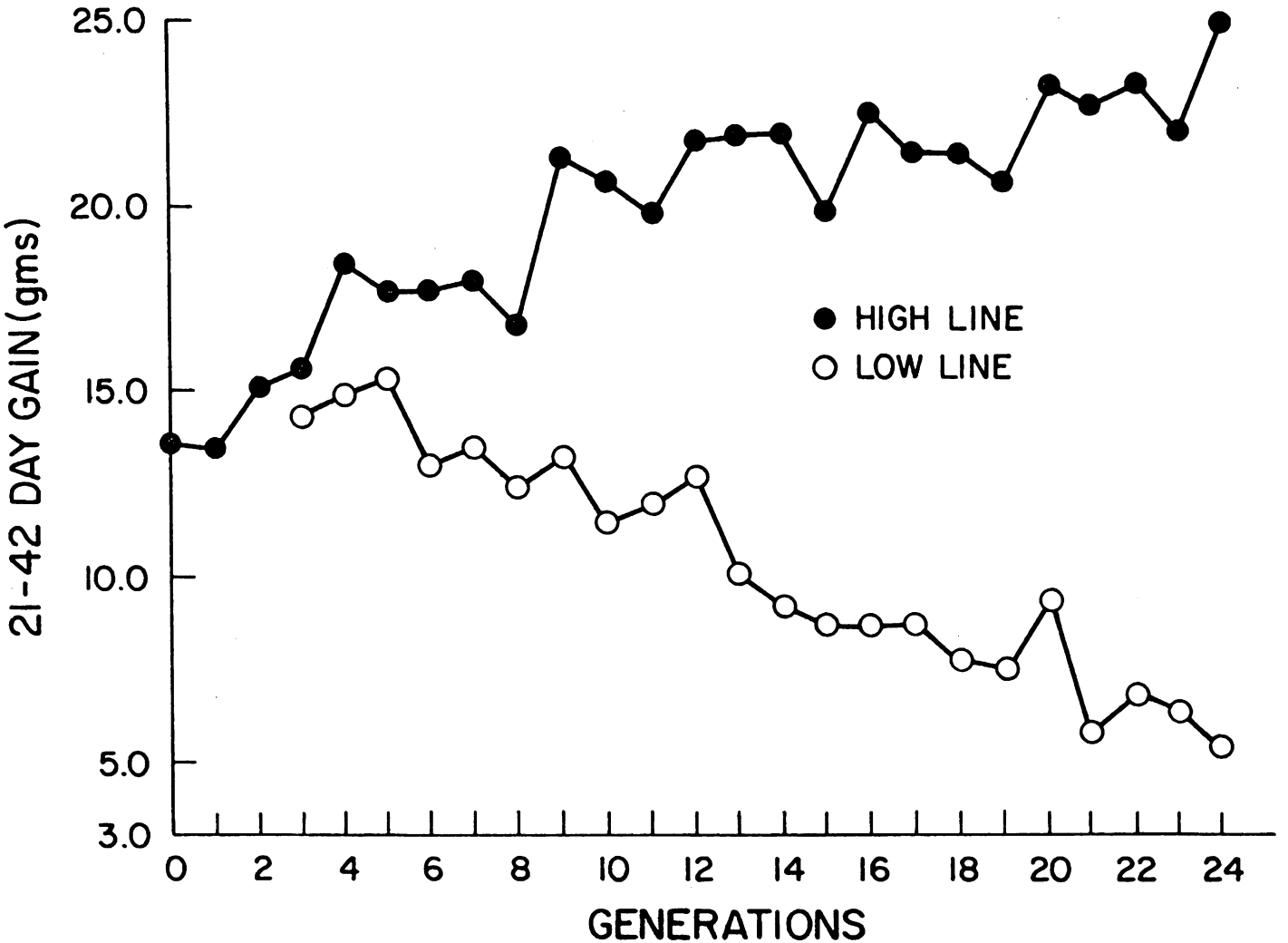


Figure 1. Response to selection for increased and decreased gain from 21 to 42 days of age

GEN 1

SIRE LINE \ DAM LINE	H	L
H	H	HL
L	LH	L

GEN 2

SIRE LINE \ DAM LINE	H	L	HL	LH
H	H	HL	x	x
L	LH	L	x	x
HL	x	x	HLHL	HLLH
LH	x	x	LHHL	LHLH

GEN 3 AND 4

SIRE LINE		DAM LINE
HLHL	x	H, L, LH, HL
HLLH	x	H, L, LH, HL
LHHL	x	H, L, LH, HL
LHLH	x	H, L, LH, HL

Figure 2. Triple test cross mating design

At birth, number of mice born, dam, sire, and litter number were recorded along with date of birth. At 5 days of age all litters were standardized to four males and four females. If a litter had less than eight but more than five, fostered mice were supplemented and later discarded at weaning. Litter traits measured on each dam were number born per litter, mortality of young from birth to 5 days expressed as a percentage, number of days from exposure of male to littering and 12-day litter weight. Weight traits measured on each offspring were 12, 21, 42 and 56 day body weights. Three gain traits were computed for each individual: 12-21, 21-42 and 42-56 day gain. Only mice surviving to 56 days of age were used in analyses of the data; 2% were eliminated. The subclass numbers for littering traits of each group are presented in Table 1. Note that litter weight at 12 days includes only those litters which have weight measurements also, while other littering traits were measured on all litters. Table 2 shows subclass numbers for weight traits of each group for both sexes. Appendix Tables 47 through 52 contain arithmetic means and standard deviations for generation 0, 1, 2, 3 and 4 for all littering and weight traits.

Statistical Analyses of Components of Means

Presence of various types of gene action can be detected using components of means. Four genetic models were tested: (1) which contained additive and dominance effects only; (2) which added non-allelic interactions; (3) which contained additive and dominance autosomal and sex-linked effects; and (4) which contained additive and dominance autosomal and maternal effects. Traits analyzed were divided

Table 1. Subclass numbers for littering traits

Group	Traits: No. born, litt. time, MB-5 days					Litt. wt. 12 days				
	Gen 0	Gen 1	Gen 2	Gen 3	Gen 4	Gen 0	Gen 1	Gen 2	Gen 3	Gen 4
P_1(H)	43	42	48	-	-	42	40	43	-	-
P_2(L)	54	49	57	-	-	50	45	46	-	-
F_{1-3}	-	48	43	-	-	-	47	41	-	-
F_{1-4}	-	42	49	-	-	-	41	42	-	-
F_2	-	-	271	-	-	-	-	190	-	-
$F_2 x P_1$	-	-	-	138	93	-	-	-	101	70
$F_2 x P_2$	-	-	-	141	99	-	-	-	102	72
$F_2 x F_{1-3}$	-	-	-	147	100	-	-	-	103	70
$F_2 x F_{1-4}$	-	-	-	147	99	-	-	-	104	72

Table 2. Subclass numbers for weight traits by sex

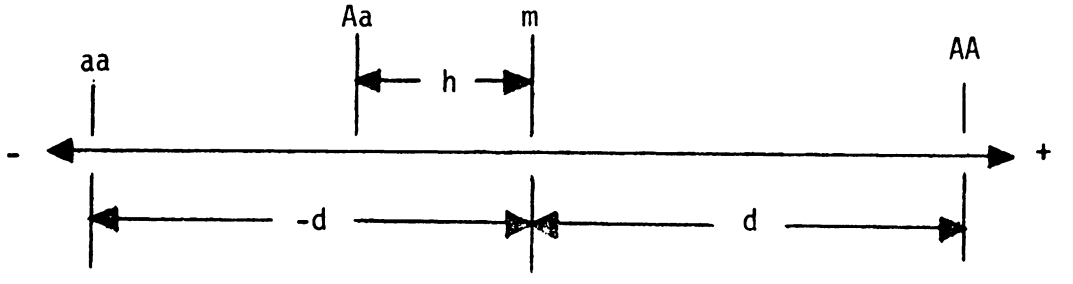
Group	Males					Females				
	Gen 0	Gen 1	Gen 2	Gen 3	Gen 4	Gen 0	Gen 1	Gen 2	Gen 3	Gen 4
P_1	143	161	155	-	-	164	140	165	-	-
P_2	147	161	196	-	-	191	172	159	-	-
F_{1-3}	-	189	158	-	-	-	173	155	-	-
F_{1-4}	-	146	151	-	-	-	171	169	-	-
F_2	-	-	747	-	-	-	-	722	-	-
$F_2 \times P_1$	-	-	-	396	286	-	-	-	395	266
$F_2 \times P_2$	-	-	-	409	272	-	-	-	378	285
$F_2 \times F_{1-3}$	-	-	-	402	282	-	-	-	390	258
$F_2 \times F_{1-4}$	-	-	-	410	279	-	-	-	402	268

into three general groupings. The first group contained the littering traits: number born, littering time, mortality from birth to 5 days and 12-day litter weights. The second and third groups contained the weight traits of males and females, respectively: 12-, 21-, 42- and 56-day body weights and 12-21, 21-42 and 42-56 day gain. A problem arises with the littering traits, a question of whose genotype is measured as number born, littering time, mortality from birth to 5 days and 12-day litter weights the mother or offspring. Analyses used here assume that these characters are determined by the genotype of the offspring with a maternal component dependent on the mother's genotype.

Additive and Dominance Effects

At one locus with two alleles, an individual will have the genotype, AA, Aa, or aa. The effects of these combinations on phenotype can be described by two parameters, d and h. d is used to represent phenotypic differences between the two homozygotes AA and aa while h represents departure in phenotype of the heterozygote Aa from the mid-point between AA and aa, m. Taking m, mid-point, as the origin, the effects on the magnitude of the characters are:

AA d, Aa h, aa -d.



The gene's contribution to additive genetic variation is proportional to d and h reflects the dominance properties of the genes. If there is no dominance, then h = 0 and Aa will be at the midpoint. If A is dominant, h is positive and if a is dominant, h is negative. If dominance is complete, h is equal to +d or -d. The degree of dominance is h/d.

If the relative frequencies of the three genotypes with respect to each gene are known for any population of individuals, the expected deviation of the mean of the population can be specified in terms of d and h. For example, in the F_2 population, half the individuals will be heterozygous and half homozygous for each segregating gene pair assuming $p_A = .5$. Among the homozygotes, half will be homozygous AA and half aa for each gene difference so their contribution to generation means will cancel out. Heterozygotes do contribute to the generation mean. Hence, summing over all segregating genes, the F_2 generation mean will equal m + 1/2[h] where [h] reflects the summed dominance deviations of all genotypes. These results can be generalized to any cross between two true breeding lines. Table 3 shows some of the relationships used in this study assuming an additive-dominance model is adequate on the scale used.

By using scaling tests described by Mather and Jinks (1971), quantities A, B and C and their variances can be used to test the adequacy of the additive-dominance model (covariances between groups were assumed to be zero).

$$A = 2\overline{F_2 x P_1} - \overline{P}_1 - \overline{F}_1 \text{ with } \hat{V}_A = 4V_{\overline{F_2 x P_1}} + V_{\overline{P}_1} + V_{\overline{F}_1}$$

Table 3. Expected means derived from crosses between two true breeding lines assuming additive-dominance model

$\bar{P}_1 = m + [d]$
$\bar{P}_2 = m - [d]$
$\bar{F}_1 = m + [h]$
$\bar{F}_2 = m + 1/2[h]$
$\overline{F_2 x P_1} = m + 1/2[d] + 1/2[h]$
$\overline{F_2 x P_2} = m - 1/2[d] + 1/2[h]$
$\overline{F_2 x F_1} = m + 1/2[h]$

$$B = 2\overline{F_2xP_2} - \overline{P}_2 - \overline{F}_1 \text{ with } \hat{V}_B = 4V_{\overline{F_2xP_2}} + V_{\overline{P}_2} + V_{\overline{F}_1}$$

$$C = 4\overline{F}_2 - 2\overline{F}_1 - \overline{P}_1 - \overline{P}_2 \text{ with } \hat{V}_C = 16V_{\overline{F}_2} + 4V_{\overline{F}_1} + V_{\overline{P}_1} + V_{\overline{P}_2}$$

If the model is adequate, quantities A, B and C will equal zero within the limits of sampling error.

Since P_1, P_2, F_1 and F_2xP_1, F_2xP_2, F_2xF_1 groups are raised in several generations, least square means adjusted for either generation or replicate effects are used for the generation mean of each.

Another test for adequacy of additive-dominance model was proposed by Cavalli (1952). This procedure consists of estimating the parameters m, [d] and [h] by using least squares means and standard errors of different groups. From the estimated parameters expected values for each group can be computed and then compared with the observed group means.

The three parameters m, [d] and [h] are estimated by using a weighted least squares procedure. Since the various group means do not have equal precision, the group means and their expectations must be weighted by the reciprocals of the squared standard errors of each group as shown in Table 4. An information matrix, J, contains the weighted coefficients of m, [d] and [h], $\hat{M}$ estimates of parameters and N a matrix of weighted observed means. The weighted least squares equations used to estimate parameters for additive-dominance model are given in Table 5. The solution is then

$$\hat{M} = J^{-1}N$$

where J^{-1} is the inverse of the information matrix and is a variance-covariance matrix, the diagonal elements of which are the standard

Table 4. Weights and coefficients of parameters used to test additive-dominance model

Groups	Weights	m	[d]	[h]	Obs mean	Expected mean
P_1	$1/(S.E.P_1)^2$	1	1	0	$\bar{P}_1$	m + [d]
P_2	$1/(S.E.P_2)^2$	1	-1	0	$\bar{P}_2$	m - [d]
F_1	$1/(S.E.F_1)^2$	1	0	1	$\bar{F}_1$	m + [h]
F_2	$1/(S.E.F_2)^2$	1	0	1/2	$\bar{F}_2$	m + 1/2[h]
F_2xP_1	$1/(S.E.F_2xP_1)^2$	1	1/2	1/2	$\overline{F_2xP_1}$	m + 1/2[d] + 1/2[h]
F_2xP_2	$1/(S.E.F_2xP_2)^2$	1	-1/2	1/2	$\overline{F_2xP_2}$	m - 1/2[d] + 1/2[h]
F_2xF_1	$1/(S.E.F_2xF_1)^2$	1	0	1/2	$\overline{F_2xF_1}$	m + 1/2[h]

Table 5. Weighted least squares equations used to estimate parameters for additive-dominance model

$$
\begin{bmatrix}
\left(\begin{array}{l} 1/(S.E.P_1)^2 + 1/(S.E.P_2)^2 + \\ 1/(S.E.F_1)^2 + 1/(S.E.F_2)^2 + \\ 1/(S.E.F_2xP_1)^2 + \\ 1/(S.E.F_2xP_2)^2 + \\ 1/(S.E.F_2xF_1)^2 \end{array}\right) & \left(\begin{array}{l} 1/(S.E.P_1)^2 - 1/(S.E.P_2)^2 + \\ 1/2(S.E.F_2xP_1)^2 - \\ 1/2(S.E.F_2xP_2)^2 \end{array}\right) & \left(\begin{array}{l} 1/(S.E.F_1)^2 + 1/2(S.E.F_2)^2 + \\ 1/2(S.E.F_2xP_1)^2 + \\ 1/2(S.E.F_2xP_2)^2 + \\ 1/2(S.E.F_2xF_1)^2 \end{array}\right) \\
 & \left(\begin{array}{l} 1/(S.E.P_1)^2 + 1/(S.E.P_2)^2 + \\ 1/4(S.E.F_2xP_1)^2 + \\ 1/4(S.E.F_2xP_2) \end{array}\right) & \left(\begin{array}{l} 1/4(S.E.F_2xP_1)^2 - \\ 1/4(S.E.F_2xP_2)^2 \end{array}\right) \\
\text{(Symmetric)} & & \left(\begin{array}{l} 1/(S.E.F_1)^2 + 1/4(S.E.F_2)^2 + \\ 1/4(S.E.F_2xP_1)^2 + \\ 1/4(S.E.F_2xP_2)^2 + \\ 1/4(S.E.F_2xF_1)^2 \end{array}\right)
\end{bmatrix}
\begin{bmatrix} \hat{m} \\ \hat{d} \\ \hat{h} \end{bmatrix}
=
\begin{bmatrix}
\left(\begin{array}{l} 1/(S.E.P_1)^2 \cdot \bar{P}_1 + \\ 1/(S.E.P_2)^2 \cdot \bar{P}_2 + \\ 1/(S.E.F_1)^2 \cdot \bar{F}_1 + \\ 1/(S.E.F_2)^2 \cdot \bar{F}_2 + \\ 1/(S.E.F_2xP_1)^2 \cdot \overline{F_2xP_1} + \\ 1/(S.E.F_2xP_2)^2 \cdot \overline{F_2xP_2} + \\ 1/(S.E.F_2xF_1)^2 \cdot \overline{F_2xF_1} \end{array}\right) \\
\left(\begin{array}{l} 1/(S.E.P_1)^2 \cdot \bar{P}_1 - \\ 1/(S.E.P_2)^2 \cdot \bar{P}_2 + \\ 1/2(S.E.F_2xP_1)^2 \cdot \overline{F_2xP_1} - \\ 1/2(S.E.F_2xP_2)^2 \cdot \overline{F_2xP_2} + \end{array}\right) \\
\left(\begin{array}{l} 1/(S.E.F_1)^2 \cdot \bar{F}_1 + \\ 1/2(S.E.F_2)^2 \cdot \bar{F}_2 + \\ 1/2(S.E.F_2xP_1)^2 \cdot \overline{F_2xP_1} + \\ 1/2(S.E.F_2xP_2)^2 \cdot \overline{F_2xP_2} + \\ 1/2(S.E.F_2xF_1)^2 \cdot \overline{F_2xF_1} \end{array}\right)
\end{bmatrix}
$$

J $\hat{M}$ = N

errors of the estimated parameters.

