A STUDY OF DIRECTIONAL DOMINANCE IN QUANTITATIVE INHERITANCE WITH SPECIAL REFERENCE TO SIZE IN THE HOUSE MOUSE.

by

St. Clair S. Taylor

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Institute of Animal Genetics
University of Edinburgh.

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I - INTRODUCTION

It has been customary to present a general view of the history of Genetics pertaining to a thesis, and this, one might imagine, is not too extensive owing to the short period over which Genetics has been studied. Nevertheless progress has been rapid, and recently, papers and essays have appeared solely concerning the historical development of Genetics. Such exceptionally good reviews of the history arose from the Anniversary Conference (especially Mather, 1950, and Wright, 1950), that it now seems unnecessary to repeat, or attempt to improve on work of such detail and brilliance. Only previous work strictly relevant to the central problem of this thesis will be discussed.

It becomes apparent from these reviews that the theory of the inheritance of quantitative characters by many genes has been widely accepted, but the success of the theory in quantitative prediction has been only mediocre. The demonstration of the existence of "quantitative" genes did not imply any fixed way in which these genes produced their effects, and indeed, the genes for quantitative characters must be allowed all the complexities displayed by major mutants. In its proper perspective, however, the theory represents a real achievement and advance, certainly opens a very wide speculative field, and provides many openings for further investigation.

Much /
Much of the work in connection with the theory has been directed towards quantitative agreement with observation, and such an approach demanded that the genes responsible for the quantitative characters be assigned a definite way in which they produce their phenotypic effects and certain quantitative values to define these effects. The simplest theoretical treatment (East, 1913, Fisher 1918, and Lerner 1950) gives all genes small and more or less equal effects, which combine additively, so that populations will differ in mean quantitative character to the same extent as they differ in mean gene-frequency. The effects of different breeding systems on gene- and zygotic frequencies were fully studied (esp. Wright, 1921, 1931, 1933, 1951).

Pertinent deductions from this additive hypothesis were that (i) the hybrid population from any cross would have the mean value of any quantitative character exactly intermediate between the two parental means; i.e. there would be no heterosis; and (ii) there would be no depression in the mean value of the character accompanying inbreeding.

The concept of the simple additive nature of the gene-effect was extended by assuming that the genes could have uniformly combining effects, e.g. all effects multiply. (East 1913; Rasmussen 1933; Wright 1920; Zeleny 1920).

This assumption of uniformity in combining implies that the effect of every allele is identical, whatever the genotype in /
in which it be included, so that the mean value of the character would be the same whether the alleles were grouped into genotypes or not, provided the mean value of the character were found by combining individual phenotypic character values in the same manner as the genes combined. This meant that under a scale transformation of data, the gene effects would behave as if additive. Criteria for discovering the proper transformation were given (Mather, 1949; Wright, 1950).

The advantage of a transformation of data to an additive scale lay in retaining simplicity of theory, while allowing for the possibility of heterosis in lines differing widely in mean phenotypic value. There exists, however, no transformation that can remove heterosis in the cross of two lines of equal mean phenotypic value; and equally none that can render identical in mean phenotype a random breeding population and a set of inbred lines taken therefrom and showing depression. Some further assumption had to be made, and it followed naturally from knowledge of the major mutants.

The original additive assumption is equivalent to giving one defining value to each gene — namely the difference in effect between the two alleles — and this is seen to be sufficient only for gross first order effects. A second defining value was introduced by carrying over to the "polygenes", the concept of dominance apparent in major genes (Fisher, 1918). Whereas previously the mean was represented by /
by summing the effects of two types of alleles, the mean now is represented by summing the effects of three types of allelic pairs (homozygous dominant, heterozygote, and homozygous recessive). The phenomena of heterosis and inbreeding depression can now be simply explained as due to excess or deficiency of heterozygotes, the effective values of which may lie at any point between the values of the corresponding homozygotes (Davenport, 1908; Jones, 1917). The two phenomena are thus complementary. Any strain that showed heterosis would be expected to show inbreeding depression, and in such a case the phenotypic effect of heterozygotes would be greater on the average than the mean phenotypic effect of the two homozygotes.

Other phenomena, such as the effect of relaxing selection, yield to this explanation, if the degree of dominance is made excessive (overdominance) and if populations are defined by a number of zygotic-pairs, necessitating the introduction of linkage values. Otherwise, a third defining quantity can be given to the genes. However, this thesis is concerned with the quantitative agreement on a hypothesis of dominance of observed inbreeding depression and heterosis only.

Experiments were carried out with a variety of selected and unselected lines in order to arrive at fairly accurate estimates of heterosis and inbreeding depression. A theoretical treatment of the hypothesis of dominance has been developed in a form suitable for assessing its adequacy over /
over the array of observed values of heterosis and inbreeding depression. In the event of the hypothesis proving adequate, the method will also allow of prediction of upper and lower limits attainable within the stock by the phenotypic mean of a character, and of inbreeding depression in lines and heterosis in crosses not observed during the present experiment.

The expectation of adequacy would seem slight on account of the possibility (i) of "scale" defects, (ii) of maternal effects, (iii) of differential changes, due to selection, in the frequency of dominant and recessive alleles, and (iv) even of alteration of the degree of dominance of the genes by selection.

The main purpose, however, of the hypothesis of dominance in its present form is to provide a rigid framework on which to assess the nature and extent of deviations from expectation; so that the deviations revealed may be discussed in the light of each, in turn, of the possible causes advanced above.

At the present stage this much can be said:

(i) A scale will first be chosen on theoretical considerations using the criteria as given by Wright (1950). If discrepancies are encountered on this scale, then these discrepancies themselves may suggest other scale transformations whereby they may be eliminated. The scale finally adopted will be that for which deviations are least.

(ii) /
(ii) The complications of maternal effect are not yet sufficiently well understood to be independently disentangled. They can, however, be eliminated experimentally to a certain extent, as by reciprocal crosses.

(iii) Every locus will be associated with a certain degree of dominance, $d$, representing on the proper scale, the relative excess of the expression of the heterozygote over the mean expression of the two homozygotes, the excess being measured in the same direction as the character. Thus $d = +1$ signifies a locus completely dominant for greater expression of the character; $d = -1$ signifies a locus completely recessive for greater expression; $|d| > 1$ signifies overdominance; $d = 0$ gives the case of additive alleles.

At the present state of our knowledge, $d$ has the possibility of values ranging between $+\infty$ and $-\infty$, with a variety of values among the different loci. The question is: Do such positive and negative values of $d$ exist to any marked extent, and, if so, how are they affected by selection, and what will be the effect on heterosis and inbreeding depression in selected lines? Curves, giving the expected changes due to selection in the frequency of dominant and recessive alleles, (inter al. Lush, 1945) indicate that for frequencies less than a half, the frequency of alleles dominant or overdominant, in the direction of selection, will be increased to a relatively greater extent than the frequency /
frequency of recessives; whereas at frequencies greater than a half, the reverse is true. Such differential changes of frequency would set up correlations between the degree of dominance and certain functions of the gene frequency. The expected effects of such correlations on heterosis and inbreeding depression are discussed in detail after the theory has been developed.

(iv) Fisher (1930 a) has advanced reasons, supported by Mather (1933 a), for expecting the genes in unselected natural populations to show a distribution of values of $d$ symmetrical about $d = 0$. Dominance, they maintain, is related to selective advantage, and since, for "polygenes" in a natural population, one allele does not have a regular but only an occasional selective advantage over the other (variation being round an optimum) there will be equal numbers of dominants in either direction. If selection is brought to bear on such a population, the equality of distribution will be lost. There will be a resultant skewing of the phenotypic frequency distribution, the tail pointing away from the direction of selection and containing the recessive less frequent phenotypes. The degree of dominance of an allele will itself increase as its frequency is increased by selection. Dominance, they say, is "evolved" in the direction of selection. Such directional dominance, Mather continues, "should most often cause hybrids to depart from the strain means in the direction of previous selection."
This implies that a cross between two lines both selected in an upward direction from an initial unselected population which showed no directional dominance, would give positive heterosis, whereas a cross between two lines both selected in the reverse direction would give negative heterosis.

The cross between a large selected line and small selected line would be relatively intermediate, but tending to the direction of the line of greatest potency (in the sense used by Wigan, 1944, and Mather, 1946 a). Inbreeding (although Mather does not actually draw this conclusion) would decrease the mean value of the character in the large selected line, and increase the mean of the small selected line. Here it has been supposed that in the initial population from which selection began the dominance of the genes were symmetrically distributed, so that inbreeding would have no effect on the mean value of the character. If, however, the initial population showed directional dominance, the above expectations would be superimposed on the main trend of dominance, tending to increase the heterosis and inbreeding depression for large selected lines, and to decrease the heterosis and inbreeding depression for small selected lines, beyond what would otherwise be expected.

The present experiments then are intended

1) to furnish estimates of heterosis and inbreeding depression with which the hypothesis of dominance can be tested for adequacy of quantitative agreement;

2) /
2) to discover, in the event of inadequacy, whether the deviations are such as would be expected either on differential selection for dominants, or on the Theory of Evolution of Dominance;

3) generally to bring to light any marked difference in behaviour of selected as opposed to unselected lines under inbreeding or crossing, so that present domestic stocks, in that they are already selected, should be treated as such.
II. EXPERIMENT

A. EXPERIMENTAL MATERIAL

It was thought that the questions posed in the Introduction might be better answered if the experimental observations were confined largely to one stock. Values of the parameters of genetic relationship (e.g., relative in-breeding coefficient) required in the theoretical treatment, can be more readily and accurately traced within a stock. The theoretical treatment also requires that single fixed values be given to certain genetical constants, and such values are likely to hold to a better degree of approximation over lines within a stock than over a variety of lines from different stocks.

A stock (Falconer, 1953) herein designated the N-stock, was available and was especially suitable for two reasons: (1) it contained three lines differing widely in mean body size, and (2) the genetic relationships within each line had been followed by means of tables of genetic covariance. The covariance technique, due to Emik and Terrill (1949), is discussed with particular reference to the N-stock by Falconer (1953).

The stock was originated by crossing four well-known inbred lines of mice (CBA x R III; and A x C) giving two $F_1$'s.
F₁'s and an "F₂" which constituted the foundation population. From this "F₂", the six largest mice of each sex, in respect of weight at six weeks after birth, were selected and mated, and likewise the six smallest mice of each sex, thereby originating a high and a low selection line. The selection lines were continued by within-litter selection.

**NC-line**

After the selection had continued for about 15 generations in both lines, the foundation population was reconstituted and became the origin of an unselected line, the NC-line, running concurrently with the large and small selected lines, and acting as a control line for the N-stock.

**LC-line**

The mean six week weight of the seventeenth generation of mice, in the line selected for large size, stood at 4.4 gm. above the mean six week weight of 21.6 gm. for the foundation population. At this point the LC-line was derived by relaxing selection for large size.

**SC-line**

The origin of the SC-line is slightly more complex. From the fourteenth generation of the line selected for small size, two lines were derived, one being a continuation of selection for small size, and the other selected backwards for large size. Two generations later, neither of these lines could /
could independently provide the requisite number of mice for the present purposes without introducing strong inbreeding. A cross was made in which both lines were equally represented, and the \( F_1 \) formed the first generation of the SC-line; and thereby both increased inbreeding and delay were avoided.

**MSG-line**

One further line, also selected for small size, was required. A line was available which had been selected for small size (weight at 60 days) by MacArthur (1949) as far as the 26th generation. At this stage the line furnished mice which were used by Falconer to initiate a line selected for low weight at six weeks; and after thirteen generations, selection on this line was relaxed, providing the fourth line, designated MSG, used in the present experiment.

These four lines (LC, NC, SC, and MSG) are usually referred to as the "control" lines of the experiment, and constitute the parental lines of the crossbred populations formed. Their function as control lines is fully discussed in the section on Control of Non-Genetic Variation.

**B. EXPERIMENTAL PROGRAMME**

The experimental programme involved:

1) maintaining the control lines described above;
2) the formation of a set of inbred lines from each control line;
3) /
3) the simultaneous crossing of the three N-stock lines in all possible ways;

4) the cross of the small line (SC) of the N-stock with the small line (MSC) of MacArthur's stock.

A diagrammatic representation of the experiment is shown. (Fig. 0).

C. BREEDING SYSTEM.

Choice of Parents

Throughout every part of the present experiment the method of selecting parents was identical. Each line was continued or represented by one female and one male chosen strictly at random from the offspring (generally the first litter) of each of the matings in the line. The randomisation was achieved by throwing lettered blocks.

Choice of Matings

Control Lines. Matings were chosen so as to achieve the maximum possible outbreeding within a line and an even distribution over the matings of the slight but inevitable increase in the degree of inbreeding. This was done by choosing those parental pairs with minimum genetic covariance from a table of genetic covariances constructed for all possible pairs.

Inbred /
Inbred Lines. Each inbred line consisted of a set of about twelve continued sib-matings. In conjunction with maximum outbreeding in the control lines, the difference in the rates of inbreeding was the greatest possible for the present size of control populations.

CROSSES. Parents of the $F_1$ were paired at random and reciprocally crossed. Reciprocal crossing made possible four types of $F_2$-matings, and each type was equally represented. (Using the first letters to indicate the maternal line so that $LS$ represents the cross between females from the large parental line and males from the small parental line, and $SL$ represents the reciprocal cross, the four types of mating equally represented in the $F_2$ are, in this case, $LS, LS, LS, LS, SL, SL, SL, SL$).