Adequacy of the additive-dominance model can be tested by comparing the observed group means and expected group means which are predicted from estimates of the three parameters using a χ^2 test. The goodness of fit can be tested by squaring the deviation of the observed from the expected value for each group mean, multiplying by the corresponding weight and summing the products over all groups. The resultant value is compared with a χ^2 distribution with degrees of freedom number of groups minus three. Since most of the χ^2 were extremely large, these values were used to compare the various models and determine which genetic model fits the data.

Non-allelic Interactions

If the additive-dominance model appears inadequate, further investigation into non-allelic interactions would be appropriate. Three more parameters are needed to test epistasis as described by Mather and Jinks (1971) assuming interactions between three or more genes are negligible. With two different genes each with two alleles, A-a and B-b, eight parameters are used to describe the different genotypes. Four of these are the d's and h's, d_a, d_b, h_a and h_b which are lumped into parameters used before d and h. Parameters corresponding to interactions between non-allelic genes are i_{ab} is the additive x additive interaction between the a^{th} and b^{th} loci; $j_{a/b}$ or $j_{b/a}$ is the additive x dominance or dominance x additive interaction and l_{ab} is the dominance x dominance interaction.

For the present study the parameters equated to their mean are shown in Table 6. Weighted least squares procedures similar to those used for the additive-dominance model are used to estimate m, [d], [h], [i], [j] and [l]. The coefficients of the interaction parameters are in all cases derived as the products of the coefficients of the corresponding pair of d's and h's taking sign into account. The expected group means are then compared with observed means using a χ^2 goodness of fit test with degrees of freedom equal to the number of groups minus six thus testing the adequacy of this model.

If quantities A, B and C used in the scaling test (discussed on page 16) are not zero, they could give some indication to the importance of combinations of interactions. Test C depends to a greater extent on the l type interaction, but it is possible that these tests will fail to detect non-allelic interactions. Since

$$A = 2\overline{F_2 x P_1} - \overline{P}_1 - \overline{F}_1 = -1/2[i] + 1/2[j] - 1/2[l]$$

$$B = 2\overline{F_2 x P_2} - \overline{P}_2 - \overline{F}_1 = -1/2[i] - 1/2[j] - 1/2[l]$$

$$C = 4\overline{F}_2 - 2\overline{F}_1 - \overline{P}_1 - \overline{P}_2 = -2[i] - [l],$$

quantities A, B or C can be zero when interaction is present largely because the sign of the i's, j's and l's may differ from one pair of interacting genes to another.

Heterosis

Heterosis can be defined as the amount by which the mean of an F_1 group exceeds its better parent. Some question arises as to which

Table 6. Weights and coefficients of parameters used to test for non-allelic interactions

Group	Weight	m	[d]	[h]	[i]	[j]	[l]	Obs. mean	Expected mean
P_1	$1/(S.E.P_1)^2$	1	1	0	1	0	0	$\bar{P}_1$	m + [d] + [i]
P_2	$1/(S.E.P_2)^2$	1	-1	0	1	0	0	$\bar{P}_2$	m - [d] + [i]
F_1	$1/(S.E.F_1)^2$	1	0	1	0	0	1	$\bar{F}_1$	m + [h] + [l]
F_2	$1/(S.E.F_2)^2$	1	0	1/2	0	0	1/4	$\bar{F}_2$	m + 1/2[h] + 1/4[l]
F_2x P_1	$1/(S.E.F_2xP_1)^2$	1	1/2	1/2	1/4	1/4	1/4	$\overline{F_2xP_1}$	m + 1/2[d] + 1/2[h] + 1/4[i] + 1/4[j] + 1/4[l]
F_2xP_2	$1/(S.E.F_2xP_2)^2$	1	-1/2	1/2	1/4	-1/4	1/4	$\overline{F_2xP_2}$	m + 1/2[d] + 1/2[h] + 1/4[i] - 1/4[j] + 1/4[l]
F_2xF_1	$1/(S.E.F_2xF_1)^2$	1	0	1/2	0	0	1/4	$\overline{F_2xF_1}$	m + 1/2[h] + 1/4[l]

is the better parent so heterosis is specified positive if $\bar{F}_1 > P_1$ and negative if $\bar{F}_1 < \bar{P}_2$ assuming P_1 corresponds to the parent with the greater mean value and P_2 to the parent with the smaller mean value.

If heterosis is measured on a scale for which an additive-dominance model is adequate, positive heterosis is

$$\text{Heterosis} = \bar{F}_1 - \bar{P}_1 = [h] - [d]$$

so that for heterosis to occur [h] must be positive and greater than [d]. For negative heterosis

$$\text{Heterosis} = \bar{F}_1 - \bar{P}_2 = [h] - [d] = [h] + [d]$$

and heterosis will occur only when [h] is negative and greater than [d].

But if non-allelic interactions are needed for an adequate model, positive heterosis is

$$\text{Heterosis} = \bar{F}_1 - \bar{P}_1 = ([h] + [l]) - ([d] + [i])$$

and negative heterosis is

$$\text{Heterosis} = \bar{F}_1 - \bar{P}_2 = ([h] + [l]) - (-[d] + [i])$$

The presence or absence of heterosis is not in itself indicative of the presence or absence of any particular type of gene action or interaction; it can result from a whole range of combinations of gene effects. Therefore, it is necessary that we know the appropriate genetic model for the trait under investigation.

Test for Sex-linkage

Differences between reciprocal crosses generally suggest the influence of sex-linkage, maternal effects or both. Diagnostic properties of sex-linkage given by Mather and Jinks (1971) are:

(1) A difference between reciprocal crosses in the F_1 generation which is confined to the heterogametic sex.

(2) A difference between reciprocal crosses in the F_2 generation which is confined to the homogametic sex.

(3) A difference between reciprocal crosses in the two backcrosses, in both sexes, but a difference between the two reciprocal crosses using the inbred line as the homogametic parent which is confined to the individuals of that sex.

Parameters used to estimate sex-linkage differ according to the sex of the animal. In the homogametic sex (XX) three genotypes are possible with respect to a gene pair: X_AX_A, X_AX_a and X_aX_a with contributions to the mean of d_x, h_x and $-d_x$, respectively. The heterogametic sex (XY) has only two genotypes possible, X_AY and X_aY with contributions of d_x and $-d_x$.

The additive-dominance model including autosomal, [d] and [h], and sex-linked, [d_x] and [h_x], effects given in Table 7 can be fitted to male and female data separately by the method of weighted least squares. In the males, number of groups minus 4 determines the degrees of freedom used for testing adequacy of the model while in females, number of groups minus 5 determines degrees of freedom. χ^2 test of goodness of fit is used to determine which of the parameters is significant.

Test for Maternal Effects

Maternal effects arise when the phenotype of the offspring is confounded with the maternal influence of its dam. Influences can be

Table 7. Coefficients of parameters used to test for sex-linkage

Group	Mating		Progeny										
			Male					Female					
	Male Parent	Female Parent	m	[d]	[h]	[d_x]	Male obs. mean	m	[d]	[h]	[d_x]	[h_x]	Female obs. mean
P_1	P_1	x P_1	1	1	0	1	$\overline{P_1}$	1	1	0	1	0	$\overline{P_1}$
P_2	P_2	x P_2	1	-1	0	-1	$\overline{P_2}$	1	-1	0	-1	0	$\overline{P_2}$
F_{1-3}	P_1	x P_2	1	0	1	-1	$\overline{F_{1-3}}$	1	0	1	0	1	$\overline{F_{1-3}}$
F_{1-4}	P_2	x P_1	1	0	1	1	$\overline{F_{1-4}}$	1	0	1	0	1	$\overline{F_{1-4}}$
$F_{2(3x3)}$	$F_1(P_1xP_2)$	x $F_1(P_1xP_2)$	1	0	1/2	0	$\overline{F_{2-3}}$	1	0	1/2	-1	1/2	$\overline{F_{2-3}}$
$F_{2(4x4)}$	$F_1(P_2xP_1)$	x $F_1(P_2xP_1)$	1	0	1/2	0	$\overline{F_{2-4}}$	1	0	1/2	1/2	1/2	$\overline{F_{2-4}}$
F_2xP_1	F_2	x P_1	1	1/2	1/2	1	$\overline{F_2xP_1}$	1	1/2	1/2	1/2	1/2	$\overline{F_2xP_1}$
F_2xP_2	F_2	x P_2	1	-1/2	1/2	-1	$\overline{F_2xP_2}$	1	-1/2	1/2	-1/2	1/2	$\overline{F_2xP_2}$
F_2xF_{1-3}	F_2	x $F_1(P_1xP_2)$	1	0	1/2	0	$\overline{F_2xF_{1-3}}$	1	0	1/2	0	1/2	$\overline{F_2xF_{1-3}}$
F_2xF_{1-4}	F_2	x $F_1(P_2xP_1)$	1	0	1/2	0	$\overline{F_2xF_{1-4}}$	1	0	1/2	0	1/2	$\overline{F_2xF_{1-4}}$

cytoplasmic inheritance, pre- or post-natal nutrition from the mother, imitative behavior, interaction of sibs, etc.

The maternal parameters contributed to their progenies by three possible genotypes of the mother AA, Aa, and aa are specified d_m, h_m and $-d_m$, respectively, (Barnes, 1968). The components of means for groups used in this experiment are shown in Table 8. As before, estimates of parameters are obtained by the method of weighted least squares. χ^2 tests with degrees of freedom 5 less than number of groups determine the adequacy of the model and which parameters are significant.

Statistical Analyses of Components of Variation

Genetic Structure of Data

The triple test cross first proposed by Comstock and Robinson (1952) and later extended by Kearsey and Jinks (1968) was executed in generations 3 and 4 as shown in Figure 2. F_2 males were mated to high line, low line and F_1 females. L_1 and L_2 designated the cross of F_2 male with high and low females and L_3 and L_4 designated the cross of F_2 male with F_{1-3} and F_{1-4} females. Generation 4 was a replicate of generation 3 with all matings repeated. Only F_2 sires which successfully mated a high, low and one F_1 female both replicates could be used in the analyses. Because of the structure of the analyses to be discussed later, the data was broken up into 3 groups, the first containing L_1, L_2 and L_3; the second containing L_1, L_2 and L_4; the third containing L_1 and L_2 only. The means and variances of these three groups are shown in Tables 9, 10 and 11. Variances are presented since they

Table 8. Coefficients of parameters used to test for maternal effects

Group	Mating		Progeny					Obs. mean
	Paternal parent	Maternal parent	m	[d]	[h]	$[d_m]$	$[h_m]$	
P_1	P_1	P_1	1	1	0	1	0	$\bar{P}_1$
P_2	P_2	P_2	1	-1	0	-1	0	$\bar{P}_2$
F_{1-3}	P_1	P_2	1	0	1	-1	0	$\overline{F_{1-3}}$
F_{1-4}	P_2	P_1	1	0	1	1	0	$\overline{F_{1-4}}$
F_2	F_1	F_1	1	0	1/2	0	1	$\bar{F}_2$
F_2xP_1	F_2	P_1	1	1/2	1/2	1	0	$\overline{F_2xP_1}$
F_2xP_2	F_2	P_2	1	-1/2	1/2	-1	0	$\overline{F_2xP_2}$
F_2xF_1	F_2	F_1	1	0	1/2	0	1	$\overline{F_2xF_1}$

Table 9. Means and variances of L_1, L_2, L_3

Group	No.	12-day wt. Mean	12-day wt. Var.	21-day wt. Mean	21-day wt. Var.	42-day wt. Mean	42-day wt. Var.	56-day wt. Mean	56-day wt. Var.	12-21 gain Mean	12-21 gain Var.	21-42 gain Mean	21-42 gain Var.	42-56 gain Mean	42-56 gain Var.
Males															
L_1	141	8.5	1.52	14.5	6.94	35.1	18.86	39.4	23.97	5.9	2.82	20.5	12.98	4.4	15.36
L_2	141	7.2	0.65	11.8	3.36	23.5	11.78	25.6	14.73	4.7	1.57	11.6	8.12	2.1	4.07
L_3	138	8.5	0.66	14.0	3.18	30.3	9.99	33.6	13.38	5.6	1.58	16.2	9.86	3.3	4.03
Females															
L_1	145	8.4	1.64	14.2	6.86	29.8	12.83	33.0	13.53	5.7	2.90	15.7	8.50	3.1	5.33
L_2	137	7.1	0.63	11.3	2.90	20.3	5.42	21.0	10.22	4.3	1.32	9.0	3.66	0.7	5.14
L_3	136	8.4	0.69	13.6	3.12	25.1	6.55	27.0	11.61	5.2	1.50	11.5	5.57	1.9	5.29

Table 10. Means and variances of L_1, L_2, L_4

Group	No.	12-day wt. Mean	12-day wt. Var.	21-day wt. Mean	21-day wt. Var.	42-day wt. Mean	42-day wt. Var.	56-day wt. Mean	56-day wt. Var.	12-21 gain Mean	12-21 gain Var.	21-42 gain Mean	21-42 gain Var.	42-56 gain Mean	42-56 gain Var.
Males															
L_1	137	9.2	1.97	15.4	6.53	36.1	19.27	40.3	27.40	6.3	3.53	20.6	15.21	4.2	16.17
L_2	146	7.4	1.38	12.0	3.60	23.7	14.02	20.6	17.93	4.6	2.34	11.7	9.35	2.3	5.33
L_4	141	8.4	1.10	14.2	5.37	30.4	13.81	33.8	14.79	5.8	2.70	16.2	8.57	3.4	3.88
Females															
L_1	145	9.0	1.93	15.2	6.72	30.7	13.99	30.1	12.84	6.1	3.39	15.5	8.93	3.4	5.29
L_2	129	7.3	1.07	11.8	2.48	20.7	6.85	21.7	8.34	4.5	1.77	8.9	4.92	1.0	3.59
L_4	148	8.4	1.18	14.1	3.86	26.0	7.76	28.0	9.97	5.7	1.71	11.9	6.03	1.9	4.59

Table 11. Means and variances L_1, L_2

Group	No.	12-day wt. Mean	12-day wt. Var.	21-day wt. Mean	21-day wt. Var.	42-day wt. Mean	42-day wt. Var.	56-day wt. Mean	56-day wt. Var.	12-21 gain Mean	12-21 gain Var.	21-42 gain Mean	21-42 gain Var.	42-56 gain Mean	42-56 gain Var.
Males															
L_1	204	8.9	1.79	15.0	6.98	35.6	19.10	40.1	23.83	6.0	3.97	20.6	14.19	4.5	13.13
L_2	203	7.3	1.13	11.9	3.12	23.4	11.85	25.5	15.23	4.6	1.91	11.5	8.46	2.1	4.94
Females															
L_1	206	8.9	1.76	14.8	6.81	30.4	12.45	33.5	12.34	5.9	3.31	15.6	8.29	3.2	4.84
L_2	195	7.2	0.90	11.5	2.63	20.4	5.86	21.1	9.44	4.4	1.63	8.8	4.35	0.7	4.65

are later used in computation of error sums of squares.

Detection of Additive, Dominance and Epistatic Variation

By using the same d and h parameters discussed previously, the contribution of a single gene difference to means and variance of backcross females (L_1, L_2 and L_3) is set out in Table 12. The genetic variances are:

$$\text{Variance of } 1/2\ (\bar{L}_{1i} + \bar{L}_{2i} + \bar{L}_{3i}) = 1/8d^2$$

$$\text{Variance of } 1/2\ (\bar{L}_{1i} - \bar{L}_{2i}) = 1/8h^2.$$

The linear contrast of $1/2\ (L_{1i} + L_{2i} - 2L_{3i})$ is used to test for epistasis. After summing over many loci for each individual and all i individuals of the population, $\Sigma d^2 = D$ and $\Sigma h^2 = H$. Combinations of L_{1i}, L_{2i} and L_{3i} yields a test for additive component (D), dominance component (H) and epistatic component as explained by Jinks and Perkins (1970). All analyses were repeated with $\bar{L}_{4i}$ in place of $\bar{L}_{3i}$ to determine if any differences arose.

Estimates of additive and dominance components are most meaningful when epistasis is negligible; therefore, the method for detecting epistasis will be illustrated first. Eighteen F_2 sires (s = 18) were successfully mated to P_1, P_2 and F_1 (either $F_{1\text{-}3}$ or $F_{1\text{-}4}$) females. Two replicates (r = 2) of each mating with an unequal number of male (or female) progeny (n = 1, 2, 3, ideally 4) per family. The linear contrast used to detect epistasis is

$$Y_{ij} = \bar{L}_{1ij} + \bar{L}_{2ij} - 2\bar{L}_{3ij} \qquad i = 1, 2 \ldots 18 \qquad j = 1, 2$$

where $\bar{L}_{1ij}$ is the mean of n males (or females) for j^{th} replicate of i^{th}

Table 12. Backcrosses of F_2 to parentals and F_1

F_2 genotype	AA	Aa	aa	Mean
Frequency	1/4	1/2	1/4	
Mean of backcross to $P_1(\bar{L}_1)$	d	1/2(d+h)	h	1/2(d+h)
Mean of backcross to $P_2(\bar{L}_2)$	h	1/2(h-d)	-d	1/2(h-d)
Mean of backcross to $F_1(\bar{L}_3)$	1/2(d+h)	1/2h	1/2(h-d)	1/2h
Variance of backcross to $P_1(L_1)$	0	$1/4(d-h)^2$	0	$1/8(d-h)^2$
Variance of backcross to $P_2(L_2)$	0	$1/4(d+h)^2$	0	$1/8(d+h)^2$
Variance of backcross to $F_1(L_3)$	$1/4(d-h)^2$	$1/2d^2 + 1/4h^2$	$1/4(d+h)^2$	$3/8d^2 + 1/4h^2$

family. The animals that make up $\bar{L}_{1i1}$ and $\bar{L}_{1i2}$ are full sibs produced by replicate matings. Animals in L_{1ij} are paternal half sibs to those in $\bar{L}_{2ij}$ and $\bar{L}_{3ij}$. Sums of squares used to detect epistasis (Jinks and Perkins, 1970) are given in Table 13. The epistatic source of variation is computed by summing squared values of $(\bar{L}_{1ij} + \bar{L}_{2ij} - 2\bar{L}_{3ij})$ after summing over replicates while the replicate families sums of squares is computed by summing squared differences between replicates. The epistasis sum of square can be subdivided into an item for one degree of freedom testing the mean value of the epistatic term $(\bar{L}_{1i} + \bar{L}_{2i} - 2\bar{L}_{3i})$ over all 18 sets of progeny families and an item for 17 degrees of freedom for the remainder which tests variation in the value of the epistatic term over the 18 sets of families around this mean value. The sums of squares of replicate families can also be partitioned into corresponding items for replicates (1 degree of freedom) and epistasis x replicates (17 degrees of freedom). Epistasis is tested using a F-ratio with replicate families as an appropriate error. If replicate or epistasis x replicates terms are significant, these would have been the appropriate error for testing the significance of the overall epistasis and epistasis items, respectively.

The method for estimating additive and dominance components is similar to that used for epistasis. The linear contrasts used are:

$$Y_{ij} = \bar{L}_{1ij} + \bar{L}_{2ij} + \bar{L}_{3ij}$$

which detects additive variation and

$$Y_{ij} = \bar{L}_{1ij} - \bar{L}_{2ij}$$

Table 13. Computation of sums of squares to test for epistasis

Source of variation	d.f.	Sums of squares
Epistasis $(\bar{L}_{1i} + \bar{L}_{2i} - 2\bar{L}_{3i})$	s	$\sum_{i=1}^{s} (\sum_{j=1}^{r} \bar{L}_{1ij} + \bar{L}_{2ij} - 2\bar{L}_{3ij})^2$
Overall epistasis (i type)	1	$[\sum_{i=1}^{s} \sum_{j=1}^{r} (\bar{L}_{1ij} + \bar{L}_{2ij} - 2\bar{L}_{3ij})]^2/s$
Epistasis (j and l types)	s-1	$\sum_{i=1}^{s} (\sum_{j=1}^{r} \bar{L}_{1ij} + \bar{L}_{2ij} - 2\bar{L}_{3ij})^2 - [\sum_{i=1}^{s} \sum_{j=1}^{r} (\bar{L}_{1ij} + \bar{L}_{2ij} - 2\bar{L}_{3ij})]^2/s$
Replicate--families	s	$\sum_{i=1}^{s} [(\bar{L}_{1i1} + \bar{L}_{2i1} - 2\bar{L}_{3i1}) - (\bar{L}_{1i2} + \bar{L}_{2i2} - 2\bar{L}_{3i2})]^2$
Replicates	1	$[\sum_{i=1}^{s} [(\bar{L}_{1i1} + \bar{L}_{2i1} - 2\bar{L}_{3i1}) - (\bar{L}_{1i2} + \bar{L}_{2i2} - 2\bar{L}_{3i2})]^2/s$
Epistasis x replicates	s-1	$\sum_{i=1}^{s} [(\bar{L}_{1i1} + \bar{L}_{2i1} - 2\bar{L}_{3i1}) - (\bar{L}_{1i2} + \bar{L}_{2i2} - 2\bar{L}_{3i2})]^2 -$
		$[\sum_{i=1}^{s} (\bar{L}_{1i1} + \bar{L}_{2i1} - 2\bar{L}_{3i1}) - (\bar{L}_{1i2} + \bar{L}_{2i2} - 2\bar{L}_{3i2})]^2/s$
Within families in reps	n..-rs	SSE_1

which detects dominance variation. Computation of sums of squares for each analysis are given in Tables 14 and 15. Presence of additive variation can be detected by a F-ratio of sums of squares and sums x replicate sums of square (or error, if not significant). Replicates are tested by using either sums x replicates (if significant) or error as appropriate error variance. Similarly, differences among $\bar{L}_{1i}$ and $\bar{L}_{2i}$ are tested for significance using diff x replicates or error as appropriate error. Which error to use in testing the F-ratios can be determined by looking at the expected mean squares shown in Tables 16 and 17. If the interaction sums of squares (sums x replicates or diff x replicates) are significant, then these sums of squares must be used as the error variance for testing the two main effects. Once the computed mean squares are equated to their expected values then variance components of the main effects can be estimated. Derivation of the expected mean squares (personal communication, Dr. K. Hinkelmann, V.P.I.) structure and explanation of coefficients are given in Appendix Table 53.

Since

$$\sigma^2_S = 1/8D \text{ and } \sigma^2_D = 1/8H,$$

estimates of additive and dominance components can be computed from analyses of variance tables. Two estimates of D, D_1 and D_2 are presented with one involving $\bar{L}_1$, $\bar{L}_2$ and $\bar{L}_3$ and the other $\bar{L}_1$, $\bar{L}_2$ and $\bar{L}_4$. For females, sex-linkage parameters, D_x and H_x can be estimated as functions of D and H as explained by Killick (1971). Also, σ^2_D/σ^2_S, a measure of average dominance, $\bar{d}_1$ and $\bar{d}_2$, can be computed.

Relative magnitudes of additive and dominance genetic variances

Table 14. Computation of sums of squares to estimate additive genetic variation

Source of variation	d.f.	Sums of squares
Sums $(L_{1i}+L_{2i}+L_{3i})$	s-1	$\sum_{i=1}^{s}(\sum_{j=1}^{r}\bar{L}_{1ij}+\bar{L}_{2ij}+\bar{L}_{3ij})^2-[\sum_{i=1}^{s}\sum_{j=1}^{r}(\bar{L}_{1ij}+\bar{L}_{2ij}+\bar{L}_{3ij})]^2/s$
Replicates	1	$[\sum_{i=1}^{s}(\bar{L}_{1i1}+\bar{L}_{2i1}+\bar{L}_{3i1})-(\bar{L}_{1i2}+\bar{L}_{2i2}+\bar{L}_{3i2})]^2/s$
Sums x replicates	s-1	$\sum_{i=1}^{s}[(\bar{L}_{1i1}+\bar{L}_{2i1}+\bar{L}_{3i1})-(\bar{L}_{1i2}+\bar{L}_{2i2}+\bar{L}_{3i2})]^2-[\sum_{i=1}^{s}(\bar{L}_{1i1}+\bar{L}_{2i1}+\bar{L}_{3i1})-(\bar{L}_{1i2}+\bar{L}_{2i2}+\bar{L}_{3i2})]^2/s$
Within families in reps	n..-rs	SSE_2

Table 15. Computation of sums of squares to estimate dominance genetic variation

Source of variation	d.f.	Sums of squares
Between parents	1	$[\sum_{i=1}^{s}\sum_{j=1}^{r}(\bar{L}_{1ij} - \bar{L}_{2ij})]^2/s$
Differences $(\bar{L}_{1i} - \bar{L}_{2i})$	s-1	$\sum_{i=1}^{s}(\sum_{j=1}^{r}\bar{L}_{1ij} - \bar{L}_{2ij})^2 - [\sum_{i=1}^{s}\sum_{j=1}^{r}(\bar{L}_{1ij} - \bar{L}_{2ij})]^2/s$
Replicates	1	$[\sum_{i=1}^{s}(\bar{L}_{1i1} - \bar{L}_{2i1}) - (\bar{L}_{1i2} - \bar{L}_{2i2})]^2/s$
Diff x replicates	s-1	$\sum_{i=1}^{s}[(\bar{L}_{1i1} - \bar{L}_{2i1}) - (\bar{L}_{1i2} - \bar{L}_{2i2})]^2 - [\sum_{i=1}^{s}(\bar{L}_{1i1} - \bar{L}_{2i1}) - (\bar{L}_{1i2} - \bar{L}_{2i2})]^2/s$
Within families in reps	$n_{..}$-rs	SSE_3

Table 16. Expected mean square structure for analyses of sums

Source	MS	EMS
Sums	MS_S	$1/2\ \{(\frac{1}{n_{11h}} + \frac{1}{n_{12h}})\sigma^2_1 + (\frac{1}{n_{21h}} + \frac{1}{n_{22h}})\sigma^2_2 + (\frac{1}{n_{31h}} + \frac{1}{n_{32h}})\sigma^2_3\} + \sigma^2_{RxS} + 2\sigma^2_S$
Replicates	MS_R	$1/2\ \{(\frac{1}{n_{11h}} + \frac{1}{n_{12h}})\sigma^2_1 + (\frac{1}{n_{21h}} + \frac{1}{n_{22h}})\sigma^2_2 + (\frac{1}{n_{31h}} + \frac{1}{n_{32h}})\sigma^2_3\} + \sigma^2_{RxS} + 18\sigma^2_R$
Sums x replicates	MS_{SxR}	$1/2\ \{(\frac{1}{n_{11h}} + \frac{1}{n_{12h}})\sigma^2_1 + (\frac{1}{n_{21h}} + \frac{1}{n_{22h}})\sigma^2_2 + (\frac{1}{n_{31h}} + \frac{1}{n_{32h}})\sigma^2_3\} + \sigma^2_{RxS}$
Error	MS_E	$1/2\ \{(\frac{1}{n_{11h}} + \frac{1}{n_{12h}})\sigma^2_1 + (\frac{1}{n_{21h}} + \frac{1}{n_{22h}})\sigma^2_2 + (\frac{1}{n_{31h}} + \frac{1}{n_{32h}})\sigma^2_3\}$

Table 17. Expected mean square structure for analyses of differences

Source	MS	EMS
Between parents	MS_P	
Differences	MS_D	$1/2\ \{(\frac{1}{\bar{n}_{11h}} + \frac{1}{\bar{n}_{12h}})\sigma^2_1 + (\frac{1}{\bar{n}_{21h}} + \frac{1}{\bar{n}_{22h}})\sigma^2_2\} + \sigma^2_{RxD} + 2\sigma^2_D$
Replicates	MS_R	$1/2\ \{(\frac{1}{\bar{n}_{11h}} + \frac{1}{\bar{n}_{12h}})\sigma^2_1 + (\frac{1}{\bar{n}_{21h}} + \frac{1}{\bar{n}_{22h}})\sigma^2_2\} + \sigma^2_{RxD} + 18\sigma^2_R$
Diff x replicates	MS_{DxR}	$1/2\ \{(\frac{1}{\bar{n}_{11h}} + \frac{1}{\bar{n}_{12h}})\sigma^2_1 + (\frac{1}{\bar{n}_{21h}} + \frac{1}{\bar{n}_{22h}})\sigma^2_2\} + \sigma^2_{RxD}$
Error	MS_E	$1/2\ \{(\frac{1}{\bar{n}_{11h}} + \frac{1}{\bar{n}_{12h}})\sigma^2_1 + (\frac{1}{\bar{n}_{21h}} + \frac{1}{\bar{n}_{22h}})\sigma^2_2\}$

can also be measured. Additive genetic variation, V_A, is 1/2D and dominance genetic variation, V_D, is 1/4H so heritabilities (Kearsey, 1965) can be computed as

$$h^2 \text{ (in narrow sense)} = \frac{V_A}{V_P} = \frac{1/2D}{1/2D + 1/4H + sE_2}$$

$$h^2 \text{ (in broad sense)} = \frac{V_G}{V_P} = \frac{1/2D + 1/4H}{1/2D + 1/4H + sE_2}$$

E_2 is measured by σ^2_{RxS}.

By using the triple test cross with extreme selection lines not only can additive and dominance components be estimated with the same precision, but presence of epistasis can also be detected. With all loci segregating, maximized percentages reveal the genetic structure of a population.

RESULTS AND DISCUSSION

Estimates of Genetic Components

Generally analyses of the data are divided into two categories. The first tests components of means and the second evaluates components of variation. The first procedure uses a weighted least squares method to compute point estimates of genetic parameters investigated. A χ^2 goodness of fit test determines the adequacy of the model and statistical significance of its parameters.

Advantages of the tests are their relative simplicity and statistical reliability. But first order tests are only complimentary to higher degree statistical tests, namely, components of variation. To estimate the contribution of non-allelic interactions unconfounded by effects of gene distribution in the original parental lines, second degree statistics must be employed. Also there is no reason to assume that the relative contributions of genetic, environmental, and interactive sources of variation are the same for differences between means of families and for differences among individuals in the same family. Thus, for a complete understanding of the genetic architecture of the measured traits, analyses at both levels should be exploited.

Epistasis

For all component of means tests, least squares means adjusted for generation or replicate effects were used for the observed group

means. Least squares means and standard errors for littering traits and weight traits for males and females are shown in Tables 18, 19 and 20. The A, B and C quantities used in the scaling test are also given in these tables. Estimates of m, [d], [h], [i], [j] and [l] for littering and weight traits are presented in Tables 21, 22 and 23.

Extremely large χ^2 values for weight traits in both males and females suggest that epistasis is not an important genetic component. Littering traits, especially length of time from exposure to male to littering time and mortality of young from birth to 5 days of age, are strongly influenced by non-allelic interactions.

Testing for presence of epistatic variation from analyses of variance, using F_{1-3} and F_{1-4} females, is shown in Tables 24, 25, 26 and 27. Epistasis can be detected for 12-day individual weight in males and females. The type of epistasis which is significant seems to depend on F_1 females. For analyses $(L_{1i} + L_{2i} - 2L_{3i})$ epistasis is [i] type or additive x additive while for $(L_{1i} + L_{2i} - 2L_{4i})$ epistasis is [j] and [l] type or additive x dominance and dominance x dominance. Weaning weight at 21 days of age appears influenced by [j] and [l] type epistasis for males and females of analyses involving F_{1-4}. In males, 21-day weight has a slight influence of [i] type epistasis for analyses involving F_{1-3}. The only other weight trait which seems to be influenced by epistasis is weight at 56 days of age. The males show a strong hint of [j] and [l] type while females show weaker amount or none.