D. EXPERIMENTAL DESIGN

The greater part of the experimental design and procedure was determined by the need for control of non-genetic variation which is discussed in the next section.

E. CHARACTERS OBSERVED

All characters recorded are quantitative. In each mating the following observations were made:

(a) /
(a) the period between pairing and birth of the first litter;
(b) the number of offspring of each sex born;
(c) the weight of the litter twelve days after birth;
(d) the individual weight of each mouse at weaning (three weeks after birth);
(e) the individual weight at four weeks after birth;
(f) the individual weight at six weeks after birth.

(a) and (b) provide measures of the fertility of the mating. (c) is a measure of the mothering ability (Falconer, 1947), and hence some indication of the maternal effect on six week weight. (d), (e) and (f) are taken as measures of body size of the mice. Weight at four weeks lies about midway between weight at weaning and weight at six weeks. Individual weight at six weeks after birth is the main character studied. All but one of the lines used in the present experiment had undergone selection for weight at six weeks, and consequently the lines differed more in mean six week weight than in any other character. Differences that do occur in the mean level of any of the other characters observed can be taken as correlated responses to selection for six week weight.
III. CONTROL OF NON-GENETIC VARIATION

Prior to any breeding experiment a detailed study of the sources of non-genetic variation in the character to be observed is necessary, it being of first importance to ensure that the observed changes in the mean value of the character are a consequence of the breeding system. Many non-genetic sources of variation in six week weight are known to be in operation, and are discussed below, according to the way in which they were controlled.

A. VARIATION IN THE CHARACTER REMOVED AS FAR AS POSSIBLE BY CONTROLLING THE SOURCE OF VARIATION.

(a) The temperature, diet, and cage conditions were kept as constant as possible.

(b) The mean six week weight of a litter varies considerably with the number of young raised by the mother, being greater if the number raised is small (Falconer, 1947). The number of mice raised by a mother was therefore standardised as far as possible till weaning age. If the number born in a litter exceeded eight, the litter size was reduced to eight by discarding at random, subject to making the sex ratio as near a half as possible. If less than eight were born in a litter, the litter size was increased to eight with fosterlings from extra matings kept for this purpose. Fosterlings were discarded at weaning. In the small lines, a litter size of eight was difficult to maintain, and where no extraneous
comparison had to be made, the litter size was standardised at six. Beyond this, no control could be put on the variation in weight of litters due to maternal effect.

(c) The weaning age was invariably three weeks after birth.

(d) At weaning the sexes were separated and the mice were placed in storage cases. Variation in individual six week weight, due to the number, size and age of cage mates, was minimised by keeping in any one cage the standard number of six mice, all of the same sex, of the same age, and from the same line. Occasional age differences of up to two or three days occurred.

(e) Matings were examined daily for the birth of litters, so that for litters recorded as born on the same day, an age difference of up to twenty-four hours is possible. The error introduced when comparing the mean six week weight of different lines will be slight since the distribution of times of birth will be more or less alike in all lines.

(f) A graph of the weights of a few mice aged about six weeks taken at hourly intervals over the normal laboratory working hours, shows a decline in weight from morning till early afternoon (Fig. 1), the mean of all morning weights exceeding the mean of all afternoon weights by 0.65 gm. An average variance for individual mice of 0.58 gm. for weighings repeated between 9.30 a.m. and 12.30 p.m. (32 weighings), and 0.08 gm. for weighings repeated between 2.30 p.m. and 5.30 p.m. (32 weighings) indicated that if the decline were real a greater /
greater accuracy of mean six week weight could be achieved by confining weighings to between the hours of 2.30 p.m. and 5.30 p.m. Further, if the decline were a definite feature of growth a serious error would be introduced in the comparison of the mean six week weight of two populations, one of which had been weighed early in the day, and the other later. The decline showed by repeated weighing, however, might be equally well ascribed to handling of the mice as to a diurnal rhythm.

An experiment was therefore carried out to determine whether or not the decline in weight was a regular feature of growth. In three lines (LC, NC, SC) the offspring in one generation were divided at random into two equal groups, one of which was weighed in the morning, and the other in the afternoon; those mice weighed in the morning were weighed again in the afternoon. The mean six week weight of the group weighed in the morning was 19.86 gm. (38 mice); when reweighed in the afternoon it was 19.41 gm.; and the mean weight of the group weighed in the afternoon only was 19.35 gm. (35 mice). The differences, however, were not significant, but a decline of 0.5 gm., that could not be ascribed to handling was suggested.

The procedure therefore adopted throughout the whole of the present experiment was to weigh all mice between 2.30 p.m. and 5.30 p.m. so that all comparisons within the experiment are valid as far as time of weighing is concerned. Should it ever be necessary to make comparisons with previous results,
results, where weighing was generally done in the morning, 
a correction of \( \frac{1}{2} \) gm. is indicated.

(g) Litter order affects individual six week weight, mice 
from a second or third litter tending to be slightly heavier 
than those from a first litter. For 126 matings from the 
éarlier generations raised, the mean weight of 2nd litters 
was 0.33 gm. greater than that of 1st litters at six weeks, 
and 0.11 gm. greater at 12 days, representing an increase of 
about 1.7% at both ages. The number of litters raised per 
mating varied with the needs of the experiment, but when 
two populations had to be compared for mean six week weight 
the number and order of the litters involved in the 
comparison were strictly alike.

B. VARIATION AVOIDED BY STATISTICAL PROCEDURE.

(h) The mean of litter means has been used to represent the 
mean six week weight of a population. Every mating in any 
generation of a line has been equally represented genetically 
in the sample of parents chosen for matings in the next 
generation, so that, in the appropriate phenotypic mean, each 
mating should also be equally represented. In the case of 
a set of sib-matings especially, where smaller litters tended 
to have a lower mean weight, a bias towards under-estimation 
of inbreeding depression was avoided by using the mean of 
litter means. In populations where the fertility of mothers 
and /
and the survivability of offspring were uniformly high, and where standardisation of litter size discussed in (b) resulted in an equal number of mice in every litter, the mean of litter means and the mean of all individual mice were, of course, identical.

(i) A combined mean of both sexes in which each individual was equally represented would give the most efficient estimate of the mean weight of a litter. If the mean of sex means were taken each individual would be equally represented only if the sex ratio were a half. Although litter number was standardised so as to bring the sex ratio closer to a half, there nevertheless remained considerable variation in sex ratio.

However, it is known that the ratio of the weight of females to the weight of males is remarkably constant from population to population. (See Tables 2 and 11).

Butler (1952), observing the mean weight of mice sixty days after birth found that the ratio of the weight of females to the weight of males had an approximately constant value of 0.85 for populations differing widely in mean weight.

Falconer and King (1952) give a value of 0.84 for the ratio of mean six week weight of females to mean six week weight of males over a variety of populations. The frequency distribution of the ratio (for six week weight) for 460 of the litters /
litters observed in the present experiment is shown. (Fig. 2). The mean value for this distribution is 0.835. For the six generations of the LC-line the mean value of the ratio over 72 litters is 0.835; for the six generations of the NC-line 0.837 (82 litters); and for the five generations of the SC-line 0.836 (55 litters). There seems little doubt that the ratio of mean weight of females to mean weight of males in a litter is normally distributed and independent of the mean weight of the litter.

Falconer and King (1953) draw the conclusion that a geometric mean for the sexes would be more appropriate than an arithmetic mean. They calculate the mean of a litter, however, by multiplying the weights of females by \( \frac{1}{2}(1 + r) \) and males by \( \frac{1}{2}(1 + \frac{1}{r}) \), where \( r \) is the ratio of the mean weight of all males to that of all females, and averaging the resultant "neutral" weights. It seems that, if the ratio were perfectly constant, this procedure would be the exact equivalent of taking the arithmetic mean of sex means. The empirical relation is \( \frac{\bar{W}_\phi}{\bar{W}_\delta} = constant = k \), say (to avoid confusion with the \( r \) which appears later in its usual symbolisation of a correlation) where \( \bar{W}_\delta \), \( \bar{W}_\phi \) represent the mean weight of males and females respectively, so that on the average \( \frac{\bar{W}_\phi}{\sqrt{k}} = \bar{W}_\delta \sqrt{k} \). An efficient estimate of a litter mean /
mean with both sexes combined and each individual equally represented is therefore achieved by taking the mean of 

\[ \frac{W}{\sqrt{k}} \]

for females and \( w \sqrt{k} \) for males. Since there are indications, (see Fig. 6, and Tables 2 and 11) that the ratio may be changed by inbreeding or may differ in reciprocal crosses the value of the ratio used for finding litter means in any population is that obtained by taking the mean value of the ratio for all litters in that population.

(j) In the case of sources of variation such as injuries and diseases, where the effect on an individual is marked but irregular, the observation on the affected individual has been rejected; e.g. in calculating the mean six week weight of the second generation in the LC-line, the weight of a hydrocephalic male which deviated from the male mean by 5 standard deviations was omitted.

C. VARIATION CONTROLLED BY EXPERIMENTAL DESIGN

(k) Genetic Sampling Variation. Part of the fluctuation in the mean six week weight of a line from generation to generation will be due to genetic sampling error. Since genetic changes in the various lines caused by selection are under investigation, it is necessary that each line be represented by genetic samples of a size such that the inbreeding /
inbreeding depression and heterosis observed can both be attributed to the line or lines and not merely each to its particular sample. Since control lines are also used, the need for which is discussed in (1) below, the ideal method would require a large sample of parents from each line, and the use of the identical sample to form control, inbred, and cross-bred populations. Although the present experiment was carried out as compactly as possible, this procedure was impossible. The maximum to the number of litters raised was set by the number of parents and cages available. To achieve as representative samples as possible, the number of different matings was increased at the expense of the number of litters per mating, and the crossing part of the programme could be started only when the inbreeding part was largely complete. Thus the six matings which comprised the seventeenth generation of the large selected line of the N-stock, each provided eight mice (the equivalent of a full litter), and one sample of two females and two males from each mating originated the large control line (LC), and another equivalent sample was used to form a set of twelve sib-matings (LI). In the first generation, first and second litters were raised in control and inbred lines, but in the second and third generations first litters only were raised. The procedure was largely similar in the unselected control line (giving the NO- and NI-lines), in the small selected line of /
of the N-stock (giving the SC- and SI-lines), and in the small
selected line of MacArthur's stock (giving the ISC- and MIS-
lines). The SI-line, however, originated from the first
generation of the SC-line, and not from the small selected
line itself, and the number of litters raised from each
control and sib-mating was increased to three in the second
and third generations, as fertility was very poor. The
genetic sample from the parental line of a cross had to be
chosen with the further requirement that the sex-linked
effects of both parental lines had to be equally represented
in the F1. In the cross of the small selected lines
(the SC- and ISC-lines) each parental line was represented
in the cross by a sample of one male and one female from each
of ten matings, and was represented in the next generation
of the control line by an equivalent sample, giving ten
matings in each control line and twenty reciprocal matings
in the crossbred population.

In the N-stock crosses, however, each of the three
control (parental) lines was represented by a sample of eighteen
females and eighteen males, three mistaken from each control
mating. The identical sample served to continue a control
line comprised of eighteen matings and to represent it in the
thirty-six different crossbred matings with each of the other
two lines. Genetic sampling variation was thus completely
absent /
absent between parental control lines and the corresponding $F_1$. In the $F_2$'s genetic sampling variation could not be avoided. The four possible types of $F_2$ mating, however, were equally represented.

(1) "Seasonal" Variation. When all the sources of variation discussed above had been controlled and bias avoided by statistical procedure, the mean six week weight of the control lines still showed random fluctuations from generation to generation. (Fig. 3).

The variance of generation means is $0.334$ (6 d.f.), $0.272$ (6 d.f.) and $0.152$ (5 d.f.) in the large, the unselected, and the small control lines respectively, giving an average value of $0.253$. Falconer (1953) gives an average value of $0.254$ for the variance of the two selected lines of the N-stock about their linear regression lines; and has shown that, under standardised conditions, largely similar to those discussed above, about two-thirds of this variance of generation means is due to sources of variation that affect all contemporaneous generations equally; that the remaining third of the variance is accounted for by the sampling error of generation means; and hence that variance of the deviation of a generation mean from the mean of another contemporaneous generation is entirely due to sampling variation in the generation means. The contemporaneous generations to which the /
the above results refer, belonged to two lines selected in opposite directions and showing an increasing divergence of generation mean. It seemed probable that if the populations entering into a comparison are both formed from two equivalent samples (or the identical sample) of parents from the same previous population, then the variance of the difference in generation means might be further reduced. In view of this, inbreeding depression and heterosis are measured as deviations of the inbred or crossbred populations from their own particular control or control populations, raised contemporaneously and from an equivalent (or identical) sample of parents. The accuracy of the estimates of inbreeding depression and heterosis will be determined by the size of the sampling variance of the generation means.

The sampling variances used were calculated as a weighted average of the variance of all female weights divided by \( k \) and the variance of all male weights multiplied by \( k \), where \( k \) is the average value of the ratio of the mean weight of females to that of males in a litter taken over all litters in the population. Since \( k \) is normally distributed (see (i) above), the covariance term in the combined sex variance will be zero. Standard errors, which for the reasons given above can be attached only to differences in mean weight between an experimental population and its control population, were calculated from these sampling variances /
variances by means of the usual formula for the standard error of a difference between two means.