Since no studies have determined the importance of non-allelic interactions in mice, no basis for comparison is available. It appears that littering traits (reproductive and maternal) are influenced

Table 18. Least square means (adjusted for generation or replicate effects) for littering traits

Groups	No.	No. born		Litt. time		Mort. B-5 days		Litt. wt. 12 days		
		Mean	S.E.	Mean	S.E.	Mean	S.E.	No.	Mean	S.E.
P_1	133	12.4	0.23	24.5	0.34	2.0	0.81	125	77.3	0.70
P_2	160	9.1	0.21	23.7	0.31	1.4	0.73	141	56.5	0.66
F_{1-3}	91	9.7	0.32	26.1	0.44	1.4	1.38	88	62.8	1.06
F_{1-4}	91	12.1	0.32	25.3	0.44	3.3	1.38	83	73.1	1.08
$F_{1-(3+4)}$	182	10.9	0.22	25.7	0.31	2.3	0.98	171	68.0	0.76
F_2	271	12.4	0.16	22.6	0.19	0.8	0.42	190	74.3	0.50
F_2xP_1	231	13.4	0.19	23.7	0.23	1.5	0.45	172	71.1	0.51
F_2xP_2	240	10.8	0.18	23.4	0.23	1.5	0.44	174	54.7	0.50
F_2xF_{1-3}	247	13.5	0.18	23.1	0.22	0.3	0.43	173	67.1	0.50
F_2xF_{1-4}	246	13.9	0.18	23.4	0.23	1.0	0.43	176	66.2	0.50
$F_2xF_{1-(3+4)}$	493	13.7	0.13	23.3	0.16	0.6	0.31	349	66.6	0.35
Scaling tests										
A		3.57	0.50	-2.80	0.66	-1.29	1.54		-2.96	1.43
B		1.52	0.49	-2.67	0.63	-0.81	1.51		-15.08	1.42
C		6.19	0.80	-9.43	0.94	-4.68	6.81		27.44	7.69

Table 19. Least squares means for weight traits of males

Group	No.	12-day wt.		21-day wt.		42-day wt.		56-day wt.		12-21 gain		21-42 gain		42-56 gain	
		Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.
P_1	459	9.8	0.05	16.8	0.09	41.2	0.19	46.7	0.18	7.0	0.07	24.3	0.15	5.5	0.12
P_2	504	7.2	0.04	11.7	0.09	18.8	0.18	20.6	0.18	4.6	0.06	7.0	0.15	1.8	0.12
F_{1-3}	349	8.0	0.06	13.9	0.12	29.3	0.19	32.1	0.20	5.9	0.08	15.5	0.15	2.7	0.10
F_{1-4}	297	9.3	0.07	15.9	0.13	32.3	0.21	35.2	0.21	6.6	0.10	16.4	0.16	2.9	0.10
$F_{1-(3+4)}$	646	8.6	0.05	14.9	0.09	30.8	0.14	33.6	0.14	6.2	0.06	15.9	0.11	2.8	0.07
F_2	747	9.4	0.03	15.9	0.07	31.6	0.14	34.2	0.15	6.6	0.05	15.7	0.11	2.6	0.07
$F_2 \times P_1$	682	9.0	0.04	15.1	0.08	36.0	0.14	40.7	0.15	6.1	0.06	20.9	0.12	4.7	0.10
$F_2 \times P_2$	681	7.0	0.04	11.5	0.08	23.0	0.14	25.0	0.15	4.5	0.06	11.5	0.12	2.0	0.10
$F_2 \times F_{1-3}$	684	8.4	0.04	14.1	0.08	30.1	0.14	33.5	0.15	5.6	0.05	16.0	0.12	3.3	0.10
$F_2 \times F_{1-4}$	689	8.4	0.04	14.0	0.08	29.8	0.14	33.1	0.15	5.6	0.05	15.8	0.12	3.3	0.10
$F_2 \times F_{1-(3+4)}$	1373	8.4	0.03	14.0	0.06	30.0	0.10	33.3	0.11	5.6	0.04	15.9	0.09	3.3	0.07
Scaling Tests															
A		-0.57	0.10	-1.51	0.20	-0.01	0.37	1.01	0.39	-0.93	0.14	1.49	0.32	-1.03	0.24
B		-1.85	0.10	-3.66	0.20	-3.65	0.37	-4.29	0.39	-1.81	0.14	0.01	0.32	-0.67	0.24
C		3.10	0.17	5.35	0.34	4.84	0.66	2.18	0.70	2.28	0.24	-0.52	5.40	-2.66	0.37

Table 20. Least squares means for weight traits of females

Group	No.	12-day wt.		21-day wt.		42-day wt.		56-day wt.		12-21 gain		21-42 gain		42-56 gain	
		Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.
P_1	469	9.7	0.04	16.5	0.08	36.0	0.15	39.8	0.15	6.8	0.05	19.5	0.12	3.8	0.11
P_2	522	7.1	0.04	11.3	0.08	16.5	0.14	17.7	0.14	4.2	0.05	5.3	0.12	1.2	0.10
F_{1-3}	330	7.9	0.06	13.5	0.11	25.4	0.15	26.9	0.15	5.6	0.07	11.9	0.12	1.5	0.09
F_{1-4}	340	9.2	0.06	15.1	0.11	26.6	0.15	28.4	0.15	5.9	0.07	11.4	0.12	1.5	0.09
$F_{1-(3+4)}$	670	8.5	0.04	14.3	0.08	26.0	0.11	27.6	0.11	5.8	0.05	11.7	0.09	1.8	0.09
F_2	722	9.3	0.04	15.4	0.07	26.4	0.12	28.0	0.12	6.1	0.05	11.0	0.09	1.5	0.07
$F_2 \times P_1$	661	8.9	0.04	14.7	0.08	30.7	0.12	33.8	0.13	5.8	0.05	16.0	0.10	3.1	0.09
$F_2 \times P_2$	663	6.9	0.04	11.2	0.07	19.9	0.11	20.8	0.13	4.3	0.05	8.8	0.10	0.9	0.09
$F_2 \times F_{1-3}$	648	8.4	0.04	13.7	0.08	25.3	0.12	27.1	0.13	5.3	0.05	11.6	0.10	1.8	0.09
$F_2 \times F_{1-4}$	670	8.3	0.04	13.7	0.08	25.5	0.12	27.3	0.13	5.4	0.05	11.8	0.10	1.8	0.09
$F_2 \times F_{1-(3+4)}$	1318	8.4	0.03	13.7	0.05	25.4	0.08	27.2	0.09	5.3	0.04	11.7	0.07	1.8	0.06
Scaling tests															
A		-0.55	0.10	-1.50	0.20	-0.66	0.30	0.11	0.32	-0.96	0.14	0.84	0.24	0.61	0.22
B		-1.92	0.10	-3.19	0.20	-2.68	0.28	-3.70	0.32	-1.27	0.14	0.54	0.24	-1.20	0.22
C		3.29	0.17	5.19	0.33	1.18	0.56	-0.93	0.58	1.91	0.22	-4.04	0.46	-2.39	0.35

Table 21. Test for non-allelic interactions for littering traits

	No. born		Litt. Time		Mort. B-5 days		Litt. wt. 12 days	
	Estimate	S.E.	Estimate	S.E.	Estimate	S.E.	Estimate	S.E.
m	14.31	0.71	20.98	0.86	-2.63	1.76	86.78	1.97
[d]	0.75	0.15	0.78	0.20	1.08	0.48	3.93	0.45
[h]	-1.89	1.89	2.38	2.32	7.08	4.76	-56.60	5.23
[i]	-3.63	0.69	3.19	0.83	4.41	1.69	-20.28	1.92
[j]	2.05	0.53	3.08	0.65	1.18	1.26	3.06	1.42
[l]	-1.52	1.27	2.33	1.59	-2.13	3.33	37.80	3.59
$x^2_{(1)}$	432.4		33.2		17.5		920.3	

Table 22. Test for non-allelic interactions for weight traits of males

	12-day wt.		21-day wt.		42-day wt.		56-day wt.		12-21 gain		21-42 gain		42-56 gain	
	estimate	S.E.	estimate	S.E.	estimate	S.E.	estimate	S.E.	estimate	S.E.	estimate	S.E.	estimate	S.E.
m	10.60	0.14	18.09	0.30	22.40	0.56	21.94	0.59	7.43	0.21	4.17	0.47	0.21	0.36
[d]	0.69	0.03	1.38	0.06	8.95	0.12	11.19	0.12	0.69	0.04	7.85	0.10	1.82	0.07
[h]	-6.30	0.38	-12.03	0.80	12.71	1.47	20.56	1.56	-5.51	0.56	25.09	1.25	6.53	0.98
[i]	-2.12	0.14	-3.84	0.29	7.49	0.54	11.63	0.58	-1.67	0.21	11.48	0.46	3.45	0.35
[j]	0.11	0.11	0.29	0.22	0.05	0.41	-0.00	0.43	0.59	0.16	0.35	0.35	0.83	0.28
[l]	4.34	0.26	8.82	0.53	-4.30	0.97	-8.85	1.00	4.31	0.37	-13.33	0.82	-3.91	0.64
$x^2_{(1)}$	2,726.4		2,317.7		9,755.3		14,670.6		1,092.4		13,394.2		1,295.3	

Table 23. Test for non-allelic interactions for weight traits of females

	12-day wt.		21-day wt.		42-day wt.		56-day wt.		12-21 gain		21-42 gain		42-56 gain	
	estimate	S.E.	estimate	S.E.	estimate	S.E.	estimate	S.E.	estimate	S.E.	estimate	S.E.	estimate	S.E.
m	10.99	0.14	17.51	0.28	17.60	0.45	17.19	0.49	6.56	0.20	0.36	0.39	-0.07	0.32
[d]	0.66	0.03	1.62	0.05	8.20	0.10	9.81	0.09	0.96	0.03	6.83	0.08	1.29	0.07
[h]	-7.55	0.38	-11.60	0.75	13.21	1.18	18.14	1.31	-4.10	0.53	24.99	1.03	3.76	0.87
[i]	-2.59	0.14	-3.67	0.28	8.61	0.44	11.50	0.48	-1.12	0.19	12.02	0.38	2.55	0.32
[j]	1.87	0.11	1.74	0.21	3.03	0.33	1.99	0.37	1.00	0.15	1.62	0.29	1.12	0.24
[l]	5.10	0.25	8.37	0.49	-4.83	0.77	-7.71	0.85	3.30	0.35	-13.17	0.67	-1.89	0.58
$x^2_{(1)}$	2,984.4		2,703.3		13,407.5		16,494.8		1,526.4		15,614.6		824.4	

Table 24. Analyses of variance to test for epistasis ($\bar{L}_{1i} + \bar{L}_{2i} - 2\bar{L}_{3i}$) of weight traits in males

Source of variation	d.f.	MS. 12-day wt.	MS. 21-day wt.	MS. 42-day wt.	MS. 56-day wt.	MS. 12-21 gain	MS. 21-42 gain	MS. 42-56 gain
Epistasis ($\bar{L}_{1i}+\bar{L}_{2i}-2\bar{L}_{3i}$)	18	13.48[b]	45.88	73.57	140.81	18.94	64.72	35.17
Overall epistasis (i type)	1	111.50[c]	168.67[c]	228.98	210.81	6.72	1,128.13	0.50
Epistasis (j and l types)	17	7.72	38.66	64.43	136.69[b]	19.66	12.75	37.21
Replicate--families	18	4.90[a]	35.60[a]	102.89[a]	87.55[a]	19.30[a]	114.34[a]	44.24[a]
Replicates	1	1.08	1.68	56.89	631.31[a]	5.78	1,620.70[a]	304.22[a]
Epistasis x replicates	17	5.12[a]	37.59[a]	105.59[a]	55.36[b]	20.10[a]	25.73[a]	28.95[a]
Within families in reps	312	1.39	6.65	20.48	26.75	3.10	17.64	10.17

[a]Significance at .01 level
[b]Significance at .05 level
[c]Significance at .10 level

Table 25. Analyses of variance to test for epistasis ($\bar{L}_{1i} + \bar{L}_{2i} - 2\bar{L}_{4i}$) of weight traits in males

Source of variation	d.f.	MS. 12-day wt.	MS. 21-day wt.	MS. 42-day wt.	MS. 56-day wt.	MS. 12-21 gain	MS. 21-42 gain	MS. 42-56 gain
Epistasis ($\bar{L}_{1i}+\bar{L}_{2i}-2\bar{L}_{4i}$)	18	14.08[b]	58.43[c]	102.00	175.68[b]	39.30	100.38	38.31
Overall epistasis (i type)	1	3.74	74.42	58.32	98.94	45.13	1,350.27	5.12
Epistasis (j and l types)	17	14.69[b]	57.49[b]	104.58	180.19[a]	33.14[b]	26.85	40.26
Replicate--families	18	5.57[a]	32.70[a]	87.90[a]	67.22[a]	23.03[a]	84.24[a]	62.08[a]
Replicates	1	0.64	175.47[a]	516.28[a]	57.60	153.13[a]	817.43[a]	228.98[a]
Epistasis x replicates	17	5.86[a]	24.31[a]	62.70[b]	67.79[b]	15.38[a]	41.11[b]	52.26[a]
Within families in reps	317	2.14	8.71	24.42	28.88	4.59	16.29	10.39

[a]Significance at .01 level
[b]Significance at .05 level
[c]Significance at .10 level

Table 26. Analyses of variance to test for epistasis ($\bar{L}_{1i} + \bar{L}_{2i} - 2\bar{L}_{3i}$) of weight traits in females

Source of variation	d.f.	MS. 12-day wt.	MS. 21-day wt.	MS. 42-day wt.	MS. 56-day wt.	MS. 12-21 gain	MS. 21-42 gain	MS. 42-56 gain
Epistasis ($\bar{L}_{1i}+\bar{L}_{2i}-2\bar{L}_{3i}$)	18	15.19[b]	42.92	69.89	93.82	16.21	47.94	29.24
Overall epistasis (i type)	1	144.50[b]	236.17	3.38	1.62	11.20	688.21	0.05
Epistasis (j and l types)	17	7.58	31.55	73.80	99.25[c]	16.51	10.28	30.96
Replicate--families	18	5.68[a]	22.27[a]	45.08[a]	43.45[b]	10.92[a]	37.03[a]	19.87[a]
Replicates	1	0.22	8.54	20.05	8.54	6.97	362.70[a]	0.08
Epistasis x replicates	17	6.01[a]	23.08[a]	46.55[a]	45.50[b]	11.15[a]	17.87[c]	21.04[b]
Within families in reps	310	1.46	5.10	13.11	20.77	2.99	10.23	9.38

[a]Significance at .01 level
[b]Significance at .05 level
[c]Significance at .10 level

Table 27. Analyses of variance to test for epistasis ($\bar{L}_{1i} + \bar{L}_{2i} - 2\bar{L}_{4i}$) of weight traits in females

Source of variation	d.f.	MS. 12-day wt.	MS. 21-day wt.	MS. 42-day wt.	MS. 56-day wt.	MS. 12-21 gain	MS. 21-42 gain	MS. 42-56 gain
Epistasis ($\bar{L}_{1i}+\bar{L}_{2i}-2\bar{L}_{4i}$)	18	16.06[c]	45,70	52.13	51.34	23.39	55.71	19.71
Overall epistasis (i type)	1	15.13	121.68	36.98	18.20	50.33	715.68	4.81
Epistasis (j and l types)	17	16.11[c]	41.24[c]	53.02	53.29	21.80	16.89	20.58
Replicate--families	18	7.06[a]	29.16[a]	50.48[a]	43.51[a]	19.27[a]	55.04[a]	16.61[a]
Replicates	1	1.44	114.51[a]	44.18	30.16	89.33[a]	636.05[a]	0.16
Epistasis x replicates	17	7.39[a]	24.13[a]	50.85[a]	44.29[a]	15.15[a]	20.86[a]	17.57[a]
Within families in reps	314	2.08	6.56	13.95	14.68	3.24	10.18	7.31

[a]Significance at .01 level
[b]Significance at .05 level
[c]Significance at .10 level

by epistasis, but weight traits are relatively free of epistatic effects. Only 12-day weight consistently showed presence of epistasis and the type varied according to the data used. An experiment using Drosophila (Kearsey and Kojima, 1967) has shown the presence of additive x additive interaction for female body weight and a weak dominance x dominance interaction for hatchability. Looking at first-order test the [j] parameter seems to be close to zero suggesting that the important epistatic interactions of 12-day weight and possibly 21-day and 56-day weights are additive x additive and dominance x dominance.

Additive and Dominance Effects

First indication of adequacy of additive-dominance model are the quantities A, B and C. If these quantities equal zero within the limits of sampling error, additive and dominance explain the gene action on the scale used. A, B and C and standard errors are given in Table 18 for littering traits and Tables 19 and 20 for weight traits. Littering traits have large values of A, B and C while weight traits have smaller values. Since these values are not zero, genetic influences other than additive and dominance might influence these traits.

Another test for adequacy of additive-dominance model was a weighted least squares approach which obtain estimates of m, [d] and [h] and determine their contribution to the model. Results appear in Table 28 for littering traits and Tables 29 and 30 for weight traits. A measure of dominance [h] seems equal to zero for all traits. This caused the degree of dominance, h/d, to be zero. χ^2 values are quite large for all first-order tests but expected means computed from estimates of parameters are

Table 28. Test for adequacy of additive-dominance model for littering traits

	No. born		Litt. time		Mort. B-5 days		Litt. wt. 12 days	
	estimate	S.E.	estimate	S.E.	estimate	S.E.	estimate	S.E.
m	12.24	0.07	23.49	0.09	1.15	0.24	66.84	0.20
[d]	2.29	0.14	0.67	0.19	0.56	0.41	12.63	0.40
[h]	0.01	0.03	0.00	0.03	-0.04	0.33	0.00	0.04
h/d	0.00		0.00		-0.07		0.00	
$\chi^2_{(4)}$	265.5		89.0		8.2		397.4	
$\chi^2_{(5)[h]=0}$	261.9		85.6		7.1		396.8	

Table 29. Test for adequacy of additive-dominance model for weight traits in males

	12-day wt.		21-day wt.		42-day wt.		56-day wt.		12-21 gain		21-42 gain		42-56 gain	
	estimate	S.E.	estimate	S.E.	estimate	S.E.	estimate	S.E.	estimate	S.E.	estimate	S.E.	estimate	S.E.
m	8.49	0.01	14.27	0.03	30.20	0.05	33.43	0.06	5.79	0.02	15.91	0.04	3.17	0.04
[d]	1.78	0.03	3.08	0.06	12.04	0.11	13.99	0.11	1.57	0.04	9.14	0.09	2.35	0.07
[h]	0.00	0.01	0.00	0.01	0.00	0.01	-0.00	0.01	0.01	0.01	0.00	0.02	-0.06	0.03
h/d	0.00		0.00		0.00		0.00		0.01		0.00		-0.02	
$\chi^2(4)$	1247.2		974.9		248.1		181.2		509.6		40.4		164.7	
$\chi^2(5)[h]=0$	1145.6		953.6		240.9		175.7		469.8		31.3		157.4	

Table 30. Test for adequacy of additive-dominance model for weight traits in females

	12-day wt.		21-day wt.		42-day wt.		56-day wt.		12-21 gain		21-42 gain		42-56 gain	
	estimate	S.E.	estimate	S.E.	estimate	S.E.	estimate	S.E.	estimate	S.E.	estimate	S.E.	estimate	S.E.
m	8.39	0.01	13.87	0.03	25.75	0.04	27.72	0.04	5.47	0.02	11.91	0.04	1.97	0.04
[d]	1.74	0.03	3.06	0.05	10.31	0.09	11.68	0.09	1.53	0.03	7.40	0.07	1.79	0.06
[h]	0.00	0.01	0.00	0.01	-0.00	0.01	-0.01	0.01	0.01	0.01	-0.01	0.01	-0.09	0.04
h/d	0.00		0.00		0.00		0.00		0.01		0.00		-0.05	
$\chi^2(4)$	1270.9		943.9		157.6		260.7		370.3		191.1		140.9	
$\chi^2(5)[h]=0$	1186.3		924.1		147.2		254.9		359.1		179.6		133.0	

very close to the observed values (Table 31).