(m) Maternal Effect. The mean weight of litters at 12 days after birth is determined largely by the mother, the component of variation due to mothers being more than 70% (Bateman, in press; Falconer, 1947; see also row and column means for the F1's in Table 15). The correlation between the mean weight of litters in a population at 12 days and that at six weeks is high. Estimates of this correlation calculated for a few NC populations were about 0.7. Hence 12 day weight can be used as some indication of the maternal effect on six week weight. The maternal effect on a litter can be controlled to a limited extent only (as discussed in (b)), so that there will always be a large maternal component (about a half) in the variance between litter means at six weeks in any generation.

Differences due to maternal effect, however, are largely eliminated in a comparison of two contemporaneous populations both of which were formed by equivalent (or identical) samples of mothers.

In the two small lines (the S- and N3-lines) the maternal quality did not differ greatly and it was deemed sufficient, when crossing the lines, simply to represent both control populations and the reciprocal crossbred populations by the same number of mothers. When forming crossbred populations between N-stock lines, which differed considerably /
considerably in maternal qualities, not only the same number of mothers but the identical mothers were used to form control and crossbred populations. Thus, of the eighteen females representing the LC-parent line, one set of six produced first litters by fathers from their own (LC) line, second litters by fathers from the NC parental line, and third litters by fathers from the SC parental line. The second set of six mothers produced first litters by fathers from the NC-line, second litters by fathers from the SC-line, and third litters by fathers of their own (LC) line. The third set of six mothers from the LC-line, and likewise the three sets of six mothers from each of the other two control lines, followed the sequence. Thus each control population was represented by eighteen litters, six of which were first litters, six were second litters, and six were third litters. Each crossbred population was represented by thirty-six litters, twelve of which were first litters, twelve second litters, and twelve third. In each set of twelve, six litters had mothers from one of the control lines, and six had mothers from the other control line.

This experimental design had the merit of controlling variation due to maternal effect, litter order, "seasonal" fluctuations, and genetic sampling of parents. Nevertheless, although experimental design can remove the maternal bias in certain comparisons of mean six week weights, three difficulties in connection with maternal effect remain:
(1) The accuracy of determination of any mean six week weight, or a difference between two generation means, will be impaired so long as there is a strong maternal component of variance between litter means.

(2) The large and small lines differed considerably in mothering ability (see Table 6) although direct selection for maternal effect had been deliberately avoided by within-litter selection for six week weight. (Falconer, 1953). Marked differences in reciprocal crosses will therefore be present in computing the mean for the crossbred population and it is not strictly legitimate to take the mid-point between the reciprocal means on the scale used. It is nevertheless the procedure adopted, as the quantitative mode of operation of maternal effect is not known.

(3) The effect of inbreeding on mothers which will lag one generation behind the effect of inbreeding on the offspring, introduces a complication, as does the hybrid maternal vigour, which will not appear till the F2 of a cross. The maternal component in the inbreeding depression and in the heterosis for six week weight cannot be accurately separated, as knowledge of its exact nature is incomplete.

The results are carefully examined for these maternal effects.
IV. OBSERVED RESULTS

This section has been confined to a direct presentation of the results for the various characters observed. A theoretically grounded synthesis has been delayed till after the section on Theory.

The results are presented in four parts. The first is a description of the four lines of house mouse which act as control lines throughout the experiment, which form the parental lines of the crosses, and from which the inbred lines are derived. The second part gives the results of inbreeding the lines. The third deals with the crossing of the three lines belonging to the N-stock. The fourth gives the results of the cross of the two lines previously selected for small size.

A. CONTROL LINES

A graph of the mean six week weight of the control lines over successive generations shows the extent to which the lines differ in this character. Random fluctuations from generation to generation are apparent, and the accompanying inset graphs for corresponding weights at 12 days indicate that these fluctuations largely originate at the stage where the maternal effect predominates (Fig. 3). A character subject to much less non-genetic variation from generation to generation than six week weight might thus be provided by gain in weight from 12 to 42 days. The effect of relaxing /
relaxing selection was observed in the Large line and in MacArthur's Small line. The divergence from the unselected level shown by the mean six week weight of the first three relaxed generations of the Large line is only about $\frac{2}{3}$ of the divergence shown by the mean six week weight (corrected for time of weighing) of the last three selected generations. This significant regression of the Large line to the unselected level occurred almost entirely in the first relaxed generation. In MacArthur's Small line, on the other hand, relaxation of selection was not accompanied by any definite change in the mean six week weight. The sex ratio at birth appeared to be upset by relaxation of selection in the Large line, for in each of the first three relaxed generations there was a significant relative increase in the number of females born, with $P(\chi^2) < 0.001$ for the three generations together. Just over 60% of the total number of mice born were females.

The coefficients of variation within and between litters for each generation indicate that the small control lines are somewhat more variable relative to their mean weight than are the Unselected and Large lines (Table 3).

Growth curves for the four control lines are shown. Clear differences in weight between the Large and Unselected lines and between the two small lines begin to appear only after /
after four weeks. Weight differences between the Large or the Unselected line and either of the two small lines, however, appear very much earlier, and there is a clear distinction between them before three weeks (Fig. 4).

The mean of the reciprocals of the number of days lapsing between the setting up of a mating and the birth of a first litter, multiplied by 22 so that an average value of unity is obtained for the Unselected line, provides a measure of the breeding speed in the various populations. Reciprocals were taken so that matings which fail to reproduce could be given the value zero. This index of breeding speed suggests that this component of natural fitness has been reduced in all three selected lines, in that its mean value over several generations in the Large line was 0.97, in the Small line was 0.87, and in MacArthur's Small line was 0.89, compared with the mean value of 1.02 for the Unselected line.

More detailed differences in the control lines, including differences for the subsidiary characters, can be found in the Tables, entries for inbred and crossbred populations being invariably accompanied by entries for the corresponding control populations.

B. INBREEDING

There was a significant depression in mean six week weight in all lines for the three generations of sib-mating combined /
combined. The Unselected line shows the greatest inbreeding depression in grams weight, followed by MacArthur's Small line. The Large line shows the least depression. The percentage decline in mean six week weight, however, is greatest in MacArthur's Small line (Table 1). The mean six week weight for inbred and control lines on the arithmetic and on the logarithmic scale are shown plotted against successive generations (Figures 5(a), (b)).

The difference in the effect of the inbreeding on males and females is interesting. The changes in the ratio of mean six week weight of females in a litter to that of males averaged over the litters in the generation are shown for inbred and control lines (Table 2, Fig. 6). The most marked and significant change occurs in the Small line where the ratio increases on inbreeding, implying that the sex difference in weight gradually diminishes with successive generations of sib-mating. It follows that males in the Small line suffer a much greater relative depression than females. The same phenomenon is present to a lesser extent in the Large line, and the mean six week weight of the females in the third inbred generation was in fact the same as that for the control line. The changes in the ratio in MacArthur's Small line were inconclusive, and for the Unselected...
Unselected line the changes were slight and random. It was considered unnecessary to give separately the weights of females and those of males, but, if desired, these can be simply found from the combined mean six week weight and the corresponding ratio.

The coefficient of variation within litters does not show the expected decrease on inbreeding, there being no significant difference between control and inbred even when combined over all lines. Likewise there is no overall significant change in the component of variation between litter means. (Table 3). The somewhat greater values of the coefficient of variation in the small lines agrees with their somewhat greater logarithmic depression.

A definite feature of the inbreeding was the absence of depression in the first inbred generations, where the offspring are inbred but their parents are not. The change in the value of the inbreeding coefficient with respect to the populations from which the present inbreeding began was from 0 to 0.25 for the first inbred generation, and therefore twice as much depression should have occurred in the first inbred generation as in either the second or third which both correspond to an increase of 0.125 in the inbreeding coefficient. In the present case, this feature might be attributed to the maternal effect, although the same feature has been remarked on by Rasmussen (1913) in connection with studies on barley, where the maternal effect is absent. Changes in 12 day weight can be taken as one measure /
measure of the changes in maternal qualities as discussed in Section III (m). Table 6 shows that, for the lines combined, there is no depression in 12 day weight in the 1st inbred generation, only slight depression in the 2nd inbred generation, while the 3rd inbred generation shows the greatest increase in depression, so that even in this measure of maternal qualities there seems to be an overall delay of one generation before the greatest depression occurs.

Fertility, also largely maternally determined (as seen from the row and column totals for the F1 in Table 15) shows the greatest increase in depression in the 2nd inbred generations of the Large and Unselected lines. In the small lines, however, a very marked depression shows in the 1st inbred generation, and thereafter is almost absent, owing to strong natural selection (Table 7, Fig. 7).

One of the most striking effects of the inbreeding was a gradual disintegration of the small inbred lines. Sterility became rife, and survivability poor. It was noticeable in the Small line that those sib-matings with offspring showing the lower mean weights produced no further. (Table 9(1)). The average number of survivors per mating set up gives a measure of the difficulty in maintaining a line, and both small lines show a rapid decline in this measure especially in the 2nd and 3rd inbred generations (Table 8, Fig. 8). Row and column totals in Tables in Table 17 indicate /
indicate that this measure is to a limited extent maternally
determined. A comparable result has been published by
Nather and Harrison (1949), who, working with bristle number
in *Drosophila*, found that continued selection threatened to
extinguish the line selected for low bristle number so that
the line had to be continued by mass-mating. Attempts to
decrease the phenotypic mean at several later stages in this
low relaxed selection line all resulted in extinction within
a few generations through sterility and inviability.

The results, so far, do not point directly to
maternal effect as the explanation of the noticeable absence
of inbreeding depression in mean six week weight in the 1st
inbred generation. A clearer picture of the situation
is given by a comparative study of the mean depression in
weight at 12, 21, 28, and 42 days after birth. Figure 9
shows the percentage depression in mean weight for successive
weighings throughout the three generations averaged over
the four lines. It is immediately apparent that, although
the increase in the depression in 12 day weight from
generation 1 to generation 2 is slight, there is a strong
increase from generation 1 to generation 2 in the depression
in weight immediately after 12 days, continuing to a peak
one week after weaning, and thereafter, up till six weeks,
there is a definite recovery of some of the depression.

The /
The absence of depression in the 1st inbred generation and the identical pattern of depression appearing in the 2nd and 3rd generations seem to point to the maternal effect (of inbred mothers) on weaning as an important factor in causing inbreeding depression. The effect of weaning is also reflected in the variance which is often greater at one week after weaning than at three weeks after weaning, the variance at weaning being much smaller than at either subsequent stage (e.g. Table 20).

A study of the average depression at the different stages of growth in the individual lines throws further light on the situation (Fig. 10). The Large line shows a slight gradual increase in depression from 12 days to six weeks; in the Unselected line the greatest depression occurs between 3 and 4 weeks; while in both small lines the greatest depression occurs between 12 days and 3 weeks, reaches a peak at 4 weeks and thereafter shows a decline from 4 weeks to 6 weeks. This might well be taken as evidence that the inbreeding depression increases from large to small lines in step with the deterioration in mothering qualities. The argument for maternal effect causing the relative differences in inbreeding depression at the various stages in the different lines is, however, not conclusive. The observed /
observed pattern of inbreeding depression may well be attributed to an inherent feature of the offspring’s growth, and may well follow naturally from changes in the relative growth rate on inbreeding.

C. CROSSING OF THE THREE N-STOCK LINES

The results of crosses between the Large and Unselected line, between the Large and the Small line, and between the Unselected and the Small line would seem very simple and conclusive in respect of mean six week weight. In every cross, in both the F₁ and the F₂, the mean of the crossbred populations on the arithmetic scale did not deviate from the mid-parent mean (Table 10, Fig. 11). The closeness of the agreement was in fact the most exceptional feature, in that the error variances imply that the proportion of times such close or closer agreement would be obtained is small. In view of this exceptional absence of heterosis on crossing, it is strange that the parental lines all showed inbreeding depression. One concludes that metrical bias is probably present, causing a false impression of simplicity. The question of scale transformation is discussed later.

The indications from several publications concerning the cross of a large line of animals with a small line are that the above result is against the normal trend which expects /
expects the crossbred population to fall somewhat nearer the mean of the smaller parental line (Castle, 1931; Johansson and Venge, 1953; Pease, 1928). On the other hand, the results of Reeve and Robertson (in press) working with Drosophila, give the mean of the crossbred population between an unselected inbred line and an inbred line taken from the line selected for small size as regressing fully to the level of the unselected inbred line—differing completely from the present result. Mather and Harrison (1949), however, also working with Drosophila, obtained results in exact agreement with those from the present crosses.

The ratio of sex weights shows one or two interesting features, namely a definite increase in the $F_1$ and $F_2$ of the cross between the Unselected and the Small line, and a difference in the reciprocal crosses between the Large and Small lines, which in a lesser degree is continued into the $F_2$. The ratios are given in Table 11. No simple explanation in terms of sex linkage is available and a long discussion of these ratios would be irrelevant to the present purpose.