Since χ^2 values are computed by

$$\sum_{i=1}^{\text{no. groups}} (\text{observed-expected})^2 \cdot \frac{1}{(\text{S.E. Group}_i)^2},$$

large values arise from the weights. For this model, weights ranged from 1 to 25 for littering traits and 39 to 1000 for weight traits. For this reason, χ^2 values are generally used to compare all models tested instead of accepting or rejecting one model. When a χ^2 test was run letting [h] = 0, χ^2 values improved only slightly. A comparison of χ^2 values testing additive-dominance model and those testing a model including nonallelic interactions, [i], [j] and [l] (Tables 21, 22 and 23) show that the additive-dominance model has a better fit for all traits except littering time and mortality of young from birth to 5 days of age.

Heterosis is described as the amount by which the means of an F_1 group exceeds its better parent. Expected positive $(\bar{F}_1-\bar{P}_1)$ and negative $(\bar{F}_1-\bar{P}_2)$ heterosis can be computed in terms of [d] and [h] (or [d], [h], [i], and [l] for littering time and mortality). Table 32 gives the observed and expected magnitude of heterosis for all measured traits. Observed heterosis for littering traits is not close to expected even using the correct model for each. Possible biases could be caused by assuming the offspring's genotype affects the littering trait measured. Weight traits of males and females had observed and expected amounts of heterosis quite similar to each other.

Significance of additive variation, obtained from triple test cross procedure, can be detected from analyses of variance Tables 33 and 34 for weight traits of males and Tables 35 and 36 for weight traits

Table 31. Comparison of observed and expected means for weight traits in males used in χ^2 test

Group	Expected gen. mean	12-day wt. Obs.	12-day wt. Exp.	21-day wt. Obs.	21-day wt. Exp.	42-day wt. Obs.	42-day wt. Exp.	56-day wt. Obs.	56-day wt. Exp.	12-21 gain Obs.	12-21 gain Exp.	21-42 gain Obs.	21-42 gain Exp.	42-56 gain Obs.	42-56 gain Exp.
P_1	m + [d]	9.8	10.3	16.8	17.4	41.2	42.2	46.7	47.4	7.0	7.4	24.3	25.1	5.5	5.5
P_2	m - [d]	7.2	6.7	11.7	11.2	18.8	18.2	20.6	19.4	4.6	4.2	7.0	6.8	1.8	0.8
F_1	m + [h]	8.6	8.5	14.9	14.3	30.8	30.2	33.6	33.4	6.2	5.8	15.9	15.9	2.8	3.1
F_2	m + 1/2[h]	9.4	8.5	15.9	14.3	31.6	30.2	34.2	33.4	6.6	5.8	15.7	15.9	2.6	3.1
F_2xP_1	m + 1/2[d] + 1/2[h]	9.0	9.4	15.1	15.8	36.0	36.2	40.7	40.4	6.1	6.6	20.9	20.5	4.7	4.3
F_2xP_2	m - 1/2[d] + 1/2[h]	7.0	7.6	11.5	12.7	23.0	24.2	25.0	26.4	4.5	5.0	11.5	11.3	2.0	2.0
F_2xF_1	m + 1/2[h]	8.4	8.5	14.0	14.3	30.0	30.2	33.3	33.4	5.6	5.8	15.9	15.9	3.3	3.1

Table 32. Observed and expected magnitude of heterosis for all measured traits

Traits	$\bar{F}_1-\bar{P}_1$	[h]-[d]	$\bar{F}_1-\bar{P}_2$	[h]+[d]
Littering				
No. born	-0.0	-2.3	3.3	2.3
Litt. time	1.9	-0.7(0.7)	-1.1(2.3)	0.7
Mort. B-5 days	-1.2	-0.6(-0.5)	-0.6(1.6)	0.6
Litt. wt. 12 days	-3.0	-12.6	17.8	12.6
Weight-males				
12-day wt.	-1.2	-1.8	1.4	1.8
21-day wt.	-1.9	-3.1	3.2	3.1
42-day wt.	-10.4	-12.0	12.0	12.0
56-day wt.	-13.1	-14.0	13.0	14.0
12-21 gain	-0.8	-1.5	1.6	1.6
21-42 gain	-6.8	-9.1	8.9	9.1
42-56 gain	-2.7	-2.4	1.7	2.4
Weight-females				
12-day wt.	-1.2	-1.7	1.4	1.7
21-day wt.	-2.2	-3.1	3.0	3.1
42-day wt.	-10.0	-10.3	9.5	10.3
56-day wt.	-12.2	-11.7	9.9	11.7
12-21 gain	-1.0	-1.5	1.6	1.5
21-42 gain	-7.8	-7.4	6.4	7.4
42-56 gain	-2.0	-1.9	0.6	1.7

Table 33. Analyses of variance used to estimate additive variation ($\bar{L}_{1i} + \bar{L}_{2i} + \bar{L}_{3i}$) of weight traits in males

Source of variation	d.f.	MS. 12-day wt.	MS. 21-day wt.	MS. 42-day wt.	MS. 56-day wt.	MS. 12-21 gain	MS. 21-42 gain	MS. 42-56 gain
Sums ($\bar{L}_{1i}+\bar{L}_{2i}+\bar{L}_{3i}$)	17	5.67[a]	19.29[b]	93.00[a]	124.98[a]	10.27	100.16[a]	30.48
Replicates	1	30.68[a]	99.87[a]	92.93[a]	60.13[a]	21.13[a]	1,350.27[a]	3.83[a]
Sums x replicates	17	1.61[b]	8.13[b]	13.96	19.95	6.24[a]	26.98[a]	38.02[a]
Within families in reps	312	0.81	3.86	11.69	14.98	1.71	8.92	6.62

[a]Significant at .01 level
[b]Significant at .05 level
[c]Significant at .10 level

Table 34. Analyses of variance used to estimate additive variation ($\bar{L}_{1i} + \bar{L}_{2i} + \bar{L}_{4i}$) of weight traits in males

Source of variation	d.f.	MS. 12-day wt.	MS. 21-day wt.	MS. 42-day wt.	MS. 56-day wt.	MS. 12-21 gain	MS. 21-42 gain	MS. 42-56 gain
Sums ($\bar{L}_{1i}+\bar{L}_{2i}+\bar{L}_{4i}$)	17	6.07	15.61	112.09[a]	163.26[a]	13.20	1.59	2.24
Replicates	1	143.93[a]	446.01[a]	16.05	70.41[a]	85.81[a]	1,298.80[a]	18.00
Sums x replicates	17	3.72[a]	17.75[a]	25.20[c]	18.27	16.17[a]	39.95[a]	25.82[a]
Within families in reps	317	1.25	4.35	13.21	16.92	2.35	9.33	7.24

[a]Significant at .01 level
[b]Significant at .05 level
[c]Significant at .10 level

Table 35. Analyses of variance used to estimate additive variation ($\bar{L}_{1i} + \bar{L}_{2i} + \bar{L}_{3i}$) of weight traits in females

Source of variation	d.f.	MS. 12-day wt.	MS. 21-day wt.	MS. 42-day wt.	MS. 56-day wt.	MS. 12-21 gain	MS. 21-42 gain	MS. 42-56 gain
Sums ($\bar{L}_{1i}+\bar{L}_{2i}+\bar{L}_{3i}$)	17	5.05[b]	19.23	37.87[b]	61.63[a]	8.42	40.32[b]	14.50
Replicates	1	51.34[a]	121.16[a]	6.24	99.87[a]	15.49	408.03[a]	118.58[a]
Sums x replicates	17	1.90	11.84[a]	16.25	9.25	6.27[a]	13.92	8.52
Within families in reps	310	1.25	4.35	13.21	16.92	2.35	9.33	7.24

[a]Significant at .01 level
[b]Significant at .05 level
[c]Significant at .10 level

Table 36. Analyses of variance used to estimate additive variation ($\bar{L}_{1i} + \bar{L}_{2i} + \bar{L}_{4i}$) of weight traits in females

Source of variation	d.f.	MS. 12-day wt.	MS. 21-day wt.	MS. 42-day wt.	MS. 56-day wt.	MS. 12-21 gain	MS. 21-42 gain	MS. 42-56 gain
Sums ($\bar{L}_{1i}+\bar{L}_{2i}+\bar{L}_{4i}$)	17	7.27[c]	16.89	48.17[b]	75.02[a]	9.69	42.65	21.20[b]
Replicates	1	146.21[a]	316.68[a]	182.41[a]	8.13	33.08	217.01[a]	125.35[a]
Sums x replicates	17	3.45[b]	14.46[a]	20.10[b]	23.51[a]	12.25[a]	25.99[a]	8.33[b]
Within families in reps	314	1.17	3.60	7.99	8.76	1.93	5.56	3.78

[a]Significant at .01 level
[b]Significant at .05 level
[c]Significant at .10 level

of females. Additive variation makes an important contribution to phenotype of 12-, 42- and 56-day body weights for analyses involving F_{1-3} and F_{1-4} females. Additive variation is not important for gain from 12 to 21 days of age. Significance for the other three traits depends on the sex of the offspring and which F_1 was used. For 21-day weight, no additive variation was found significant for females but analyses ($\bar{L}_{1i} + \bar{L}_{2i} + \bar{L}_{3i}$) showed significance in males while analyses ($\bar{L}_{1i} + \bar{L}_{2i} + \bar{L}_{4i}$) did not. Gain from 21 to 42 days of age showed no significant additive component for analyses ($\bar{L}_{1i} + \bar{L}_{2i} + \bar{L}_{3i}$) but did show a significant additive component for analyses ($\bar{L}_{1i} + \bar{L}_{2i} + \bar{L}_{4i}$). Gain from 42 to 56 days of age in males showed no significant contribution to additive variation while in females, analyses using F_{1-3} showed no significance for the additive component but analyses using F_{1-4} did.

Significance of dominance variation was detected from analyses of variance Tables 37 and 38. Traits, 21-day weight, 12-21, 21-42, and 42-56 day gains, did not show significant dominance variation. Traits showing significant dominance effects for both sexes were 12- and 56-day weight. In males 42-day weight was significantly influenced by dominance but in the females it was not important.

After mean squares are equated to their expected values, variance components, σ^2_S and σ^2_D can be computed. Since $\sigma^2_S = 1/8D$ and $\sigma^2_D = 1/8H$, estimates of D and H are given in Table 39. The two analyses of sums produced two D's and $\bar{d}$'s (σ^2_D/σ^2_S), a measure of average dominance. Estimates of D_1 and D_2 differ from each other even though in theory they should not. Possible causes include inadequate numbers of observations, linkage bias or some maternal force. As shown in Table 39, dominance

Table 37. Analyses of variance used to estimate dominance variation of weight traits in males

Source of variation	d.f.	MS. 12-day wt.	MS. 21-day wt.	MS. 42-day wt.	MS. 56-day wt.	MS. 12-21 gain	MS. 21-42 gain	MS. 42-56 gain
Between parents	1	281.82	1,054.74	15,019.23[b]	21,341.38	246.77	8,099.59[b]	566.84
Differences ($\bar{L}_{1i}$-$\bar{L}_{2i}$)	25	5.54[b]	14.07	41.82[b]	46.44[c]	5.07	26.13	15.24
Replicates	1	16.32[b]	54.38[b]	18.45	517.35[a]	11.78	8.77	215.19[a]
Diff x replicates	25	2.68[a]	10.80[a]	20.20[a]	27.10[a]	7.24[a]	16.60[a]	21.67[a]
Within families in reps	304	0.83	2.87	8.83	11.15	1.53	6.44	5.13

[a]Significant at .01 level
[b]Significant at .05 level
[c]Significant at .10 level

Table 38. Analyses of variance used to estimate dominance variation of weight traits in females

Source of variation	d.f.	MS. 12-day wt.	MS. 21-day wt.	MS. 42-day wt.	MS. 56-day wt.	MS. 12-21 gain	MS. 21-42 gain	MS. 42-56 gain
Between parents	1	273.98	1,030.68	9,968.57[b]	15,582.01[c]	240.04	4,585.85[c]	588.53
Differences ($\bar{L}_{1i}$-$\bar{L}_{2i}$)	25	5.09[b]	9.77	23.35	23.29[c]	4.39	14.60	6.29
Replicates	1	17.61[b]	82.45[a]	15.54	97.31[b]	22.90[c]	24.62	44.20[a]
Diff x replicates	25	2.92[a]	9.88[a]	18.33[a]	13.63[a]	6.68[a]	17.73[a]	5.30[b]
Within families in reps	297	0.75	2.66	5.18	6.27	1.40	3.59	2.76

[a]Significant at .01 level
[b]Significant at .05 level
[c]Significant at .10 level

Table 39. Estimates of D_1, D_2, H and $\bar{d}$ for males and females

	12-day wt.	21-day wt.	42-day wt.	56-day wt.	12-21 gain	21-42 gain	42-56 gain
Males							
D_1	13.04[a]	29.20[b]	269.44[a]	360.24[a]	9.28	257.04[a]	0.00
D_2	4.40	0.00	294.72[a]	512.32[a]	0.00	0.00	0.00
H	8.08[b]	1.60	51.12[b]	32.72[c]	0.00	0.00	0.00
$\bar{d}_1$	0.62	0.05	0.19	0.09	0.00	0.00	0.00
$\bar{d}_2$	0.54	0.00	0.17	0.06	0.00	0.00	0.00
Females							
D_1	7.60[b]	12.16	33.60[b]	141.84[a]	0.00	68.32[b]	0.00
D_2	10.56[c]	0.00	85.60[b]	170.96[a]	0.00	44.64	36.32[b]
H	7.68[b]	0.00	0.00	13.52[c]	0.00	0.00	0.00
D_{X1}	3.80	6.08	16.80	70.92	0.00	34.16	0.00
D_{X2}	5.28	0.00	42.80	85.48	0.00	22.32	18.16
H_X	3.84	0.00	0.00	6.76	0.00	0.00	0.00
$\bar{d}_1$	1.01	0.00	0.00	0.09	0.00	0.00	0.00
$\bar{d}_2$	0.73	0.00	0.00	0.08	0.00	0.00	0.00

[a]Significant at .01 level
[b]Significant at .05 level
[c]Significant at .10 level

deviated little from mid-parent value except for 12-day weight. Average dominance for 12-day weight ranges from .54-.62 in males to .73-1.01 in females.

Heritability estimates appear in Table 40 along with the percent contribution of additive, dominance and environmental variations make to the phenotypic variation. Heritabilities from triple test cross designs can only be obtained when L_1 and L_2 are divergent selection lines, thus maximizing the number of loci segregating. Because selection was practiced for one trait only, 21-42 gain, one would question whether loci for unselected traits were segregating maximally. This is a difficult question. Figure 3 shows the responses of 12-, 21-, 42- and 56-day weights after 24 generations of selecting for 21-42 day gain. A divergent phenotypic response would suggest that most loci are segregating for the trait measured. 12- and 21-day body weights show little divergence while 42- and 56-day body weights diverge considerably. Realized correlated responses presented by LaSalle et al. (1974) for these lines after 12 generations of selection for increased 21-42 gain were $-.12 \pm .72$, $.04 \pm .03$, $.80 \pm .11$ and $.80 \pm .12$ for 12-, 21-, 42- and 56-day weights, respectively. This might suggest that heritabilities for 12- and 21-day weights in Table 40 are lower than expected. Comparison of heritabilities obtained in this study and those cited in literature are:

Table 40. Heritabilities and estimates of additive, dominance and epistatic components

	12-day wt.		21-day wt.		42-day wt.		56-day wt.		12-21 gain		21-42 gain		42-56 gain	
	actual	percent	actual	percent	actual	percent	actual	percent	actual	percent	actual	percent	actual	percent
Males														
$V_{A(2)}$	2.20		0.00		147.36		256.16		0.00		0.00		0.00	
$V_{A(1)}$	6.52	17.4	14.60	9.0	134.72	33.8	180.12	32.9	4.64	4.0	128.52	20.9	0.00	0.0
V_D	2.02	5.4	0.40	0.3	12.70	3.2	8.18	1.4	0.00	0.0	0.00	0.0	0.00	0.0
E	28.98	77.2	146.34	90.7	251.28	63.0	359.10	65.7	112.32	96.0	485.64	79.1	684.36	100.0
h^2_N	0.17		0.09		0.34		0.33		0.04		0.21		0.00	
h^2_B	0.23		0.09		0.37		0.34		0.04		0.21		0.00	
Females														
$V_{A(2)}$	5.28		0.00		42.80		85.48		0.00		22.32		18.16	
$V_{A(1)}$	3.80	9.5	6.08	2.8	16.80	5.4	70.92	29.5	0.00	0.0	34.16	12.0	0.00	0.0
V_D	1.92	4.8	0.00	0.0	0.00	0.0	3.38	1.4	0.00	0.0	0.00	0.0	0.00	0.0
E	34.20	85.7	213.12	97.2	292.50	94.6	166.50	69.1	112.86	100.0	250.86	88.0	153.36	100.0
h^2_N	0.10		0.03		0.05		0.29		0.00		0.12		0.00	
h^2_B	0.19		0.03		0.05		0.31		0.00		0.12		0.00	

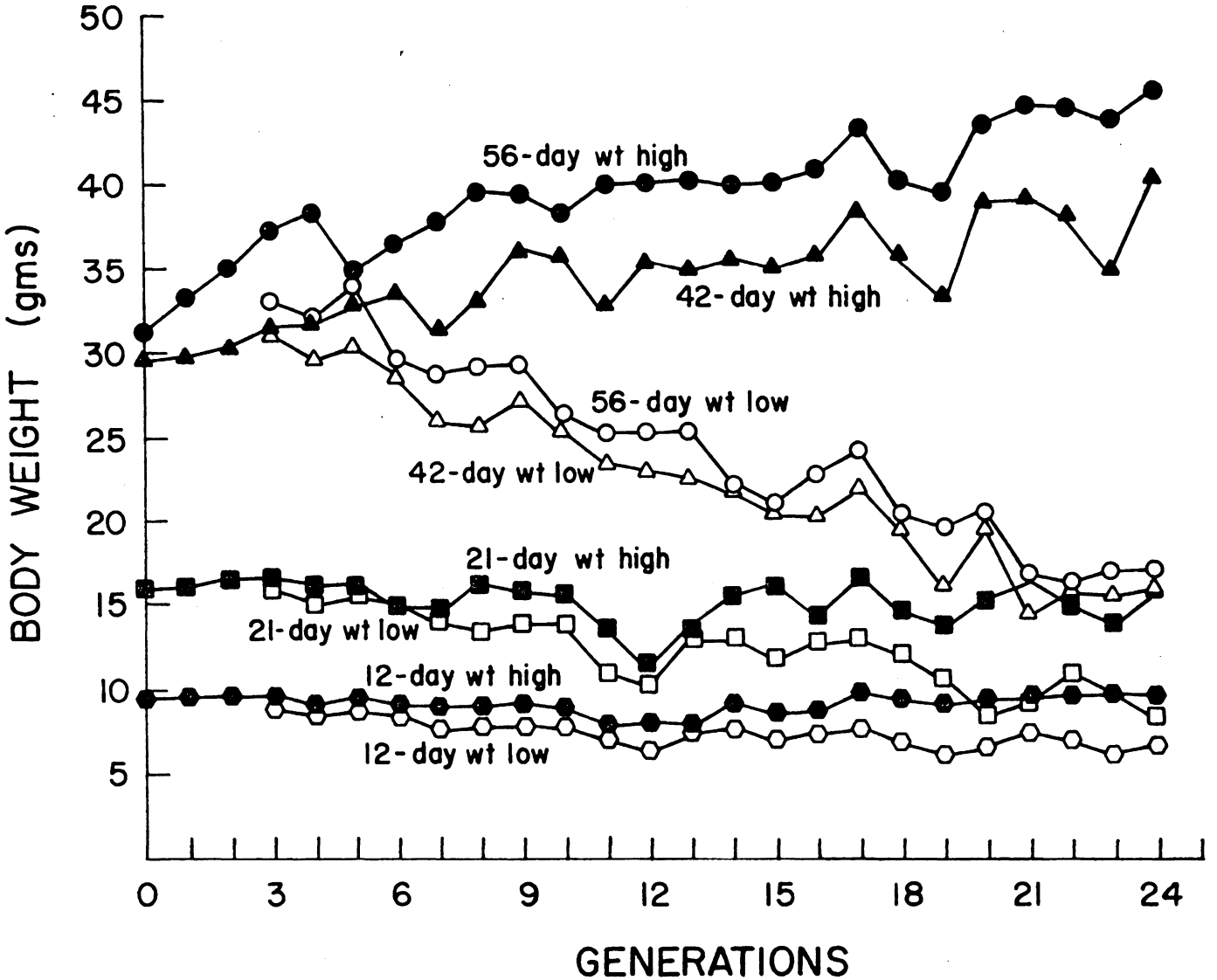


Figure 3. Responses of 12-, 21-, 42-, and 56-day weights in lines selected for increased and decreased gain from 21-42 days of age

	21-day wt.	42-day wt.	56-day wt.	21-42 gain	42-56 gain
Miller et al. (1963)	.16	.16	-	.12	-
Vinson et al. (1969)	.23	.24	.29	.27	-
Jara-Almonte and White (1973)	.14	.33	.29	.22	.19
present study	.03-.09	.05-.34	.29-.33	.12-.21	.00

Except for 21-day weight all heritabilities are similar with some differences arising from separation of sexes.

Studies with mice have found no evidence for dominance in 21-day and 42-day body weight (Godwin, 1972 and Miller et al., 1963). Miller et al. (1963) reported that dominance accounted for 28% of total variance for number of mice born in a litter. Evidence from first-order tests have shown little or no dominance for 21- and 42-day body weight and 12-21, 21-42, and 42-56 day gains but 12-day and 56-day weights did have a dominance contribution of 5.0% and 1.4%, respectively.

Sex-Linkage and Maternal Effects

Sex-linkage parameters differ according to the sex of the animal. In the homogametic sex, two sex-linkage parameters, $[d_x]$ and $[h_x]$ can be estimated along with autosomal parameters [d] and [h]. The heterogametic sex can generate only one sex-linkage parameter, $[d_{x'}]$. Estimates of sex-linkage parameters for males and females are given in Tables 41 and 42. χ^2 goodness of fit tests determine adequacy of the sex-linkage model. Since χ^2 values are very large, rejection of this

Table 41. Test for sex-linkage in males for weight traits

	12-day wt.		21-day wt.		42-day wt.		56-day wt.		12-21 gain		21-42 gain		42-56 gain	
	estimate	S.E.	estimate	S.E.	estimate	S.E.	estimate	S.E.	estimate	S.E.	estimate	S.E.	estimate	S.E.
m	8.50	0.03	14.13	0.06	30.28	0.11	34.03	0.11	5.74	0.04	16.22	0.09	3.74	0.07
[d]	0.71	0.05	1.55	0.11	9.72	0.19	11.44	0.19	0.91	0.07	8.18	0.15	1.82	0.11
[h]	-2.77	0.05	-4.64	0.11	-15.07	0.19	-18.75	0.19	-1.68	0.07	-10.63	0.15	-2.60	0.11
$[d_{x'}]$	0.63	0.04	1.00	0.07	1.55	0.12	1.82	0.13	0.32	0.05	0.53	0.10	0.22	0.06
x^2	8,622		7,483		29,694		39,965		2,050		19,185		1,025	

Table 42. Test for sex-linkage in females for weight traits

	12-day wt.		21-day wt.		42-day wt.		56-day wt.		12-21 gain		21-42 gain		42-56 gain	
	Estimate	S.E.	Estimate	S.E.	Estimate	S.E.	Estimate	S.E.	Estimate	S.E.	Estimate	S.E.	Estimate	S.E.
m	6.88	0.03	10.75	0.05	13.39	0.09	14.55	0.09	3.84	0.03	2.94	0.07	0.53	0.06
[d]	23.53	0.10	52.21	0.20	233.35	0.34	294.42	0.35	30.45	0.13	167.34	0.27	28.18	0.21
[h]	17,588.64	0.05	8,075.89	0.10	6,545.86	0.15	6,145.54	0.15	6,689.80	0.06	4,182.21	0.13	947.30	0.10
$[d_x]$	23.69	0.11	52.97	0.20	239.57	0.35	302.15	0.36	31.02	0.14	172.95	0.28	29.44	0.22
$[h_x]$	-17,585.52	0.00	-8,069.45	0.00	-6,521.63	0.00	-6,119.56	0.00	-6,686.34	0.00	-4,164.55	0.00	-944.82	0.00
χ^2	2,973,393		4,234,264		28,874,940		44,657,800		3,444,203		21,075,950		807,095	

model is appropriate. Large χ^2 values for females seem related to the unrealistic estimates of [h] and [h_x].

As reported by Killick (1971), sex-linkage variance components for females can be estimated from σ^2_S, variance component for sums, and σ^2_D, variance components for differences.

$$\sigma^2_S = 1/4D_x, \text{ and}$$

$$\sigma^2_D = 1/4H_x.$$

Remembering that σ^2_S is computed from two analyses, one involving ($\bar{L}_{1i} + \bar{L}_{2i} + \bar{L}_{3i}$) and the other ($\bar{L}_{1i} + \bar{L}_{2i} + \bar{L}_{4i}$), estimates of D_{x1}, D_{x2} and H_x appear in Table 39. These estimates could possibly suggest some additive sex-linkage variation in 12-, 42- and 56-day weight and sex-linked dominance variation in 12-day weight. But due to the overwhelming failure of sex-linkage model in first-order tests, sex-linkage does not appear to be an important genetic force. Using crosses among selected and control lines of mice, White et al. (1970) indicated that sex-linked genes probably have little effect on body weight and gain traits. These results tend to agree.

Unlike sex-linkage, maternal effects lead to a greater resemblance of the progeny to the maternal parent irrespective of whether this happens to be the homogametic sex in the species under consideration. Two parameters [d_m] and [h_m] are used to define the maternal component contributed by the mother's genotype. Estimates of maternal and autosomal parameters are given in Tables 43, 44 and 45. χ^2 values for all traits, except for 56-day weight in males, are the smallest for any first-order test. In this analyses, as in the one for additive-dominance, the [h]

Table 43. Test for maternal effects for littering traits

	No. born		Litt. time		Mort. B-5 days		Litt. wt. 12 days	
	estimate	S.E.	estimate	S.E.	estimate	S.E.	estimate	S.E.
m	11.20	0.14	23.59	0.20	1.50	0.49	65.29	0.44
[d]	0.53	0.27	0.67	0.37	-0.25	0.99	4.95	0.85
[h]	0.57	0.27	1.04	0.37	0.23	0.99	-1.25	0.85
$[d_m]$	1.12	0.18	-0.25	0.24	0.28	0.63	5.54	0.57
$[h_m]$	1.72	0.14	-1.15	0.17	-0.91	0.37	4.54	0.40
$x^2(3)$	85.6		38.4		1.66		217.6	

Table 44. Test for maternal effects for weight traits in males

	12-day wt.		21-day wt.		42-day wt.		56-day wt.		12-21 gain		21-42 gain		42-56 gain	
	estimate	S.E.	estimate	S.E.	estimate	S.E.	estimate	S.E.	estimate	S.E.	estimate	S.E.	estimate	S.E.
m	8.30	0.03	13.84	0.06	29.57	0.12	31.56	0.11	5.54	0.04	15.85	0.09	3.71	0.07
[d]	0.71	0.05	1.56	0.11	9.72	0.20	3.03	0.19	0.93	0.08	8.18	0.15	1.81	0.11
[h]	-0.08	0.05	0.21	0.11	0.77	0.19	8.35	0.19	0.25	0.08	0.25	0.15	-0.84	0.11
$[d_m]$	0.62	0.04	0.99	0.07	1.54	0.12	8.47	0.13	0.30	0.05	0.53	0.10	0.22	0.06
$[h_m]$	0.49	0.03	0.78	0.06	0.59	0.11	-2.13	0.11	0.31	0.04	-0.16	0.09	-0.31	0.07
$x^2_{(3)}$	736.5		688.3		138.5		2065.7		350.5		14.0		72.2	

Table 45. Test for maternal effects for weight traits in females

	12-day wt.		21-day wt.		42-day wt.		56-day wt.		12-21 gain		21-42 gain		42-56 gain	
	estimate	S.E.	estimate	S.E.	estimate	S.E.	estimate	S.E.	estimate	S.E.	estimate	S.E.	estimate	S.E.
m	8.21	0.03	13.51	0.05	25.70	0.09	28.44	0.09	5.31	0.03	12.54	0.08	2.49	0.06
[d]	0.62	0.05	1.76	0.09	9.08	0.15	10.25	0.15	1.13	0.06	7.37	0.12	1.34	0.10
[h]	-0.10	0.05	0.11	0.09	-0.39	0.15	-1.19	0.15	0.16	0.06	-0.71	0.12	-1.01	0.10
$[d_m]$	0.69	0.04	0.86	0.06	0.98	0.09	0.99	0.09	0.17	0.04	-0.16	0.08	0.15	0.06
$[h_m]$	0.53	0.03	0.74	0.05	0.23	0.09	-0.37	0.09	0.24	0.04	-0.73	0.07	-0.28	0.06
$x^2_{(3)}$	706.2		678.9		264.3		109.9		303.2		50.4		42.1	

parameter is small and close to zero. The additive maternal, [d_m], and dominance maternal component, [h_m], are almost as large as the additive autosomal component, [d], for littering traits and 12-day individual body weight. For the remaining traits, the additive component is the larger. Many experiments (Rutledge et al., 1972; Miller et al., 1963; Jamison et al., 1975) have found that maternal influences in mice have a significant effect on body weight from birth to weaning but decline rapidly as the animal matures. This study shows similar results except that maternal influences remain with the animal as it matures. Breakdown of maternal variation as shown by Godwin (1972) was 25%, 0% and 0% for additive maternal; 6%, 26% and 19% for dominance maternal of total phenotypic variation for 21-, 42- and 60-day weights, respectively. These results here show the importance of the additive and dominance maternal components in the genetic model for littering and weight traits in mice.

Efficiencies and Biases of Triple Test Cross

The triple test cross is used to determine the genetic architecture of traits within a population. Phenotypically divergent tester lines will detect genetic sources of variation for the sample of loci for which the testers differ. Tester lines should be developed from the population to be studied. Models used are rated only within a population. The same allele showing different dominance in different populations would be detected as epistasis, but it would not in fact be a type of epistasis found within a population. It is a well known phenomenon that wide crosses exhibit a type of non-additive variation not present within a

population. Thus, a mating design used to estimate genetic parameters must use the genetic material from the population to be studied.

Efficiencies of this design over other genetical designs are numerous. Importance of detection of epistasis cannot be underemphasized. To obtain valid estimates of additive and dominance components, the effect of variation in genotype at any single locus cannot be modified by genes at other loci. Maternal effects are not confounded with detection of epistatic, additive, and dominance variation. Number of animals needed to detect dominance when $p = q = .5$ and $h^2 = .25$ for diallel and triple test cross procedure are given by Kearsey (1970).

$\bar{d}$ =	0.2	0.4	0.6	0.8	1.0
Diallel	9,088	2,240	960	512	320
TTC	5,904	1,464	624	336	216

As shown above the triple test cross is a more efficient design in terms of experimental sizes. A half-sib and full-sib structure of data, however, makes obtaining the same number of observations as in a diallel a bit more difficult.

Possible sources of bias in the triple test cross model include multiple allelism and linkage. No multiple allelism is assured by origin of the population. Multiple alleles in an F_2 of homozygous lines can result from mutation only when $q = 1.0$ in the P_1. Since mutation would be expected to occur very infrequently, the only possible bias would be linkage. Furthermore, specific linkage relationships in

an F_1 of homozygous lines must be in either the coupling or repulsion phase and equilibrium between the phases cannot occur in the F_2. The effect of linkage bias on estimation of additive and dominance variance using inbred lines was summarized by Robinson et al. (1960).

Initial linkage phase	σ^2_S	σ^2_D	dominance ratio
Cancellation of repulsion and coupling	decrease	no change	decrease
Predominantly repulsion	decrease	increase	decrease
All coupling	decrease	decrease	no change
Predominantly coupling	decrease	decrease	increase or decrease

Kearsey and Jinks (1968) stated that when L_1 and L_2 are extreme high and low selection lines a high degree of gene association exists which inflates coupling linkages by the same amount. Thus, the ratio, σ^2_D/σ^2_S, is a measure of average dominance irrespective of gene distributions in the population.

SUMMARY

Reproductive and growth traits in mice were subjected to various statistical approaches in order to investigate the genetic architecture of these traits. Reproductive traits, number mice born per litter, littering time, mortality of young from birth to 5 days, 12-day litter weight and growth traits, 12-, 21-, 42- and 56-day body weight, gain from 12-21, 21-42 and 42-56 days of age were analyzed to evaluate additive, dominance, epistatic, sex-linkage and maternal effects. Two basic levels of statistical analyses were used: first-order tests using component of means determined estimates and adequacy of various genetic parameters and second-order tests using components of variation allowed estimation of additive, dominance and environmental sources of variation and detection of epistasis. Summarization of results from both levels of analyses are presented in Table 46.