The total variance of six week weight does not show any significant change in the $F_1$'s of the $N$-stock crosses, and the variances of reciprocal crosses are more or less equal. The mean variance for the crossbred populations in the $F_1$ is $3.283$ and for the parental control populations is $3.436$.
In the \( F_2 \) of the cross of the Large and the Small line, there is a significant increase in the variance even after the component between mothers for reciprocal crosses has been removed. The other two \( N \)-stock crosses, however, do not show any change in variance in the \( F_2 \), their mean variance being 3.188 and the corresponding parental control variance being 3.350 (Table 12). Corresponding to inbreeding depression in the maternal characters of fertility and 12 day weight which was expected but not found in the second inbred generation, heterosis in these maternal characters is expected in the \( F_2 \) of the crosses but not in the \( F_1 \). The expectation is not realised for 12 day weight, the average percentage heterosis for the three crosses combined being 2.3% in the \( F_1 \) and 0.38% in the \( F_2 \) (Table 15). Significant heterosis in fertility occurs only in the \( F_2 \) of the cross between the Unselected and the Small line. There is, however, a significant increase in fertility from the \( F_1 \) to the \( F_2 \) for the three crosses combined (Table 16).

The average number of survivors per mating set up provides the only character that showed considerable improvement on crossing. The changes in this character were very pronounced only in the \( F_2 \)'s of the crosses where both the mothers and their offspring were crossbred, just as similar changes were pronounced only in the 2nd inbred generations.
generations where both the mothers and their offspring were inbred. The least increase in an F2 was 13.2%, and the least decrease in a 2nd inbred generation was 14.4%, while a change of as much as 50.5% occurred in a 2nd inbred generation. Such changes were very noticeable in working with the mice (Table 17, and Table 8). Graphs of the percentage heterosis in the mean weights at 12, 21, 28 and 42 days in the F1 and the F2 of the three crosses show that in the F1 there is some heterosis in all weights prior to six weeks, and that there is a fall in every mean weight of the crossbred populations from the F1 to the F2, except in the case of the two earliest mean weights in the cross of the Unselected and the Small line (Figure 12(a)). It was expected that any decline in weight from the F1 to the F2 would have been obscured by the appearance of maternal hybrid vigour in the F2, but this has not been the case, and if an average for the three crosses is taken, the heterosis at each successive weighing over the F1 and F2 shows a regular percentage decrease from that of the previous weighing. (Fig. 12(b)).

Differences in mean six week weight between reciprocal crosses in the F1 are very marked, being least in the cross of the Large and the Unselected line, and greatest in the cross/
cross of the Unselected and the Small line. The reciprocal differences are thus not directly related to the difference between the parental lines, but rather to the mid-parent weight. Differences in the F₁'s of reciprocal crosses are very much present in all weights prior to six weeks, (Table 18(a) ). In the F₂'s also, reciprocal differences are present generally to a smaller extent, but in the cross of the Large and Unselected lines the difference is as great as in the F₁ but the sign is reversed. Reciprocal crosses of the reciprocal crosses in the F₁ also differ significantly and the differences are even greater than those of the F₂'s of the reciprocal crosses (Table 18(b) ). These F₂ differences can be split into "maternal" differences and "sex" differences (Table 18(c) ). Significant differences due to both maternal effects and sex chromosome effects are present, with, however, strong interaction between the two effects in certain cases. A detailed discussion of these effects is irrelevant.

D. CROSSES OF THE TWO SMALL LINES

The results of the cross between the two lines both previously selected for low weight at six weeks, were very different from those of the N-stock crosses. Highly significant heterosis in mean six week weight appeared in the F₁, and diminished only very slightly in the F₂. The mean six/
six week weight of the crossbred population exceeded the 
mid-parent value by 2.00 gm. in the F₁, a superiority of 
14.5%, and by 1.93 gm. in the F₂, a superiority of 14.0% 
(Table 19). In both F₁ and F₂, the mean for the crossbred 
population was greater than that of either parental population 
(Fig. 13).

The ratio of sex weights has much the same value for 
crossbred as mid-parent in the F₁, but there is a difference 
in the ratio for reciprocal crosses, which suggests that the 
value is determined by the male parent. The ratio in the 
F₂ has the same value as that for the Small parental line 
(Table 21).

There is the expected increase in variance from the 
F₁ to the F₂. The F₂ variances, however, all have values 
intermediate between those of the parental control lines, 
and the increase in variance from the F₁ to the F₂ is due to 
a significant decrease in the values of the F₁ variances 
below those of the parental control lines. The decrease 
is apparent in both the within litter and between litter 
components of the F₁ variance. (Table 20). Reeve and 
Robertson (1952), working with Drosophila, give fairly 
conclusive evidence for exceptionally low values of the 
variance in the F₁'s of several crosses.

The /
The $F_2$ mean six week weight did not show the expected regression towards the mid-parental mean. Mean 12 days weights, however, show that the regression has been obscured by maternal hybrid vigour, since the heterosis in 12 day weight was 0.3% in the $F_1$ and 10.6% in the $F_2$. Thus, for the character gain in weight from 12 to 42 days, the heterosis becomes 23.0% in the $F_1$ and 16.2% in the $F_2$, revealing the regression of the $F_2$ mean. Considerable heterosis is also displayed by weights at three weeks and four weeks (Table 19). The average percentage increase of the crossbred means over the mid-parental means for weights earlier than six weeks was 5.6% in the $F_1$ and 10.5% in the $F_2$. In conjunction with corresponding combined percentages averaged for the two small parental lines of 0.7% in the 1st inbred generation and 8.4% in the 2nd inbred generation, the figures provide strong evidence for a pronounced maternal effect on weight in the small lines.

The fertility improved by 27.4% in the $F_1$, but fell to an improvement of only 7.7% in the $F_2$. Since fertility is determined largely maternally, the strong increase occurring in the $F_1$ (comparable with the strong decrease in fertility in the 1st inbred generation of both small lines) was not expected till the $F_2$ where it failed to appear (Table 21).

The /
The average number of survivors per mating set up was greatly increased in the F₁, and to a somewhat lesser extent in the F₂ (Table 21). The index for breeding speed (see page 32) was greater in both the F₁ and the F₂ than in either parental line. Both small lines bred rather slowly compared with the Unselected line, but the F₂ of their cross equalled the Unselected line in breeding speed (Table 21).

Summarily, the main results of the experiment were:

1. Significant inbreeding depression in mean six week weight occurred in all four lines, with the depression much greater in the small lines than in the Large line.

2. The mean six week weights of both F₁ and F₂ of the N-stock crosses fell with exceptional accuracy on the mid-parental means.

3. The cross of the two small lines showed considerable heterosis in almost every character. The variance of weights at 3, 4, and 6 weeks in the F₁, however, were all significantly less than the corresponding mean parental variances.

The observed changes in several characters for several lines and for different breeding systems have been presented above more or less independently of each other. One of the main purposes of the experiment, however, was to furnish estimates of inbreeding depression and heterosis in the character that had undergone previous selection so that these /
these estimates could be subjected to a comparative study.
A certain amount of theory is required before such a comparative study can be made, and the necessary theory is therefore developed in the next section.
In its origin, genetics was essentially mathematical, and is at present the only branch of biology that has yielded largely to mathematical treatment. In particular, population genetics is essentially the study of gene frequencies, and quantitative genetics the study of gene frequencies together with the phenotypic effects of the genetic units.

The genes responsible for quantitative characters must be assigned a definite way in which they produce their phenotypic effects, and given certain quantitative values to define these effects; and therein lies the central theoretical difficulty of quantitative genetics. To discover the quantitative effect of a single gene-pair, AA', one has to ask: What quantitative attribute is common to all members of the class of genotypes in which the gene-pair, AA', is present? In general one might be tempted to answer: Probably none. The current assumption is that the substitution of AA for AA' has the same quantitative effect for all genotypes, and that the cumulative effect of successive substitutions is independent of the order in which the substitutions are carried out. This assumption makes it possible to represent the effects /
effects as an additive scheme, wherein deductions of theoretically expected values can be more simply made. Agreement with observed values is then considered only after a proper scale transformation of data has been made.

On the current assumption, then, the mean value of a phenotypic character in a population will be given by the sum of the different effects of the genetic units multiplied by the frequencies with which they occur.

In this thesis, the chief interest is in the separation of the mean additive effects at the different loci from the dominance effects. Two defining quantities are therefore given to each locus. The mean additive effect, $a_r$, at the $r$th locus, is taken as half the difference in effect between the two homozygotes, and is always positive; and the degree of dominance, $d_r$, is taken to measure the relative excess of the effect of the heterozygote over that of the mid-homozygote, and can have any value, positive or negative. One homozygous effect is thus $a_r(1 - d_r)$, the other homozygous effect $-a_r(1 + d_r)$, and the heterozygous effect is zero.

The mid-homozygous value is thus $-a_r d_r$. Since the heterozygous effects are all taken as zero, the constant term required in the expression for the mean value of the phenotypic character will be the phenotypic value of the unique genotype heterozygous at all loci. If there are $n$ loci /
loci involved, and if the frequency of the homozygote at the
rth locus taken as having the greater effect, \( a_r (1 - \delta_r) \), is
\( y_r \), and the frequency of the other homozygote with the lesser
effect, \(-a_r (1 + \delta_r)\), is \( \delta_r \), then for the population to which
these frequencies apply, the mean phenotypic value will be
given by

\[
\mu = c + \sum_{r=1}^{n} a_r \left\{ (y_r - \delta_r) - \delta_r (y_r + \delta_r) \right\},
\]

where \( c \) is the phenotypic value of the complete heterozygote.
The mean is seen to depend on the sum and difference of the
frequencies of homozygotes in opposite phases.

The genetic component of the phenotypic variance is
given by

\[
\sigma_{\text{Ph}}^2 = \sum_{r=1}^{n} a_r^2 \left\{ (1-\delta_r)^2 (y_r - \delta_r^2) + 2y_r \delta_r (1-\delta_r^2) + (1+\delta_r)^2 (\delta_r - \delta_r^2) \right\}
\]

These expressions for mean and variance apply to populations
under any breeding system. For a random mating population,
\( y_r = p_r^2 \), \( \delta_r = q_r^2 \), where \( p_r \) and \( q_r \) are the allelic
frequencies for the \( r \)th locus, so that the expressions become

\[
\mu = c + \sum_{r=1}^{n} a_r \left\{ (p_r - q_r) - \delta_r (1 - 2p_r q_r) \right\}
\]

\[
\mu = \mu_0 + \sum_{r=1}^{n} a_r (p_r - q_r) + \sum_{r=1}^{n} 2a_r \delta_r p_r q_r, \]

where \( \mu_0 = c = \sum_{r=1}^{n} a_r \delta_r \); and

\[
\sigma_{\text{Ph}}^2 = \sum_{r=1}^{n} 2p_r q_r a_r^2 \left\{ 1 - 2 \delta_r (p_r - q_r) + \delta_r^2 (1 - 2p_r q_r) \right\}.
\]
These expressions correspond exactly to those given by Mather (1949), although a different notation has been used. Mather used $d$ to represent the additive effect, and $h$ to represent the deviation of the heterozygote from the mid-homozygote, and $u, v$, for gene frequencies. In quantitative genetics, $h$ has generally been used to represent the square root of a heritability, and gene frequencies are usually denoted $p$ and $q$. Mather's notation was therefore avoided.

**MEAN**

The mean is seen to have three terms - a constant, an "additive" term, and a "dominance" term.

Let this be represented by

$$\mu = A + D,$$

where

$$A = \mu_0 + \sum_{r=1}^{n} a_r (p_r - q_r),$$

and

$$D = \sum_{r=1}^{n} 2a_r d_r (p_r - q_r).$$

Hereafter, $A$ will be designated the additive term, and $D$ the dominance term.

**A. DOMINANCE AND INBREEDING**

If a line be fully inbred, $D = 0$, and if

$$\sum_{r=1}^{n} a_r (p_r - q_r) = 0,$$

and $D = 0$, then

$$\mu = \mu_0,$$

so that in the case of equal additive effects, $\mu_0$ represents the mean phenotypic value of a fully inbred line with equal numbers of genes fixed in either direction, i.e., $\bar{p} = \bar{q}$.

$$\sum_{r=1}^{n} a_r d_r$$

represents the maximum value of the dominance term, occurring when all loci are heterozygous, so that

$$C = \mu_0 + \sum_{r=1}^{n} a_r d_r$$

will be the mean phenotypic value of a population in which every animal is heterozygous at every locus.