Sex-linkage is not an important genetic force in growth traits of mice. Maternal effects, both additive and dominance, are large genetic contributors to the phenotypic variation for littering and weight traits. For all reproductive traits and 12-day individual body weight, estimates of maternal components are as large as the additive component, but for 21-, 42- and 56-day weights and 12-21, 21-42 and 42-56 gain, additive effects are much larger. Traits for which epistatic interaction are important genetic influences are littering time, mortality for birth to 5 days and 12-day individual weight for

Table 46. Genetic architecture of littering and weight traits

Traits	Additive	Dominance	Epistasis	Maternal	Sex-Linkage
Littering					
No. born	Yes	No	No	Yes	-
Litt. time	Weak	No	Yes	Yes	-
Mort. B-5 days	No	No	Yes	Yes	-
12-day Litt. wt.	Yes	No	No	Yes	-
Weight-males					
12-day wt.	Yes	Yes	Yes	Yes	No
21-day wt.	Weak	No	Weak	Yes	No
42-day wt.	Yes	Yes	No	Yes	No
56-day wt.	Yes	Weak	Weak	No	No
12-21 gain	No	No	No	Yes	No
21-42 gain	Yes	No	No	Yes	No
42-56 gain	No	No	No	Yes	No
Weight-females					
12-day wt.	Yes	Yes	Yes	Yes	No or weak
21-day wt.	No	No	Weak	Yes	No
42-day wt.	Yes	No	No	Yes	No or weak
56-day wt.	Yes	Weak	Weak	Yes	No or weak
12-21 gain	No	No	No	Yes	No
21-42 gain	Yes	No	No	Yes	No
42-56 gain	Weak	No	No	Yes	No

males and females. Weaker epistatic interactions were found for body weights at 21 and 56 days of age. Estimates of dominance components for littering traits were all zero. A few weight traits showed dominance to be a significant source of genetic variation but percent contribution to phenotypic variation was quite small. Body weight at 12 days of age has the largest dominance component, 5.4 and 4.8% for males and females, respectively, while 3.2% of phenotypic variation for 42-day body weight in males was attributable to dominance. Traits showing smaller dominance contributions were 56-day weight for males and females at 1.4% for each. Additive effects were important for littering traits except littering time and mortality of young from birth to 5 days, 12-, 42- and 56-day body weights in both sexes had significant additive variance components. Percent contributions of additive variation to the phenotypic expression for body weight were 17.4 and 9.5% of 12-day weights, 33.8 and 5.4% of the 42-day weights, and 32.9 and 29.5% of 56-day weights for males and females, respectively. For 21-day weight in males and females, only 9.0 and 2.8% of phenotypic variation was due to additive gene action. As for gain traits, only gain from 21-42 days of age showed any significant additive genetic variation, 20.9 and 12.0% in males and females, respectively.

In conclusion, this experiment has attempted to determine the relative importance of most genetic parameters--additive, dominance, epistatic, maternal and sex-linkage effects for reproduction and growth traits in mice. Genetic influences in reproductive traits are direct additive and maternal (additive and non-additive) effects. Epistatic interactions are involved in gene action of traits measuring length

of time from exposure of males to littering and mortality of young from birth to 5 days. For weight traits additive and maternal genetic variation are the main genetic forces. Epistatic and dominance variations are significant genetic influences for 12-day weights. Gain traits are influenced less by additive and maternal effects than weight traits. Sex-linked genes have little or no effect in body weight and gain traits.

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Table 47. Arithmetic means and standard deviations of littering traits for generations 0, 1 and 2

			No. born		Litt. time		MB-5 Days		Litt. wt. 12-days		
Gen	Line	No.	Mean	S.D.	Mean	S.D.	Mean	S.D.	No.	Mean	S.D.
0	P_1	43	13.6	2.7	23.7	4.2	1.3	4.8	42	72.0	9.5
	P_2	54	9.1	2.0	21.7	2.1	2.2	13.7	50	50.5	7.9
1	P_1	42	11.7	3.3	25.1	4.4	0.8	3.0	40	79.5	8.2
	P_2	49	8.5	2.4	25.6	3.9	1.0	5.5	45	58.3	5.5
	F_{1-3}	48	9.5	1.6	26.1	4.0	2.1	14.4	47	61.7	11.3
	4	42	12.2	3.7	25.9	4.1	0.7	3.5	41	74.2	7.1
2	P_1	48	11.9	3.6	24.8	4.5	3.7	15.3	43	80.3	8.1
	P_2	57	9.8	2.0	23.9	3.9	1.1	4.1	46	60.7	7.7
	F_{1-3}	43	9.9	2.4	26.1	4.5	0.6	2.4	41	64.0	6.7
	4	49	12.0	3.7	24.7	9.2	5.8	20.5	42	72.0	12.6
	F_{2-5}	68	12.6	2.0	22.7	3.0	0.5	2.0	47	73.5	5.9
	6	70	12.0	2.9	22.3	2.9	1.6	12.0	51	74.4	8.1
	7	67	12.5	2.7	22.7	3.0	0.7	5.0	45	74.5	5.5
	8	66	12.5	3.0	22.5	3.2	0.5	3.2	47	74.8	7.4

Table 48. Arithmetic means and standard deviations of littering traits for generation 3

Gen	Line	No.	No. born		Litt. time		MB-5 Days		Litt. wt. 12-days		
			Mean	S.D.	Mean	S.D.	Mean	S.D.	No.	Mean	S.D.
3	F_2xP_1-51	32	13.3	3.6	25.2	4.6	1.5	6.1	26	72.9	10.2
	61	35	11.5	3.8	23.1	2.8	3.6	17.0	25	73.5	6.4
	71	36	12.3	2.8	23.9	3.6	0.2	1.3	26	75.0	6.6
	81	35	12.8	3.5	23.4	2.6	0.0	0.0	25	75.8	5.3
	F_2xP_2-52	36	10.1	2.2	24.3	3.9	0.4	1.8	26	53.7	6.7
	62	34	9.5	1.7	24.6	3.6	1.0	3.2	25	54.8	6.4
	72	35	9.9	2.1	23.9	4.1	0.6	3.7	25	54.1	4.8
	82	36	10.1	1.3	23.5	3.5	2.5	9.4	26	57.3	4.6
	F_2xF_1-53	35	11.8	3.0	23.1	3.5	0.8	4.8	26	69.3	6.2
	63	37	12.5	2.4	24.5	3.8	0.3	1.4	25	66.8	7.2
	73	38	12.1	2.3	23.3	2.8	0.2	1.3	26	69.9	5.6
	83	37	12.8	2.2	23.8	3.6	0.3	1.8	26	68.4	5.4
	F_2xF_1-54	35	12.8	2.5	23.1	3.6	1.3	3.6	26	69.2	6.0
	64	36	12.4	3.2	23.6	2.5	0.6	2.6	26	70.6	6.5
	74	38	13.6	2.4	23.9	4.3	0.1	1.0	26	70.4	5.4
	84	38	12.8	2.4	23.4	3.4	0.6	2.7	26	69.3	4.9

Table 49. Arithmetic means and standard deviations of littering traits for generation 4

Gen	Line	No.	No. born		Litt. time		MB-5 Days		Litt. Wt. 12-days		
			Mean	S.D.	Mean	S.D.	Mean	S.D.	No.	Mean	S.D.
4	F_2xP_1-51	21	14.9	2.9	23.2	2.9	4.8	21.8	18	69.3	10.2
	61	25	13.9	3.7	23.5	3.6	0.3	1.3	18	67.4	8.1
	71	25	13.9	4.5	23.5	3.1	1.4	4.4	16	67.7	6.9
	81	22	15.1	3.3	23.6	3.8	0.6	2.0	18	67.5	5.8
	F_2xP_2-52	25	11.7	2.9	22.9	3.2	4.2	20.0	18	54.4	5.3
	62	24	10.9	3.2	22.4	2.6	1.4	6.8	18	52.8	6.8
	72	25	11.9	2.7	22.3	3.0	0.6	2.0	18	52.5	7.0
	82	25	12.0	2.8	23.1	3.9	1.0	3.6	18	57.9	4.5
	F_2xF_1-53	25	14.9	1.8	22.6	3.4	0.0	0.0	17	68.2	5.2
	63	24	14.1	3.9	23.1	4.1	0.0	0.0	18	62.7	7.3
	73	25	14.6	2.5	22.2	2.8	0.0	0.0	17	65.9	4.7
	83	26	15.3	1.9	22.2	2.1	0.8	2.2	18	65.3	4.2
	F_2xF_1-54	23	15.6	3.2	22.6	2.9	4.9	11.7	18	63.1	6.5
	64	26	14.0	3.8	22.9	3.5	0.0	0.0	18	63.2	8.6
	74	24	15.2	2.5	23.4	3.7	0.6	2.0	18	61.1	6.2
	84	26	14.9	2.6	24.3	3.8	0.0	0.0	18	63.1	8.2

Table 50. Arithmetic means and standard deviations of weight traits for generations 0, 1 and 2

Gen.	Line	Sex	No.	12-day wt.		21-day wt.		42-day wt.		56-day wt.		12-21 gain		21-42 gain		42-56 gain	
				Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.
0	P_1	M	143	9.3	1.1	15.1	2.4	38.2	5.9	45.5	4.9	5.8	1.7	23.2	5.0	7.3	3.8
		F	164	9.1	1.1	14.6	2.2	34.2	4.9	38.8	4.0	5.5	1.4	19.6	4.0	4.6	3.3
	P_2	M	147	6.6	0.6	10.4	1.3	17.0	3.0	19.1	2.5	3.8	0.9	6.6	2.8	2.1	2.2
		F	191	6.5	0.7	10.0	1.3	15.4	2.3	16.8	1.7	3.6	0.8	5.4	2.2	1.3	1.9
1	P_1	M	161	10.0	1.2	17.6	2.5	42.6	4.2	47.2	4.4	7.5	1.7	25.0	2.6	4.6	2.9
		F	140	10.0	1.2	17.4	2.2	37.1	3.9	40.6	4.2	7.4	1.3	19.7	2.7	3.5	2.6
	P_2	M	161	7.4	0.7	12.5	1.5	19.0	2.9	21.1	3.1	5.1	1.0	6.5	3.0	2.0	1.6
		F	172	7.3	0.8	11.7	1.3	16.7	2.4	18.0	2.5	4.4	0.8	5.0	2.4	1.3	1.7
	F_1-3	M	189	7.9	0.8	14.0	1.6	29.2	2.9	31.9	2.9	6.1	1.0	15.2	2.8	2.7	1.7
		F	173	7.9	0.9	13.7	1.6	25.4	2.3	27.0	2.5	5.9	0.9	11.6	2.0	1.6	1.7
	4	M	146	9.3	1.1	16.4	2.1	32.5	4.5	35.7	4.6	7.1	1.2	16.1	3.5	3.2	1.7
		F	171	9.2	1.2	15.5	1.7	26.6	3.2	28.5	3.1	6.3	1.3	11.2	2.6	1.9	1.8

Table 50 - continued

Gen.	Line	Sex	No.	12-day wt. Mean	12-day wt. S.D.	21-day wt. Mean	21-day wt. S.D.	42-day wt. Mean	42-day wt. S.D.	56-day wt. Mean	56-day wt. S.D.	12-21 gain Mean	12-21 gain S.D.	21-42 gain Mean	21-42 gain S.D.	42-56 gain Mean	42-56 gain S.D.
2	P_1	M	155	10.2	1.2	17.8	2.5	42.7	5.0	47.4	4.8	7.6	1.8	24.8	3.6	4.7	3.3
		F	165	10.2	1.1	17.6	2.2	36.8	3.0	40.0	3.6	7.9	1.5	19.3	2.4	3.2	2.6
	P_2	M	196	7.5	0.9	12.3	1.7	20.3	3.1	21.6	3.5	4.8	1.1	8.0	2.5	1.3	1.5
		F	159	7.5	0.9	12.0	1.3	17.5	2.3	18.4	2.5	4.5	0.8	5.5	1.9	0.9	1.4
	F_1-3	M	158	8.1	1.0	13.7	2.3	29.4	3.0	32.2	3.1	5.6	1.5	15.7	2.3	2.8	1.6
		F	155	7.9	0.8	13.2	2.0	25.4	2.3	26.8	2.6	5.3	1.4	12.2	2.2	1.4	1.5
	4	M	151	9.3	1.6	15.4	2.9	32.1	4.1	34.7	4.1	6.1	1.8	16.7	2.7	2.7	2.0
		F	169	9.2	1.5	14.8	2.4	26.5	3.2	28.2	2.9	5.6	1.5	11.7	2.3	1.7	1.6
	F_2-5	M	194	9.2	0.8	15.6	2.0	31.9	3.7	34.8	4.1	6.4	1.6	16.3	3.1	2.9	1.9
		F	178	9.2	0.9	15.2	1.9	26.5	3.1	28.1	3.6	5.9	1.5	11.3	2.4	1.6	1.7
	6	M	202	9.4	1.0	16.3	1.9	31.9	3.5	34.1	3.9	6.8	1.3	15.6	2.8	2.2	1.9
		F	191	9.3	1.0	15.5	1.9	26.5	3.2	27.7	3.2	6.2	1.2	11.1	2.4	1.2	2.0
	7	M	173	9.4	0.8	16.0	1.8	31.6	3.9	34.0	4.2	6.6	1.3	15.6	3.1	2.4	2.1
		F	167	9.3	0.9	15.5	1.6	26.4	2.9	27.9	3.0	6.2	1.1	10.9	2.5	1.5	2.0
	8	M	178	9.4	1.0	15.9	2.1	31.1	3.7	33.9	3.9	6.4	1.4	15.2	3.1	2.8	2.0
		F	186	9.4	1.0	15.5	1.8	26.3	3.2	28.1	3.3	6.1	1.2	10.8	2.7	1.9	1.9

Table 51. Arithmetic means and standard deviations of weight traits for generation 3

Gen.	Line	Sex	No.	12-day wt.		21-day wt.		42-day wt.		56-day wt.		12-21 gain		21-42 gain		42-56 gain	
				Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.
3	F_2xP_1-51	M	104	9.2	1.5	14.9	3.2	36.8	5.6	42.1	4.1	5.7	2.4	21.8	4.3	5.3	2.7
		F	101	9.1	1.4	14.5	3.0	30.9	4.1	34.4	3.7	5.4	2.2	16.5	2.8	3.4	2.0
	61	M	83	9.2	0.9	15.6	2.1	36.0	3.7	41.3	3.8	6.4	1.6	20.4	3.7	5.3	3.3
		F	106	9.3	0.8	15.6	1.9	31.3	3.2	34.5	3.3	6.3	1.4	15.7	3.1	3.2	3.0
	71	M	104	9.4	0.9	16.0	2.0	36.0	4.0	40.7	3.9	6.6	1.6	20.1	3.6	4.7	2.6
		F	95	9.3	1.1	15.5	2.2	31.7	3.5	33.6	3.6	6.2	1.7	16.1	3.1	1.9	2.6
	81	M	105	9.5	0.9	15.9	1.8	35.8	4.4	40.7	4.0	6.4	1.3	20.0	3.8	4.9	3.8
		F	93	9.4	0.9	15.3	1.9	30.4	3.7	33.0	3.8	6.0	1.4	15.1	2.9	2.6	2.3
	F_2xP_2-52	M	97	7.1	1.3	11.2	2.2	22.1	2.6	24.5	3.3	4.0	1.9	10.9	2.6	2.4	1.7
		F	94	6.7	2.0	10.9	1.6	19.4	2.3	20.4	2.7	4.2	1.5	8.4	2.2	1.0	1.6
	62	M	109	6.9	0.9	11.3	2.4	22.3	3.6	24.3	3.8	4.4	1.8	11.1	3.0	2.0	2.2
		F	88	6.8	0.8	11.1	1.9	19.6	2.6	20.3	2.5	4.3	1.4	8.4	2.1	0.7	1.9
	72	M	100	6.9	0.6	11.3	1.6	23.2	2.9	24.6	3.7	4.4	1.2	11.9	2.5	1.4	1.8
		F	92	6.8	0.6	10.7	1.6	19.9	2.0	20.3	2.6	3.9	1.3	9.2	2.1	0.4	2.0
	82	M	103	7.3	0.6	12.4	1.3	22.7	2.9	24.3	3.3	5.2	0.9	10.2	2.5	1.6	1.7
		F	104	7.0	0.8	11.7	1.4	20.1	2.2	20.5	3.3	4.7	0.9	8.4	2.2	0.5	2.5

Table 51 - continued

Gen.	Line	Sex	No.	12-day wt. Mean	12-day wt. S.D.	21-day wt. Mean	21-day wt. S.D.	42-day wt. Mean	42-day wt. S.D.	56-day wt. Mean	56-day wt. S.D.	12-21 gain Mean	12-21 gain S.D.	21-42 gain Mean	21-42 gain S.D.	42-56 gain Mean	42-56 gain S.D.
3	F_2xF_1-53	M	93	8.8	0.8	14.6	2.1	29.9	3.7	33.2	3.9	5.8	1.5	15.3	3.4	3.3	2.6
		F	107	8.7	0.9	14.0	1.9	25.5	2.9	27.1	3.6	5.3	1.4	11.5	2.5	1.6	2.3
	63	M	100	8.4	1.0	14.2	2.0	30.8	4.2	33.1	4.6	5.8	1.3	16.6	3.4	2.3	2.7
		F	97	8.4	0.9	13.9	1.6	25.7	2.9	27.1	3.3	5.6	0.9	11.8	2.5	1.3	2.5
	73	M	98	8.8	0.8	14.5	2.1	28.9	3.8	32.1	4.1	5.7	1.7	14.4	3.3	3.2	2.4
		F	94	8.7	0.9	13.9	2.1	24.1	2.8	25.7	3.2	5.2	1.7	10.2	2.5	1.6	2.0
	83	M	111	8.5	0.8	14.7	1.8	28.0	4.3	32.2	4.9	6.2	1.3	14.0	3.7	3.4	2.4
		F	92	8.4	0.8	14.4	1.8	25.1	3.0	27.0	3.7	5.9	1.2	10.8	2.6	1.9	2.6
	F_2xF_1-54	M	102	8.7	0.9	14.9	1.6	29.8	4.1	33.0	5.0	6.2	0.9	14.9	3.6	3.2	2.6
		F	99	8.5	0.8	14.3	1.5	25.4	3.3	26.8	3.4	5.8	0.9	11.1	2.8	1.4	1.9
	64	M	93	8.8	0.9	14.7	2.0	30.5	3.2	33.2	3.5	5.9	1.4	15.9	3.0	2.7	2.7
		F	110	8.8	1.0	14.5	2.0	26.1	3.4	27.6	3.9	5.6	1.3	11.6	2.7	1.5	2.0
	74	M	114	8.7	0.9	14.9	1.9	29.8	4.2	32.6	4.5	6.2	1.2	14.9	3.3	2.8	2.5
		F	89	8.8	0.8	14.5	1.7	25.1	3.0	26.4	3.4	5.7	1.1	10.6	3.0	1.3	2.2
	84	M	101	8.6	0.7	14.8	1.6	30.5	3.3	33.2	3.7	6.2	1.2	15.7	3.2	2.6	2.4
		F	104	8.7	0.8	14.4	1.5	26.2	2.9	27.6	3.5	5.7	1.0	11.9	3.0	1.4	2.0