Consider
Consider now the mean phenotypic value of several inbred lines taken from a population. The mean value of the gene frequency does not change and the changes in the individual $p_x$ in any line will be at random with respect to the effects of the genes, so that the additive term, $A$, does not change. The dominance term, $D$, will change to $D(1 - F)$, where $F$ is Wright's inbreeding coefficient. The actual value of $D$ can thus be ascertained, and will be given by

$$D = \frac{\langle u \rangle_2 - \langle u \rangle_1}{F_2 - F_1},$$

where $F_1$, $F_2$ are the inbreeding coefficients at any two stages, and $\langle u \rangle_1$, $\langle u \rangle_2$ are the corresponding observed mean values. The dominance term obtained will be that of the population which has been taken as origin for the inbreeding coefficients. The removing of the dominance term from the observed phenotypic mean gives the relation

$$\mu = \mu - D = A = \mu_0 + \sum_{x=1}^{r} \alpha_x (p_x-q_x).$$

Now

$$\sum_{x=1}^{r} \alpha_x (p_x-q_x) = n \bar{a} (p-q) + n \text{cov} \{\alpha_x, (p_x-q_x)\},$$

and

$$\sum_{x=1}^{r} 2 \alpha_x p_x q_x = 2 n \bar{a} \bar{p} q + 2 n \text{cov} \{\alpha_x, p_x q_x\}.$$

The
The covariance term in both cases will depend on correlations between gene frequencies and gene effects. Certain theoretical considerations mentioned in the Introduction lead one to expect selection to set up non-zero correlations between gene frequencies and gene effects, and the investigation of such correlations forms a major part of the present work. Initially the absence of correlation between gene frequencies and gene effects is assumed, and deductions based on this assumption are taken as giving "expected" values for various quantities. Later, the effect of non-zero correlations is discussed. If, then, the absence of correlation between gene frequencies and gene effects is assumed,

\[ A = \mu_0 + n\bar{a}(\bar{p} - \bar{q}) \]

where \( \bar{a} \) is the additive equation, and \( D = 2n\bar{a}d. \bar{p}q = 2n\bar{a}d(\bar{p}q - \bar{a}^2) \)

where \( \bar{a}^2 \) is the variance of the gene frequency at the different loci; this latter equation may be called the dominance equation. For two lines, \( X, Y \), the subtraction of their additive equations gives

\[ 2n\bar{a}(\bar{p}_x - \bar{p}_y) = A_X - A_Y \]

For a third line, \( Z \),

\[ 2n\bar{a}(\bar{p}_z - \bar{p}_y) = A_z - A_Y \]

Hence

\[ (\bar{p}_x - \bar{p}_y) = \left( \frac{A_X - A_Y}{A_z - A_Y} \right)(\bar{p}_z - \bar{p}_y) \]

which gives the relative change in mean gene frequency of two lines measured from the mean gene frequency of some third line.
It is now necessary to study the meaning of $F$, as defined by Wright. If $F_{21}$ is the inbreeding coefficient of population 2 referred to population 1 as origin, and if population 1 is in turn inbred to a degree $F_{10}$ referred to a population 0, then

$$\left(1 - F_{20}\right) = \left(1 - F_{21}\right) \left(1 - F_{10}\right)$$

gives the inbreeding coefficient of population 2 referred to population 0 as origin.

Now

$$D_2 = D_1 \left(1 - F_{21}\right) = D_0 \left(1 - F_{10}\right) \left(1 - F_{21}\right)$$

$$\therefore F_{21} = 1 - \frac{\left(\frac{p}{q} - 1\right)^2}{\left(\frac{p}{q}\right)^2} = \frac{\left(\frac{p}{q}\right)^2 - \left(\frac{p}{q}\right)^3}{\left(\frac{p}{q}\right) - \left(\frac{p}{q}\right)^3}$$

likewise

$$F_{20} = \frac{\left(\frac{p}{q}\right)^2 - \left(\frac{p}{q}\right)^3}{\left(\frac{p}{q}\right) - \left(\frac{p}{q}\right)^3}.$$ 

Define a hypothetical population with $\left(\frac{p}{q}\right)^2 = 0$, to be taken as origin, so that

$$F_{20}^* = \frac{\left(\frac{p}{q}\right)^2}{\left(\frac{p}{q}\right)}.$$ 

Hence $F$ can be written for $\frac{\sigma_{p}^2}{\sigma_{p}^2}$, provided it is understood that $F$ refers essentially to the specified hypothetical origin — a population with all genes at the same frequency as the mean frequency for the line.

The dominance equation can then be written

$$D = 2n\sigma_{d} \left(\frac{p}{q}\right) \left(1 - F\right).$$

The mean value, $\overline{X}$, has already been expressed in terms of $\overline{X}$ and $\mu_0$, and can be substituted in the above expression. Hence, by inbreeding a population, an equation in the three genetical /
genetical constants \( \mu_0 \), \( n^a \), \( n^n \), and the inbreeding coefficient, \( F \), is obtained. If the inbreeding coefficients were known, observation on three populations at different levels of \( y \) would suffice to determine the genetical constants, and thereafter the mean and variance of the gene frequencies. Once the genetical constants were known, then the mean and variance of the gene frequencies of any line could be determined simply by inbreeding.

The difficulty is that the values of \( F \) cannot be strictly followed when there is assortative mating. The case of three lines at different levels of \( y \), obtained by two-way selection from an initial population and by maintaining the unselected line, has the virtue of fixing a common origin from which inbreeding can be measured, but the \( F \)-values are no longer identical to those of lines unaccompanied by selection. The alternative of three lines with three different origins leaves us ignorant of the relative inbreeding of the three original populations.

**GENERAL SOLUTION FOR ADDITIVE AND DOMINANCE EQUATIONS**

Take the minimum requirement for solution of three lines \( X, Y, Z \), at different levels of \( y \). The additive equations are:

\[
\mu_0 + n^a (\bar{a}_x - \bar{a}_x^t) = A_x
\]

The dominance equations are:

\[
2n^a (\bar{a}_x \cdot \bar{a}_x^t (1 - F_{to})) = D_x
\]

Eliminate \( \mu_0 \) from the additive equations:

\[
\bar{a}_x = \bar{a}_y + \frac{A_x - A_y}{2n^a}
\]

\[
\bar{a}_x^t = \bar{a}_y^t - \frac{(A_x - A_y)(\bar{a}_y^t - \bar{a}_y)}{2n^a} - \frac{(A_x - A_y)^2}{(2n^a)^2}.
\]

Whence,
Whence, substituting in the dominance equations,

\[ (A_x - A_Y)x + (A_x - A_Y)^2 y = \frac{D_Y}{1 - F_{yo}} - \frac{D_x}{1 - F_{xo}}, \]

where \( x = (\bar{p}_Y - \bar{q}_Y) \cdot \frac{2nad}{2na} \),

and \( y = \frac{2nqad}{(2na)^2} \).

An equation in this form may be called the inbreeding equation.

If \( F_{yo} \) is taken as origin for inbreeding,

\[ (A_x - A_Y)(1 - F_{yo}) + (A_x - A_Y)^2 y(1 - F_{yo}) = D_Y - \frac{D_x}{1 - F_{xy}}, \]

where \( F_{xy} \) is the inbreeding coefficient of \( X \) with respect to \( Y \). Two such equations can be solved for \( x(1 - F_{yo}) \) and \( y(1 - F_{yo}) \). Providing \( x \neq 0 \), in which case \( \bar{y} = \frac{1}{2} \), one has

\[ \frac{x}{2y} = n\bar{a}(\bar{p}_Y - \bar{q}_Y), \]

and \[ \mu_0 = A_Y - \frac{x}{2y}. \]

Let \( \lambda = \frac{x(1 - F_{yo})}{y(1 - F_{yo})} = 2nqad(1 - F_{yo})(\bar{p}_Y - \bar{q}_Y)^2. \)

\[ \frac{\lambda}{D_Y} = \frac{(\bar{p}_Y - \bar{q}_Y)^2}{\bar{p}_Y \cdot \bar{q}_Y}, \]

whence \[ \bar{p}_Y = \frac{1}{2} \pm \frac{1}{2} N\sqrt{\frac{\alpha}{\alpha + 4D_Y}}, \]

\[ 2nqad(1 - F_{yo}) = \alpha + 4D_Y, \]

Therefore...
and \( n\bar{a} = \pm \frac{x}{2y} \sqrt{\frac{\alpha + 4.\overline{D}y}{\alpha}} \), the positive sign of the root being taken if \( \overline{P}_y > \frac{1}{2} \), and the negative if \( \overline{P}_y < \frac{1}{2} \).

The value of \( \overline{P}_x \) is obtained from

\[
\overline{P}_x = \overline{P}_y + \frac{(A_x - A_y)}{2n\bar{a}},
\]

and similarly for \( \overline{P}_z \).

It is seen that the values of \( \mu_o, n\bar{a} \), and the mean gene frequencies are independent of the origin taken for inbreeding. Whatever the previous inbreeding of a line, the dominance term at any stage can be experimentally obtained and removed from the observed phenotypic mean, leaving the additive term which will always remain the same; and it is on this additive term and the relative inbreeding in the different lines that the values of \( \mu_o, n\bar{a} \), and the mean gene frequencies depend. The term \( 2n\bar{a}d(1 - F_yo) \) represents the maximum value of the dominance term for the original population, i.e., the non-segregating genes are excluded.

The solution depends essentially on the ratio

\[
D_x : D_y : D_z \propto \frac{P_x \bar{q}_x(1 - F_xo)}{P_y \bar{q}_y(1 - F_yo)} : \frac{P_z \bar{q}_z(1 - F_zo)}{P_x \bar{q}_x(1 - F_xo)}.
\]

It is seen that the observed ratios can be attributed either to differences in mean gene frequencies or to differences in the degrees of inbreeding. Thus if the inbreeding were the same in the three lines, the ratios determine

\[ \frac{P_x \bar{q}_x}{P_y \bar{q}_y} \propto \frac{P_z \bar{q}_z}{P_x \bar{q}_x} \]

and for three unselected lines from the same original population,

\[
D_x : D_y : D_z \propto (1 - F_xo) : (1 - F_yo) : (1 - F_zo),
\]

i.e., the ratios determine the relative degrees of inbreeding of
of the three lines. Again if \( A_x > A_y > A_z \) so that
\[ F_x > F_y > F_z \], if \( D_x < D_y < D_z \), and if the degree of
inbreeding were the same in the three lines, then one can
conclude that \( \bar{F}_y > \frac{1}{2} \). Thus inbreeding of actual experimental
lines immediately throws some genetic light on the difference
in breeding behaviour and mean character of the lines.

B. DOMINANCE AND HETEROsis

If two lines, \( X, Y \), are crossed, the mean pheno-
typic value of the \( F_1 \) generation, written \( \mu_{xy} \), will be
\[ \mu_{xy} = \mu_0 + \frac{n}{2} \left( \bar{F}_x + \bar{F}_y - 1 \right) + \frac{ad}{n^2} \sum_{r=1}^{n} \left( p_{xr} q_{yr} + p_{yr} q_{xr} \right), \]

since the proportion of homozygotes in opposite phases is
\[ \frac{1}{n} \sum_{r=1}^{n} p_{xr} p_{yr} \] and \[ \frac{1}{n} \sum_{r=1}^{n} q_{xr} q_{yr} \]
respectively, the difference of these being \( (\bar{F}_x + \bar{F}_y - 1) \),
and the sum being \[ \frac{1}{n} \sum_{r=1}^{n} \left( 1 - p_{xr} q_{yr} - p_{yr} q_{xr} \right) \).

Thus the dominance term of the \( F_1 \) generation is
\[ D_{xy} = \frac{ad}{n^2} \sum_{r=1}^{n} \left( p_{xr} q_{yr} + p_{yr} q_{xr} \right) \]
\[ = n \bar{d} \left( \bar{F}_x \bar{q}_y + \bar{F}_y \bar{q}_x - 2 \bar{F}_x \bar{q}_y \bar{p}_x \bar{p}_y r_{xy} \right), \]
where \( r_{xy} \) is the correlation between the gene frequency, \( p_{xr} \),
at the \( r \)th locus in line \( X \), and the gene frequency, \( p_{yr} \),
at the corresponding locus in line \( Y \); \( r_{xy} \) will be referred
to as the gene frequency correlation for the two lines.

Similarly /
Similarly the $F_2$-generation mean, written $\mu_{x+y}$, is

$$\mu_{x+y} = \mu_0 + n\bar{a}(\bar{f}_x + \bar{f}_y - 1) + \bar{a}\bar{d} \sum_{r=1}^{r} \left( \frac{\bar{p}_{xr} + \bar{p}_{yr}}{2} \right) \left( \frac{\bar{e}_{xr} + \bar{e}_{yr}}{2} \right)$$

$$= \mu_0 + n\bar{a}(\bar{f}_x + \bar{f}_y - 1) + n\bar{a}\bar{d} \left\{ \frac{(\bar{p}_{x+y})^2}{2} - \sigma_{p_{x+y}}^2 \right\}.$$  

Hence $D_{x+y} = n\bar{a}\bar{d} \left\{ \frac{(\bar{p}_{x+y})^2}{2} - \sigma_{p_{x+y}}^2 \right\}$.

Combining the $F_1$- and $F_2$-generation means, one gets the well-known cross relation that the $F_2$-generation mean should lie on the mid-point between the $F_1$-generation mean and the parental mean, i.e.

$$2\mu_{x+y} = D_{x+y} + \frac{1}{2}(D_x + D_y),$$

or

$$2\mu_{x+y} = \mu_{x+y} + \frac{1}{2}(\mu_x + \mu_y)$$

since the additive term is identical on both sides.

The heterosis in the $F_1$-generation will be measured by

$$H_{xy} = \mu_{xy} - \frac{1}{2}(\mu_x + \mu_y)$$

$$= D_{xy} - \frac{1}{2}(D_x + D_y)$$

$$= \bar{a}\bar{d} \sum_{r=1}^{r} \left( \bar{p}_{xr} - \bar{p}_{yr} \right)^2.$$  

$$H_{xy} = n\bar{a}\bar{d} \left\{ \left( \bar{p}_{x-y} \right)^2 + \sigma_{p_{x-y}}^2 \right\},$$

which may be called the heterotic equation. Similarly for the $F_2$-generation,

$$H_{x+y} = D_{x+y} - \frac{1}{2}(D_x + D_y)$$

$$= \frac{1}{2} H_{xy}$$

from the cross relation.
Since the heterosis $H_{xy} = 2D_{x+y} - (D_x + D_y)$, a very useful experimental check both on theory and on the estimates of heterosis is provided by obtaining the value of $D_{x+y}$ by inbreeding the $F_2$ generation of the cross. In all, three estimates of heterosis are available: $H_{xy}$ in the $F_1$, $H_{x+y}$ in the $F_2$, and $D_{x+y}$ subsequently by inbreeding, the three being related by $H_{xy} = 2H_{x+y} = 2D_{x+y} - (D_x + D_y)$. If the genetic relationship between lines crossed is to any extent known, the most convenient form for the heterotic equation from which to obtain a solution for the genetical constants is

$$D_{xy} = m_{x+y} \left( \frac{P_x \cdot P_y}{\bar{r}_x \cdot \bar{r}_y} + \frac{P_y \cdot P_x}{\bar{r}_y \cdot \bar{r}_x} - 2 \theta \alpha \theta \beta \theta \gamma \theta \delta \theta \epsilon \theta \zeta \theta \eta \theta \zeta \theta \eta \right),$$

the $\theta \alpha \theta \beta \theta \gamma \theta \delta \theta \epsilon \theta \zeta \theta \eta \theta \zeta \theta \eta$ being expressed in terms of $\bar{r}_x$ and $m_{x+y}$ from the dominance equation; the $\bar{r}_x$ in turn being expressed in terms of $\bar{r}_x$, $m_\alpha \theta \gamma \theta \delta \theta \epsilon \theta \zeta \theta \eta \theta \zeta \theta \eta$ from the additive equation; and the three estimates of $D_{xy}$ being obtained from the relations:

1. $D_{xy} = H_{xy} + \frac{1}{2} (D_x + D_y)$
2. $D_{xy} = 2H_{x+y} + \frac{1}{2} (D_x + D_y)$
3. $D_{xy} = 2D_{x+y} - \frac{1}{2} (D_x + D_y)

Every cross in conjunction with the additive and dominance equations corresponding to the lines crossed will thus give an equation in the genetical constants $\bar{r}_x$, $m_\alpha \theta \gamma \theta \delta \theta \epsilon \theta \zeta \theta \eta \theta \zeta \theta \eta$, and the correlation between the gene frequencies (at the various loci) of the different lines. In the heterotic equation, $\bar{r}_{x+y}$ is on the same footing as $\bar{r}_x$ in the inbreeding equation, in that its value can be traced to a certain extent but not absolutely.
As with $F$ at a similar stage, it is necessary to study the meaning of $\Gamma_{P_{X}\Gamma_{X}}$.

Now
\[
D_{X+Y} = 2n \overline{a}(\overline{F_{X}})^2 (\overline{F_{X}})(1 - \overline{F_{X+Y}}),
\]
where $F_{X+Y}$ is the inbreeding coefficient from zero origin of the offspring in the $F_2$-generation. Using the cross relation
\[
D_{X+Y} = 2D_{X+Y} - \frac{1}{2}(D_{X} + D_{Y}),
\]
or much more simply the relation
\[
\sigma_{p_x}^2 + \sigma_{y}^2 + 2\sigma_{p_x} \sigma_{p_y} \Gamma_{P_{X}\Gamma_{X}} = \sigma_{p_{X+Y}}^2,
\]
one has
\[
\overline{F_{X+Y}} = 2\overline{F_{X}} - \frac{1}{2}(\overline{F_{X}} + \overline{F_{Y}}),
\]
a relation connecting the inbreeding coefficients and the gene frequency correlation and involving the mean gene frequencies.

This relation provides the link between the values of $F$ used for a solution from the inbreeding equations and the values of $\Gamma_{P_{X}\Gamma_{X}}$ used for a solution from the heterotic equations.

The relation can also give the fractional recovery of the inbreeding depression on crossing.

It should be noted that this correlation is not the same as the coefficient of relationship, defined by Wright (1922) as
\[
\Gamma_{X,Y} = \frac{2F_{X+Y}}{\sqrt{(1+F_{X}) (1+F_{Y})}},
\]
and which is therefore always positive. When the mean gene frequencies are equal, as in the case of two lines $X$, $Y$, inbred without selection from the same zero inbred initial population,
\[
\Gamma_{P_{X}\Gamma_{X}} = \frac{4F_{X+Y} - (F_{X} + F_{Y})}{2\sqrt{F_{X}F_{Y}}},
\]
and
and the two parameters of relationship are related by
\[ r_{xy}^2 = 2 \sqrt{(1 + F_x)(1 + F_y)} \cdot r_{xy}^2 \cdot \frac{F_x}{F_y} + \frac{F_y}{F_x} + 1.

Consider now the heterotic equation:
\[ H_{xy} = n \frac{1}{n} \left( \frac{p_x - p_y}{2} \right)^2 + \sigma_{p_x - p_y}^2 \]

The two terms within the brackets are both essentially positive or zero, the first representing the square of the difference in mean gene frequency of the two lines crossed, and the second representing the variance of the difference in gene frequency of the two lines at the various loci. For better understanding, the effects of the two terms may be considered separately. Thus for two lines with \((p_x - p_y) \) constant for all r loci, \( \sigma_{p_x - p_y} = 0 \), as in the case of only one segregating gene; or in a situation one might imagine resulting from two-way selection from a cross of two inbred lines with no accompanying inbreeding, where selection, acting equally on all genes, changes their frequency to the same extent in any one direction; or in the extreme case where all genes in one line were \( p_x = 1 \) and \( p_y = 0 \) in the other. In the latter case, the term \( (p_x - p_y)^2 = 1 \), so that the heterosis has the extreme value \( n \). In general, with \( \sigma_{p_x - p_y} = 0 \), the heterosis will be directly proportional to the squared difference in mean gene frequency, so that the heterosis increases parabolically with difference in mean gene frequency. The additive equations give the difference in mean gene frequency as directly proportional to \( A_x - A_y \), so that, in the case considered, \( \sqrt{H_{xy}} \propto |A_x - A_y| \), i.e. the square root of the heterosis is directly proportional to the difference of the additive terms for the lines, the constant /
constant of proportionality being \( \frac{\sqrt{n \alpha \delta}}{\eta q} \).

The second case that can be considered has \( \bar{p}_x = \bar{p}_y \), i.e., the mean gene frequencies are equal so that \( A_x = A_y \), and \( \mu_x = \mu_y \) if the lines are fully inbred. For two such lines the heterosis depends only on the variance of the difference in gene frequency at the various loci. Now

\[
\sigma_{p_x - p_y}^2 = 2\sigma_{p_x}^2 + 2\sigma_{p_y}^2 - \sigma_{p_x + p_y}^2
\]

\[
= 2F_{x_0} \bar{p}_x \bar{q}_x + 2F_{y_0} \bar{p}_y \bar{q}_y - (F_{x_0 + y_0})(\bar{p}_x + \bar{q}_x)\frac{(\bar{p}_x + \bar{q}_x)}{2}
\]

\[
= \bar{p}_x \bar{q}_x (2F_{x_0} + 2F_{y_0} - (F_{x_0 + y_0}))
\]

since \( \bar{p}_x = \bar{p}_y \).

\[
H_{xy} = 2n \alpha \delta \bar{p}_x \bar{q}_x (F_{x_0} + F_{y_0} - \frac{1}{2} F_{(x+y)} 0)
\]

\[
= \frac{D_x}{1 - F_{x_0}} (F_{x_0} + F_{y_0} - \frac{1}{2} F_{(x+y)} 0), \text{if } F_{x_0} \neq 1,
\]

and, if the lines are uncorrelated, \( F_{(x+y)} 0 = \frac{1}{2} (F_{x_0} + F_{y_0}) \), so that

\[
H_{xy} = \frac{1}{4} n \alpha \delta (\bar{p}_x \bar{q}_x (F_{x_0} + F_{y_0})
\]

\[
= \frac{r}{8} D_x \left( \frac{F_{x_0}}{1 - F_{x_0}} \right) + \frac{r}{8} D_y \left( \frac{F_{y_0}}{1 - F_{y_0}} \right), \text{if } F_{x_0}, F_{y_0} \neq 1.
\]

If the lines are both uncorrelated and fully inbred,

\[
H_{xy} = \frac{1}{4} n \alpha \delta \bar{p}_x \bar{q}_x
\]

so that \( H_{xy} \propto \bar{p}_x \bar{q}_x \), again parabolically dependent on /
on mean gene frequency, but in this case with the heterosis a
maximum for $\text{f} = \frac{1}{2}$, and very slight towards the extreme
values $\text{f} = 1, 0$.

In general, however, both terms will contribute to the
heterosis, and a complete solution of the general case
becomes necessary.

**GENERAL SOLUTION FOR THE HETEROOTIC EQUATIONS**

The mean gene frequency, $\text{f}_x$, of a line, has been
given by $\text{f}_x = \text{f}_y + \frac{(A_x - A_y)}{2n\alpha}$

from the additive equations.

$\therefore \text{f}_x \bar{x} + \text{f}_z \bar{z} = 2 \left\{ \frac{\text{f}_y \bar{y}}{X} - \frac{(A_x + A_z - 2A_y)}{z} \frac{\text{f}_y \bar{y}}{2n\alpha} - (A_x - A_y)(A_z - A_y) \frac{1}{(2n\alpha)^2} \right\}.$

From the heterotic equation one has

\[2 \text{nad} \bar{p}_x \bar{q}_z r_{p_x p_z} = \text{nad} \left\{ \bar{p}_x \bar{q}_z + \bar{p}_z \bar{q}_x \right\} - D_{xz}\]

Let \[2 \text{nad} \bar{p}_x \bar{q}_z r_{p_x p_z} = C_{xz}\]

; substitute for

$\bar{p}_x \bar{q}_z + \bar{p}_z \bar{q}_x$ ; and use x and y as before.

$\therefore C_{xz} = 2 \text{nad} \bar{p}_y \bar{q}_z - D_{xz} - \frac{(A_x + A_z - 2A_y)}{2} \bar{x} - (A_x - A_y)(A_z - A_y) \bar{y}$

\[= \frac{D_y}{1 - F_{y_0}} - D_{xz} - \frac{(A_x + A_z - 2A_y)}{2} \bar{x} - (A_x - A_y)(A_z - A_y) \bar{y},\]

from the dominance equation.

Also /
Also from the dominance equation, one has
\[ 2n_{A}d e_{p}^{2} = 2n_{A}d \bar{p}_{x} \bar{q}_{x} - D_{x} \]

Let \[ 2n_{A}d e_{p}^{2} = V_{x} \]

and substitute for \( \bar{p}_{x} \bar{q}_{x} \)
from the additive equation.

\[ V_{x} = \frac{D_{y}}{1 - F_{y_{o}}} - D_{x} - (A_{x} - A_{y}) x - (A_{x} - A_{y}) y. \]

Now \( V_{x} V_{z} \rho_{p_{x} p_{z}}^{2} = C_{xz}^{2} \)

by definition, and this relation gives the form of three equations in \( x, y, (1 - F_{y_{o}}) \),

and the gene frequency correlations. The equations are implicit cubics in \( x \) and \( y \) and are rather difficult to solve.

An equation in the heterotic form, however, is highly suitable when it is known or assumed that the lines crossed are uncorrelated, so that \( C_{xz} = 0 \), and hence

\[ \frac{1}{2} (A_{x} + A_{z} - 2A_{y}) x + (A_{x} - A_{y})(A_{z} - A_{y}) y = \frac{D_{y}}{1 - F_{y_{o}}} - D_{xz} \].

**GENERAL SOLUTION FROM CROSSING IN THE FORM OF AN INBREEDING EQUATION FOR THE OFFSPRING OF THE CROSS.**

A much simpler alternative for the heterotic equation is possible if the inbreeding coefficient of the offspring of the \( F_{2} \)-generation of the cross is used.

Now \( D_{x+z} = 2n_{A}d \left( \frac{\bar{p}_{x} + \bar{p}_{z}}{2} \right) \left( \frac{\bar{q}_{x} + \bar{q}_{z}}{2} \right) \left( 1 - F_{x+z} \right) \),

and /
and substitution for the mean gene frequencies can be made by using the additive equations, and for the dominance equation.

\[
D_{x+z} = \frac{1}{4} \left( 1 - \frac{F_{x+z}}{F_{0}} \right) \left\{ \frac{4D}{1 - F_{0}} - 2(A_x + A_z - 2A_y)x - (A_x - A_y)(A_z - A_y)y \right\},
\]

which is linear in \(x, y, \) and \(\frac{1}{1 - F_{0}}\). The value of \(D_{x+z}\) is found from the relation

\[
D_{x+z} = \frac{1}{2} \left( H_{xz} + D_{x} + D_{z} \right).
\]

The genetical constants and mean gene frequencies are found from \(x\) and \(y\) as before.

In the \(V_x, V_z, C_{xz}\) notation,

\[
D_{x+z} = \frac{t}{4} \left( 1 - \frac{F_{x+z}}{F_{0}} \right) \left\{ V_x + D_x + 2(C_{xz} + D_{xz}) + V_z + D_z \right\}.
\]

These equations, derived from crosses but in the form of the inbreeding equations of the crossbred populations, will have all the properties ascribed to inbreeding equations, and in particular they can be solved without knowing the extent of the inbreeding in the population used as origin for all inbreeding coefficients.