Table 52. Arithmetic means and standard deviations of weight traits for generation 4

Gen.	Line	Sex	No.	12-day wt.		21-day wt.		42-day wt.		56-day wt.		12-21 gain		21-42 gain		42-56 gain	
				Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.
4	F_2xP_1-51	M	73	8.7	1.4	14.7	2.6	35.9	3.5	40.0	3.5	6.0	1.4	21.2	2.9	4.1	1.9
		F	70	8.6	1.4	14.0	2.7	30.7	2.8	34.0	3.2	5.4	1.7	16.7	2.3	3.3	1.8
	61	M	73	8.6	1.2	14.7	2.2	35.2	4.1	40.4	3.4	6.0	1.1	20.5	3.4	5.2	3.0
		F	66	8.5	1.1	14.3	1.9	30.0	3.0	33.0	3.1	5.8	1.1	15.6	2.5	3.0	2.4
	71	M	61	8.6	1.1	14.3	2.2	35.6	3.6	39.8	4.2	5.7	1.4	21.3	3.4	4.3	2.8
		F	66	8.3	1.0	13.9	1.9	30.2	2.7	34.2	3.9	5.5	1.1	16.3	2.3	4.0	3.8
	81	M	79	8.5	0.9	14.6	1.8	36.4	2.8	40.3	4.5	6.1	1.1	21.7	2.1	3.9	4.0
		F	64	8.3	1.0	14.2	1.7	30.1	2.2	33.3	2.5	5.8	1.1	16.0	2.0	3.1	1.6
	F_2xP_2-52	M	65	6.9	0.8	11.7	1.5	23.3	3.1	25.6	3.9	4.8	0.9	11.6	2.7	2.3	2.3
		F	75	6.7	0.8	11.5	1.5	20.1	2.4	21.4	2.9	4.6	0.9	8.6	2.0	1.4	1.8
	62	M	73	6.7	0.9	11.0	1.7	23.0	3.1	24.8	3.6	4.3	0.9	12.0	2.5	1.8	1.5
		F	70	6.5	0.8	10.8	1.7	19.5	2.7	20.4	2.5	4.3	1.3	8.7	2.4	0.9	1.6
	72	M	66	6.8	0.8	11.2	1.6	23.4	2.6	25.5	3.2	4.3	1.1	12.3	2.1	2.1	1.7
		F	66	6.8	0.9	11.1	1.7	20.4	2.5	21.6	2.8	4.3	1.0	9.4	2.1	1.2	1.6
	82	M	68	7.2	0.6	11.7	1.3	23.7	2.4	26.2	3.0	4.5	0.9	12.0	2.4	2.5	1.4
		F	74	7.2	0.7	11.6	1.4	20.4	1.9	21.6	2.1	4.3	0.9	8.9	2.0	1.1	1.1

Table 52 - continued

Gen.	Line	Sex	No.	12-day wt. Mean	12-day wt. S.D.	21-day wt. Mean	21-day wt. S.D.	42-day wt. Mean	42-day wt. S.D.	56-day wt. Mean	56-day wt. S.D.	12-21 gain Mean	12-21 gain S.D.	21-42 gain Mean	21-42 gain S.D.	42-56 gain Mean	42-56 gain S.D.
4	F_2xF_1-53	M	73	8.6	0.8	14.3	1.6	31.7	3.1	35.3	3.6	5.8	1.1	17.4	2.6	3.7	1.5
		F	63	8.4	0.9	13.9	1.7	25.7	2.9	28.0	3.7	5.5	1.2	11.8	2.5	2.3	2.0
	63	M	73	8.0	0.9	13.1	1.6	29.9	2.8	33.7	3.4	5.0	1.0	16.8	2.3	3.8	1.6
		F	62	8.0	0.9	12.7	1.8	24.8	2.5	26.4	3.1	4.7	1.3	12.1	2.3	1.6	2.1
	73	M	65	8.3	0.8	13.7	1.8	31.6	3.8	34.7	3.8	5.4	1.2	17.9	2.9	3.1	1.5
		F	68	8.3	0.8	13.3	1.7	25.8	3.1	27.6	3.2	5.0	1.2	12.4	2.3	1.9	1.0
	83	M	71	8.2	1.0	13.6	2.1	29.5	3.2	33.9	3.4	5.4	1.5	16.0	3.0	3.8	2.3
		F	65	8.2	0.8	13.2	1.7	25.3	2.5	27.8	2.7	5.0	1.3	12.2	2.5	2.5	2.4
	F_2xF_1-54	M	67	8.1	0.9	14.0	1.8	30.5	3.1	34.6	3.4	5.9	1.3	16.5	3.0	4.1	1.6
		F	66	8.1	0.8	13.9	1.6	25.5	2.7	27.5	3.4	5.8	1.0	11.6	2.3	2.0	2.4
	64	M	74	8.0	1.1	13.2	2.0	30.1	3.4	33.2	3.7	5.3	1.2	16.9	2.9	3.1	1.8
		F	69	7.9	1.1	13.0	1.8	25.7	2.9	27.3	3.0	5.2	1.0	12.6	2.4	1.7	1.5
	74	M	71	7.7	1.1	11.8	2.8	27.9	4.4	32.2	4.4	4.2	2.0	16.1	3.1	4.3	3.3
		F	69	7.7	1.0	11.7	2.5	24.4	3.2	27.1	3.6	4.0	1.8	12.7	2.7	2.7	2.9
	84	M	67	8.3	0.9	13.6	1.7	29.3	3.2	33.0	3.8	5.3	1.3	15.7	3.5	3.7	2.1
		F	64	8.1	1.1	13.2	1.8	25.3	2.7	27.8	3.1	5.1	1.2	12.1	2.9	2.5	1.6

Table 53. Derivation of expected mean squares for analysis of sums

Let $Y_{ij} = \bar{L}_{1ij} + \bar{L}_{2ij} + \bar{L}_{3ij}$ $\quad 1 = 1, 2 \ldots s \quad j = 1, 2$

The model is $Y_{ij} = \mu + s_i + r_j + (sr)_{ij} + \varepsilon_{ij}$ with

$$\text{variance } (s_i) = \sigma^2_S$$

$$\text{variance } (r_j) = \sigma^2_R$$

$$\text{variance } (sr)_{ij} = \sigma^2_{RxS}$$

$$\text{variance } (\varepsilon_{ij}) = \sigma^2_1/n_{1ij} + \sigma^2_2/n_{2ij} + \sigma^2_3/n_{3ij}$$

where n_{1ij} is the number of animals produced by the j^{th} mating of the i^{th} sire with line 1 female.

$$SS(\text{sums}) = 2 \sum_{i=1}^{s} (\bar{y}_{i.} - \bar{y}_{..})^2$$

and

$$\sum_{j=1}^{2} Y_{ij} = Y_{i.} = 2\mu + 2s_i + \sum_{j=1}^{2} r_j + \sum_j (sr)_{ij} + \sum_j \varepsilon_{ij}$$

$$\sum\sum_{ij} Y_{ij} = Y_{..} = 2n\mu + 2\sum_i s_i + s\sum_j r_j + \sum\sum_{ij} (sr)_{ij} + \sum\sum_{ij} \varepsilon_{ij}$$

$$\sum_i Y_{ij} = Y_{.j} = s\mu + \sum_i s_i + sr_j + \sum_i (sr)_{ij} + \sum_i \varepsilon_{ij}$$

so

$$SS(SUMS) = 2\sum_i [\mu + s_i + \sum_j r_j/2 + \sum_j (sr)_{ij}/2 + \sum_j \varepsilon_{ij}/2 - \mu - \sum_{i'} s_{i'}/s$$

$$-\sum_j r_j/2 - \sum_{i'j} (sr)_{i'j}/2s - \sum_{i'j} \varepsilon_{i'j}/2s]^2$$

$$= 2\sum_i [(1-1/s)s_i - \sum_{i' \neq i} s_{i'}/s + 1/2(1-1/s) \sum_j (rs)_{ij} -$$

$$1/2s \sum_{i' \neq i} \sum_j (rs)_{i'j} + 1/2(1-1/s) \sum_j \varepsilon_{ij} - 1/2\, s \sum_{i' \neq i} \sum_j \varepsilon_{i'j}]^2$$

$$E(SS(SUMS)) = 2s\{[(s-1/s)^2 + s-1/s^2]\sigma^2_S + 2s(s-1)/4s^2\ \sigma^2_{RxS}\} + 2\sum_i\{[(s-1/2s)^2 (\sigma^2_1/n_{1i1} + \sigma^2_2/n_{2i1} + \sigma^2_3/n_{3i1} + \sigma^2_1/n_{1i2} + \sigma^2_2/n_{2i2} + \sigma^2_3/n_{3i2}) + 1/4s^2 \sum_{i'\neq 1} (\sigma^2_1/n_{1i'1} + \sigma^2_2/n_{2i'1} + \sigma^2_3/n_{3i'1} + \sigma^2_1/n_{1i'2} + \sigma^2_2/n_{2i'2} + \sigma^2_3/n_{3i'2})\}$$

$$= 2(s-1)\sigma^2_S + (s-1)\sigma^2_{RxS} + (s-1)/2s[\sigma^2_1(\sum_i 1/n_{1i1} + \sum_i 1/n_{1i2}) + \sigma^2_2(\sum_i 1/n_{2i1} + \sum_i 1/n_{2i2}) + \sigma^2_3(\sum_i 1/n_{3i1} + \sum_i 1/n_{3i2})$$

Define

$$\bar{n}_{11h} = \frac{s}{\sum_{i=1}^{s} 1/n_{1i1}}$$

$$\bar{n}_{12h} = \frac{s}{\sum_{i=1}^{s} 1/n_{1i2}}$$

$$\bar{n}_{21h} = \frac{s}{\sum_{i=1}^{s} 1/n_{2i1}}$$

$$\bar{n}_{22h} = \frac{s}{\sum_{i=1}^{s} 1/n_{2i2}}$$

$$\bar{n}_{31h} = \frac{s}{\sum_{i=1}^{s} 1/n_{3i1}}$$

$$\bar{n}_{32h} \quad \frac{s}{\sum_{i-1}^{s} 1/n_{3i2}}$$

$$E(MS(SUMS) = 1/2[(1/\bar{n}_{11h} + 1/\bar{n}_{12h})\sigma^2_1 + (1/\bar{n}_{21h} + 1/\bar{n}_{22h})\sigma^2_2 + (1/\bar{n}_{31h} + 1/\bar{n}_{32h})\sigma^2_3] + \sigma^2_{RxS} + 2\sigma^2_S$$

$$SS(\text{replicates}) = s \sum_j (\bar{y}_{.j} - \bar{y}_{..})^2$$

$$= s \sum_j [\mu + \sum_i s_i/s + r_j + \sum_i (sr)_{ij}/s + \sum_i \varepsilon_{ij}/s - \mu - \sum_i s_i/s - \sum_{j'} r_{j'}/2 -$$

$$\sum_{ij'} (rs)_{ij'}/2s - \sum_{ij'} \varepsilon_{ij'}/2s]^2$$

$$= s \sum_j [(1-1/2)r_j - 1/2 \sum_{j' \neq j} r_{j'} + 1/s(1-1/2) \sum_i (rs)_{ij} -$$

$$1/2s \sum_i \sum_{j' \neq j} (rs)_{ij'} + 1/2s \sum_i \varepsilon_{ij} - 1/2s \sum_i \sum_{j' \neq j} \varepsilon_{ij'}]^2$$

$$E(SS(\text{replicates})) = 2s\{(1/4 + 1/4)\sigma^2_R + 2s/4s^2\ \sigma^2_{RxS} + s\Sigma\Sigma_{ij}\ 2s/4s^2$$

$$(\sigma^2_1/n_{1ij} + \sigma^2_2/n_{2ij} + \sigma^2_3/n_{3ij})$$

$$E(MS(\text{replicates})) = 1/2[(1/\bar{n}_{11h} + 1/\bar{n}_{12h})\sigma^2_1 + (1/\bar{n}_{21h} + 1/\bar{n}_{22h})\sigma^2_2 +$$

$$(1/\bar{n}_{31h} + 1/\bar{n}_{32h})\sigma^2_3]\sigma^2_{RxS} + s\sigma^2_R$$

$$SS(\text{sums x replicates}) =$$

$$\sum_i \sum_j (y_{ij} - \bar{y}_{i.} - \bar{y}_{.j} + \bar{y}_{..})^2$$

$$\sum_i \sum_j \{[(rs)_{ij} - (\overline{rs})_{i.} - (\overline{rs})_{.j} + (\overline{rs})_{..}] + [\varepsilon_{ij} - 1/2\sum_{j'} \varepsilon_{ij'} -$$

$$1/s \sum_{i'} \varepsilon_{i'j} + 1/2s \sum_{i'j'} \varepsilon_{i'j'}]\}$$

$$E(SS(\text{sums x replicates})) =$$

$$(s-1)\sigma^2_{RxS} + \sum_i \sum_j \{(s-1/2s)^2\ E(\varepsilon_{ij}{}^2) + (s-1/2s)^2 \sum_{j' \neq j} E(\varepsilon^2_{ij'}) +$$

$$(1/2s)^2 \sum_{i' \neq i} E(\varepsilon^2_{i'j}) + (1/2s)^2 \sum_{i' \neq i} \sum_{j' \neq j} E(\varepsilon^2_{i'j'})\}$$

$$= (s-1)\sigma^2_{Rxs} + (s-1/2s) \sum_{ij} E(\varepsilon^2_{ij})$$

$$E(MS(\text{sums x replicates})) = 1/2\ [(1/\bar{n}_{11h} + 1/\bar{n}_{12h})\sigma^2_1 + (1/\bar{n}_{21h} + 1/\bar{n}_{22h})\sigma^2_2$$

$$+ (1/\bar{n}_{31h} + 1/\bar{n}_{32h})\sigma^2_3] + \sigma^2_{RxS}$$

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GENETIC ARCHITECTURE OF REPRODUCTIVE AND GROWTH TRAITS IN LABORATORY MICE

by

Margaret Godwin Jamison

(ABSTRACT)

This investigation was undertaken to determine the relative importance of additive, dominance, epistatic, maternal and sex-linkage effects for reproduction and growth traits in mice.

Two selected lines of mice, extremes in phenotype for gain from 21 to 42 days of age, were used in a triple test cross design. The high line had completed 24 generations of selection for increased postweaning gain while the low line was three generations behind. Generations 1 and 2 generated F_1 and F_2 lines, generations 3 and 4, replicates, were the backcross of F_2 males to high, low and F_1 females. Reproductive traits measured on each dam were number born per litter, mortality of young from birth to 5 days, number of days from exposure of male to littering and 12-day litter weight. Weight traits measured on each offspring were 12-, 21-, 42- and 56-day body weights. Three gain traits were computed for each individual: 12-21, 21-42 and 42-56 day gain.

Analyses of the data were of two levels. The first-order tests used components of means to determine adequacy of various genetic models and obtain estimates of their parameters. Four genetic models

tested were: (1) containing additive-dominance effects only, (2) adding non-allelic interactions, (3) containing additive and dominance autosomal and sex-linked effects and (4) containing additive and dominance autosomal and maternal effects. Second-order tests using components of variation were used to detect epistasis and estimate additive, dominance and environmental sources of variation.

Results showed that additive effects were important for reproductive traits except littering time and mortality of young from birth to 5 days. Body weights at 12, 42 and 56 days of age in both sexes had significant additive variance components. Percent contributions of additive variation to the phenotypic expression for body weight were 17.4 and 9.5% of 12-day weights, 33.8 and 5.4% of the 42-day weights, and 32.9 and 29.5% of 56-day weights for males and females, respectively. Gain from 21-42 days of age showed significant additive genetic variation, 20.9 and 12.0% in males and females, respectively. Estimates of dominance components for littering traits were all zero. A few weight traits showed dominance to be a significant source of genetic variation but percent contribution to phenotypic variation was quite small. Traits for which epistatic interaction were important genetic influences were littering time, mortality from birth to 5 days and 12-day individual weight for males and females. Weaker epistatic interactions were found for body weights at 21 and 56 days of age. Maternal effects, both additive and dominance, were large genetic contributors to the phenotypic variation for littering and weight traits. For all reproductive traits and 12-day individual body weight, estimates of maternal components were as large as the additive component, but for 21-, 42- and

56-day weights and 12-21, 21-42 and 42-56 gain, additive effects are much larger. Sex-linkage is not an important genetic force in growth traits of mice.