It has been shown that a solution is possible if the inbreeding coefficients are given for three lines at different phenotypic levels, or if the gene frequency correlations are given for the crosses between three such lines, or if the inbreeding /
inbreeding coefficients of the offspring in the $F_2^-$ generation of the crosses are given. It is possible, however, to obtain a solution on any three assumptions concerning the parameters or their interrelations, e.g. $F_{x_0} = F_{z_0}$, $r_{x\cdot y} = r_{z\cdot y}$, and solve for $n \text{ad} (1 - F_{y_0})$. Observations on the inbreeding of two lines and on their cross is theoretically sufficient for solution, if the mean phenotypic levels of the lines are different. In actual solution, the extent and nature of one's knowledge concerning the parameter values and the interrelations in the lines in question will determine both the type and number of the equations used. It may be of interest to determine initially a solution from the inbreeding of several lines, and a separate solution from their crosses to check the extent of the agreement, but a better solution would always be achieved by combining every available equation and adopting a least squares method.

An exact solution is, of course, impossible, but, for a sufficient number of lines, a large number of observed values have to form a consistent pattern subject to many restrictions which together may often turn out to be very stringent. Thus (i) not only must the solution of the inbreeding equations be fully consistent within itself, but (ii) this solution must also agree with the solution from the heterotic equations (providing an excellent check on the solving assumptions); further (iii) the relation between the parameters/
parameters P and r must be satisfied for each cross; (iv) the value of many quantities are restricted by definition, e.g. \( 0 \leq p, F, \leq 1 \), \(-1 \leq r \leq 1\), and again \( n\bar{a} \geq \) the maximum range already observed, \( n\bar{a}\bar{r} \geq \) twice the maximum value observed for a dominance term, and other conditions of a similar nature; and (v) if the genetical constants are given approximate values in accordance with (i) - (iv), these values, if they are to be valid, must remain consistent with all further work that may be done on the same or similar strains. The idea is that reasonably accurate values could be ascertained by the accumulation of sufficient data.

VARIANCE

In general, the total genetic variance is far too complex to be of value in the present treatment. For a random breeding population, assuming no correlation between gene frequency and gene effects, the total genetic variance is given by

\[
\sigma^2 = 2na^2 - npq - 4nqad - npq(\mu - q) + na^2d^2 + 2pq(1 - 2pq),
\]

which cannot be evaluated, except for \( n = 1\), unless the distribution of \( p_r \) is known. The first term depends on the variance of the \( p_r \) distribution, the second term on the skewness of the \( p_r \) distribution, and the third on the variance of the \( p_r \) and the variance of the proportion of heterozygotes at the different loci. A case might possibly be considered
where a population is formed by crossing four uncorrelated
lines at the same level of mean gene frequency, \( \overline{y} \). The
distribution of \( p_2 \) in the \( F_2 \) generation will be given by
\((\overline{y} + t)^4\)
so that the genetic variance, \( g_H^2 \), can be given in
terms of \( \overline{y} \) and the genetical constants for the variance.

For example, if \( \overline{y} = \frac{1}{2} \), the term for skewness vanishes and
\[
g_H^2 = \frac{3}{8} n\overline{a}^2 + \frac{27}{128} n\overline{a} \overline{c}^2,
\]
so that
\[
ng_H^2 = \frac{3}{8} (n\overline{a}^2) + \frac{27}{128} (n\overline{a} \overline{c}^2),
\]
\[
= \frac{3}{8} (n\overline{a}^2) + \frac{27}{128} (n\overline{a} \overline{c}^2)^2
\]
if the gene effects are equal. The right hand side of the
expression could be evaluated if the genetical constants for
the mean were known, and \( g_H^2 \) could be evaluated from the
variance of the parents and \( F_1 \) generations, and the \( F_3 \)
generation. A value of \( n \), the number of genes, would result.

If, however, the additive component of the variance,
\( g_G^2 \), is considered in conjunction with the dominance term,
\( D \), of the mean, one has
\[
g_G^2 = 2n\overline{a}^2 \overline{p} \overline{q},
\]
and
\[
D = 2n\overline{a} \overline{d} \overline{p} \overline{q},
\]
so that
\[
g_G^2 = \frac{n\overline{a}^2}{n\overline{a} \overline{d}} \overline{D} = k \overline{D}, \text{ say,}
\]
i.e. the additive genetic variance is directly proportional
to the dominance term of the same population. If \( g_G^2 \)
is determined from heritability estimates, and \( D \) by inbreeding,
the constant of proportionality, \( k \), can be determined. It
will be seen that once the constant of proportionality, \( k \),
has /
has been determined, the heritability in any further population can be estimated from the total phenotypic variance, \( \sigma_p^2 \), and the dominance term, \( D \), obtained by inbreeding the population. The relation is

\[
\hat{h}^2 = \frac{kD}{\sigma_p^2}.
\]

Further, if the genetical constants \( n \bar{a} \) and \( \bar{a} \bar{d} \) have been determined in connection with the mean, the genetical constant of the variance, \( \bar{n}^2 \), will be given by \( \bar{n}^2 = k \cdot \bar{a} \bar{d} \); hence, if the additive gene effects are equal, the number of genes, \( n \), will be given by

\[
n = \frac{(\bar{n}a)^2}{k \cdot (\bar{n}a)^2}
\]

and the additive gene effect by

\[
a = \frac{k \cdot \bar{n}d}{(\bar{n}a)}.
\]

The present treatment indicates that it is theoretically possible to determine values for the genetical constants, \( \mu \), \( n \bar{a} \), \( \bar{n} \bar{d} \), and \( \bar{n}^2 \); and although initially only approximate estimates could be given, the errors in estimation could gradually be reduced as more work is done over similar strains. Once values had been determined, the only requirements in finding the mean gene frequency, the degree of fixation, and the heritability of a population would be the phenotypic mean and variance of the population and the change in the mean on inbreeding.
The objections that might be raised are:

1. that the absence of correlation between gene frequency and gene effect has been assumed. The deviations expected from such correlations, however, can be deduced and are discussed later;

2. that epistatic interactions are not considered. This is not entirely true, for it is postulated that the scale of measurement be chosen so that interactions are a minimum.

3. that overdominance has not been considered. This is not so, since the degree of dominance, \( d \), can have any value from \( +\infty \) to \( -\infty \).

4. that the genetical constants will have different values in different strains. Genetics, however, interprets the phenotypic differences between strains as essentially due to differences in gene frequencies, and so long as two strains are alike in chromosomal content, so their genetical constants will be alike. If this is not the case, and if the genetical constants, at least \( \mu_0 \) and \( \bar{m} \), do not hold within close limits over all the populations used in the present experiment, the problem posed in the thesis disintegrates. The main determinants of the extent of inbreeding depression and heterosis are the mean gene frequencies and the relative amount of fixation in /
in the populations, and unless these can first be allowed for by use of genetical constants or some other means, lesser effects such as those caused by differential selection for dominants cannot begin to be detected.
The hypothesis of dominance in the form developed in the last section is intended to furnish not so much an accurate numerical interpretation, as a means of collating an increasing number of somewhat diverse results and a rigid framework on which to assess the extent of their agreement and so reveal the nature and extent of discrepant features.

This section, then, will be devoted to determining the proportions of the framework, as it were, by finding those values of the genetical constants which best agree with the present experimental estimates of phenotypic mean, inbreeding depression, and heterosis. Thereafter an attempt is made to assess the extent of the agreement between values theoretically expected and values expected on other grounds. The probable deviations from expectation of the observed estimates of inbreeding depression and heterosis are then given.

**DETERMINATION OF GENETICAL CONSTANTS**

Since the hypothesis essentially postulated that the effects of different loci had to be additive on the scale used, the first question to be considered is that of "scale".

**ARITHMETIC SCALE**

The criteria for scale given by Wright (1950) are not contradicted within the present experiment when applied to the untransformed (arithmetic) data. Since the heterosis in the N-stock /
N-stock crosses have almost negligible values in the $F_1$ and $F_2$, the $F_2$ mean can be said to fall halfway between the $F_1$ and mid-parent means. Yet, if a solution for the genetical constants is attempted using the recorded values of the inbreeding coefficients ($F_{LN} = 0.3 = F_{SN}$), the result is an absurdity, for it gives as a maximum to the range a value already exceeded by the large selected line. The solution from the heterotic equations is also absurd, since the absence of heterosis in all N-stock crosses implies that the dominance constant, $\delta$, must be zero, while these very lines gave marked inbreeding depression and the cross of the small lines gave marked heterosis, both implying that the dominance constant is considerably greater than zero.

It may be of interest, however, to give arithmetic estimates of the dominance terms found from the mean of three successive generations of sib-mating. Allowance was made for the slight inbreeding of the control lines. $D_L$ (large selected line) = 1.26 gm., $D_N$ (unselected line) = 2.46 gm., $D_S$ (small selected line) = 1.42 gm., and $D_{MS}$ (MacArthur's small selected line) = 2.16 gm. Separate estimates of $D_N$ are available from the data for the crosses of the four initial inbred lines (Falconer, 1953). The phenotypic mean of the $F_3$-generation of the cross can be predicted by

$$\mu(F_3) = \frac{1}{2} \mu(F_2) + \frac{1}{4} \mu(F_1) + \frac{1}{4} \mu(F_2),$$
the usual cross relation. The dominance term,

\[ D_N = \mu(\frac{1}{3}) - \mu(\frac{2}{3}) \]

whence \(D_N\) (original cross) = 2.82 gm., and \(D_N\) (repeat cross) = 2.20 gm., with an average of 2.51 gm. to be compared with the estimate from inbreeding of 2.46 gm. An estimate of \(D_N = 3.30\) gm., using the mean of 6 generations in the unselected (NG) line, which represent the \(F_3\) level in the repeat cross, shows a slight excess, attributable to the persistency of maternal hybrid vigour; for, if the phenotypic mean is taken over the later generations only, the estimate becomes 2.89 gm., almost the same as for the original cross.

The separate estimates of the dominance term from different sources are in very good agreement. This seems to indicate that the theory is adequate in that it gives agreement within a restricted part of the range, and that the disagreement between widely separated levels can be attributed to the arithmetic scale.

LOGARITHMIC SCALE

The logarithmic scale has been given considerable favour by many workers, and indeed there is certain evidence in its favour in the present case.

(1) It has been found from general experience that the logarithmic transformation most satisfactorily dealt with individuals' growth and changes in six week weight can be largely attributed to changes in growth rate.

(2) /
(2) The sex difference in weight is independent of the mean weight on the logarithmic scale (See Section III (1)).

(3) The major gene, "pygmy", discovered by King (1950) has a multiplicative effect.

(4) The standard deviations of six week weight seem to be proportional to the mean; although there is no strong evidence from the present experiment. The proportionality of standard deviation and mean has held throughout the N-stock populations as far as the large selected line, the unselected line, and the first 3 - 10 generations of the small selected line are concerned. The small selected line of the N-stock, however, experienced a sudden marked increase in variance about the 9th selected generation, so that the proportionality was destroyed. (Falconer, 1953).

None of these facts imply that the gene effects are, in general, multiplicative, but they are suggestive, and the logarithmic transformation is one of the simplest in calculation and interpretation. The data were therefore transformed to the logarithmic scale, and multiplied by 100 to bring a suitable significance to the figures at the decimal point.

The dominance hypothesis becomes tenable again, with the N-stock crosses now showing heterosis, so that the previous contradiction is removed. Further substantiation for the use of the logarithmic scale is that the $F_2$ means invariably /
invariably show a decline from the $F_1$ level, with the cross relation approximately satisfied (Table 23). A preliminary survey of the logarithmic estimates showed no apparent inconsistency. The results were thus subjected to a complete and detailed study.

Firstly, take the logarithmic estimates of the dominance terms from inbreeding:

\[
D_L = 2.30 \pm 1.08; \quad D_N = 5.33 \pm 0.31; \quad D_S = 4.72 \pm 1.73; \quad D_{M1} = 7.47 \pm 1.62
\]

The standard errors are calculated from variances transformed according to the formula given by Wright (1950). The estimates of $D_N$ from other sources as discussed for the arithmetic scale were:

\[
\begin{align*}
D_N \text{ (original cross)} & = 6.33 \\
D_N \text{ (repeat cross)} & = 5.05 \\
\text{and } D_N \text{ (unselected line)} & = 7.34
\end{align*}
\]

The best estimate of $D_N$ is a mean of these four separate estimates, weighted according to accuracy and reliability, giving $D_N = 5.50$.

The logarithmic estimates of the additive terms can now be made. The logarithmic mean of the large selected control line (LC) over six generations was 138.21 units. There was an average increase of 0.068 in the inbreeding coefficient, so that the mean from which inbreeding began can be taken as $138.21 + 0.068 \times 2.30 = 138.36$.

Hence /
Hence $A_L = \mu_L - D_L = 136.06$.

Likewise $A_N = 125.91$, with $\mu_N = 131.41$; $A_3 = 111.45$, with $\mu_3 = 116.17$; and $A_{MS} = 103.29$, with $\mu_{MS} = 110.76$. The estimates of heterosis are shown in Table 23, and the best estimates were calculated as the mean of the $F_1$ and $F_2$ estimates weighted according to their error variances. Since the error variances in the $F_1$'s are much the same as in the corresponding $F_2$'s (see Table 10), the best estimates can be taken as

$$\frac{2}{3} \left(2H_{F1} + H_{F2} \right).$$

All the estimates required to give the inbreeding and heterotic equations have now been given.

The inbreeding equations for the large (L) and small (S) lines of the N-stock are:

\[(L) \quad 10.15x + 103.0y = 5.5 - \frac{2.80}{1 - F_{L,N}}\]

\[(S) \quad -15.25x + 232.7y = 5.5 - \frac{4.72}{1 - F_{S,N}}\]

The inbreeding equation for MacArthur's small line (MS) is:

\[(MS) \quad -22.62x + 512.0y = 5.5 - \frac{7.47}{1 - F_{MS,N}}\]

The N-stock crosses provide three equations, given in the form of the inbreeding equations for the crossbred populations:

\[(L+N) \quad 20.3x + 103.0y = 22.0 - \frac{16.40}{1 - F_{L+N,N}}\]

\[(L+S) \quad -10.2x + 26.0y = 22.0 - \frac{16.64}{1 - F_{L+S,N}}\]

\[(N+S) \quad -30.5x + 232.7y = 22.0 - \frac{21.70}{1 - F_{N+S,N}}\]
The cross between the two small lines provides the equation:

\[
(S+MS) - 74.18x + 1377.0y = 22.0 - \frac{37.82}{1 - F(S+MS)N}
\]

The inbreeding coefficients are all given with respect to an origin in the unselected line of the N-stock, which also acts as the reference line from which the other lines, all previously selected, are measured, and so does not appear independently.

These seven equations summarise the experimental observations on the mean six week weight of the 20 control, 12 inbred, and 8 crossbred populations. Within these equations are concealed values of the genetic constants, and the success or failure in determining such values depends on the possibility of finding a solution for the equations. The numerical figures are all subject to experimental errors, and the inbreeding coefficients are, in the strictest sense, unknown. The hope of solution lies partly in the fact that each inbreeding coefficient can be given a maximum and minimum value as well as a probable one, and that the inbreeding coefficients of the crossbred lines are related to the inbreeding coefficients of their parent lines within limits set by the gene frequency correlations.

Perhaps /
Perhaps the greatest help, however, in arriving at a satisfactory solution is the necessity for consistency. Thus, for example, if the (S) and (MS) equations are solved together, negative values of x and y result — an obvious absurdity. The reason for such negative values is apparent, for lines near the same mean six week weight will be represented graphically by almost parallel lines, so that the slightest error would change the point of intersection by a great amount. The accuracy of solution will be greater the further apart the lines in mean weight.

A preliminary solution, using only the (L) and (S) inbreeding equations and making the assumption that the recorded values of $F_{2N} = F_{5N} = 0.3$ represent the true situation, gives the genetical constants as $\mu_0 = 111.2$, $n\bar{a} = 34.9$, $n\bar{ad}(1-F_{no}) = 13.39$.

A solution, using estimates of heterosis from the crosses, ought to give values for the genetical constants largely similar to those obtained from estimates of inbreeding depression. The three heterotic equations for the N-stock crosses only were used since it is imagined that within the stock there is a further knowledge of genetic relationship on which to base the necessary solving assumptions. The assumption made is that the gene frequency correlation between the large and unselected line, between the large and small line, and between the unselected and small line will not differ in value to any great extent.
No actual value is assumed, but becomes part of the solution. The detailed arguments leading to this assumption are not given, as the assumption turns out to be of little importance. It is not possible in this case to solve for \( \overline{\text{ad}} (1 - F_{NO}) \), so that some value must be assumed also for \( F_{NO} \). Falconer (1953) has given reasons for taking \( F_{NO} = 0.25 \), and this value is used.

The actual solution of the equations involved an implicit cubic in \( x \) and \( y \), giving three sets of values for \( x \) and \( y \), but there was no difficulty in deciding which applied. The genetical constants are calculated as \( \mu_0 = 116.9 \), \( \overline{\text{na}} = 27.0 \), and \( \overline{\text{ad}} = 16.5 \); hence \( \overline{\text{ad}} (1 - F_{NO}) = 12.4 \).

The values deduced from the estimates of inbreeding depression and those deduced from estimates of heterosis thus agree favourably with each other.

The equations could therefore be combined, and a more accurate solution obtained by the least squares method. The heterotic equations were unsuited to such a method, and so were replaced in linear form as inbreeding equations for the \( F_2 \)'s of the crosses. The values given to the inbreeding coefficients of the crossbred populations were found from the formula connecting the inbreeding coefficients of parents and offspring of a cross (Page 60), and based on the recorded values of the inbreeding coefficients for the parental lines and the assumption of fairly high gene frequency correlations.
The equations used in the two previous solutions, when combined, gave a "least squares" solution with $\mu = 115.60$, $\mu = 34.02$, and $\mu(1-F_{N0}) = 12.12$.

The first solution used estimates of inbreeding depression and assumed that the recorded values of the inbreeding coefficients were the correct values. The second solution used estimates of heterosis together with assumptions regarding the gene frequency correlations. The third solution used both estimates of inbreeding depression and heterosis together with assumptions regarding the inbreeding coefficients of the offspring of the crosses. Now the assumptions concerning the parameters of genetic relationship were largely equivalent in the three cases, all being based on the recorded equality of the inbreeding coefficients in the large (L) and small (S) lines of the N-stock. Agreement between solutions depends on two things: (1) that the estimates of inbreeding depression and the estimates of heterosis are complementary, each measuring correctly the same genetic situation from a different stand-point; and (2) that the assumptions regarding the genetic relationships of the lines are equivalent in the different solutions. If the assumptions made were altered, but kept equivalent in the different solutions, then agreement would not necessarily be /
be impaired. If, as in the present case, agreement is obtained between solutions, then the conclusion is that the same genetic situation has been reflected by the inbreeding and by the crossing, but that the actual values obtained for the genetical constants may be incorrect to the extent that the values assumed for the parameters of genetic relationships are incorrect.

Unfortunately, in the present case, the values obtained for the genetical constants cannot be correct. In the first solution a gene frequency correlation greater than unity between the large (L) and small (S) lines is implied, and will remain greater so long as the inbreeding coefficients in these lines are taken as equal. In the second solution, all gene frequency correlations are greater than unity, and will remain greater so long as the gene frequency correlation between the large (L) and unselected (N) lines and that between the unselected (N) and small (S) lines are taken as equal. In order to bring the gene frequency correlations down to reasonable values, it is necessary to have the inbreeding coefficient for the large line greater than that for the small line. This would have the effect of increasing the upper limit of the range. The second solution, which contains the greatest number of inconsistent features, also gives /
gives the least value for the upper limit (143.9). The first solution, in which several inconsistencies appear, gives a slightly higher value for the upper limit (146.1). The least squares solution, which shows no inconsistent features when applied to the five equations used in the solution, gives the highest value for the upper limit (149.6), and also requires that the inbreeding coefficient for the large (L) line be 10% greater than recorded, and that for the small (S) line be 10% less than recorded.

If, now, the information from the cross of the two small lines (S x MS) is introduced, and used in conjunction with the genetical constants found by the least squares method, it can be shown that a negative value of the inbreeding coefficient for the crossbred population (−0.66%) is necessary to give agreement with the observed estimate of heterosis. The nature of the situation is similarly reflected in the inbreeding equation for the extreme line for small size (M3), which to be in agreement also requires a negative inbreeding coefficient (−0.42%) (See Fig. 15). If, however, the values of the genetical constants were altered so as to render positive the inbreeding coefficients for these populations at low levels of weight, those inconsistencies associated with a low upper limit would appear /
appear in connection with the observed estimates on populations at intermediate levels of weight. There is an even greater necessity for maintaining a high upper limit than that required by the intermediate lines. An upper limit, adequate for consistency at intermediate levels, is totally inadequate for the extreme lines for large size. Two large lines, one of which belonged to the same strain as the present extreme line for small size (12) were crossed by Falconer and King (1953), and the mean of the large selected line derived from the crossbred population has surpassed the upper limit given by the least squares solution for the intermediate lines.

The conclusion is that consistency cannot be achieved simultaneously at all levels for both additive and dominance terms. Had the experimental estimates and the parameter values used been randomly in error, then an approximately correct solution would have been given by the least squares method, with the deviations from expectation randomly distributed over the different lines, and the genetic situation would have been more or less as at present imagined. The deviations, however, as measured in terms of the inbreeding coefficient, are excessively negative in the small lines and change to positive in all the larger lines. The errors (Table 22, and Fig. 14) can be taken as systematic. It is this /
this systematic trend, representing a discrepant feature, which has made impossible a solution consistent at all levels.

The accuracy of the estimates of additive terms far exceeds that of the dominance terms, and reasons have already been given in the introduction for expecting the dominance terms to deviate from the simple hypothesis. The procedure therefore adopted is to find values of the genetical constants such that the systematic trend of the errors is reduced to the minimum compatible with consistency for additive terms over the whole range. Those systematic deviations still remaining, can then be taken as real as far as the hypothesis is concerned.

It was shown in the theory that the dominance term was dependent on the mean gene frequency and on the inbreeding coefficient for the line: \( D = 2 \bar{m} \bar{Q} (1 - F) \). If the decreasing trend of the inbreeding coefficient from high to low levels of mean six week weight that appears in all the solutions is to be removed, the observed dominance terms will have to be accounted for by increasing values of \( \bar{m} \bar{Q} \) as the levels of six week weight declines, and consequently by a high value of \( V_N \), the mean gene frequency of the unselected reference line. A high value of \( V_N \), however, forces the upper limit to a very low value. The dominance terms, then, demand a high value of \( V_N \) while the upper limit demands a low value of \( V_N \) or a greater range. But if \( V_N \) is maintained sufficiently high to satisfy the dominance terms, and the range is taken sufficiently great to satisfy the upper /
upper limit, then the lower limit becomes unreasonably small. The most consistent solution rests in narrow limits set by

1. the necessity for a low value of $F_N$ to ensure an adequate range and a satisfactory upper and lower limit, and

2. the necessity for a high value of $F_N$ to achieve agreement for the dominance terms. The situation is expressed in the relation:

$$F_N = \frac{A_N - \mu_{\text{min.}}}{\mu_{\text{max.}} - \mu_{\text{min.}}}.$$

The most consistent solution is given by answering this question: What is the greatest value of $F_N$ possible, along with the greatest value of $\mu_{\text{max.}}$ while $\mu_{\text{min.}}$ is kept within the limits of reasonableness? It is not a question that can be answered with any great accuracy, but the order of the answer is firmly fixed.

As it turns out, the actual values of the genetical constants do not affect the conclusion (Fig. 14). Within the limits set by the question, the systematic trend is not reduced to any extent, but only relatively altered at the high and low levels of mean six week weight. An adequate answer to the question, however, gives $F_N = 0.65$, $\mu_{\text{max.}} = 161.05$, and $\mu_{\text{min.}} = 60.65$, whence $\mu_0 = 110.85$, $\overline{a} = 50.20$, and $\overline{ad}(1 - F_{\text{no.}}) = 12.09$. The detailed consequences of these values of the genetical constants are given at the end of this section. The only obvious difference /
difference between this solution and the least squares solution is an increase in \( nr \). For these present values of the genetical constants, the deviations measured in terms of the inbreeding coefficient are given (Table 22), and are shown plotted against the additive terms (Fig. 14). The deviations for the small lines are less than for the least squares solution, but are still very pronounced. The deviations for the larger lines have somewhat increased, but are still not so pronounced as those for the small lines.

The nature of the systematic error is such that the observed estimates of both inbreeding depression and heterosis for the larger lines are less than expected, and the corresponding estimates for the smaller lines are much greater than expected. These discrepancies must be regarded as a definite feature of the solution, and possible explanations are considered in the next section.

DEDUCTIONS FROM THE VALUES OBTAINED FOR THE GENETICAL CONSTANTS

The mean six week weight of a fully inbred population with \( \gamma = \frac{1}{2} \) is \( \mu_0 = 110.85 \) logarithmic units (approx. 12.8 gm.). The half range, \( na_2 = 50.2 \), whence the upper limit for any population /
population is \( \mu_{N\infty} = 161.05 \) (approx. 40.8 gm.), and the lower limit for any population is \( \mu_{N\infty} = 60.65 \) (approx. 14.4 gm.). The dominance constant for the N-stock, \( \bar{a}(1 - F_{N\infty}) = 12.09 \), and if \( F_{N\infty} \) is taken as 0.25, the general dominance constant, \( \bar{a} = 16.12 \).

The mean six week weight for any population, \( X \), with an inbreeding coefficient \( F_{AN} \) referred to an origin in the foundation population of the N-stock, will be given by

\[
\mu_X = 110.85 + 50.2 (\bar{p}_X - \bar{p}_x) + 24.18 \bar{p}_X \bar{p}_x (1 - F_{AN}).
\]

The mean gene frequencies for the lines discussed are given as \( p_L \) (large selected control) = 0.751, \( p_N \) (unselected control) = 0.650, \( p_S \) (small selected control) = 0.506, and \( p_{MS} \) (MacArthur's small selected control) = 0.425.

The inbreeding coefficients necessary for exact agreement with observed inbreeding depression and heterosis have been given in Table 22. Again if \( F_{N\infty} \) is taken as 0.25, the gene frequency correlations required for exact agreement with observation are \( r_{LN} = 0.88 \), \( r_{LS} = 0.69 \), and \( r_{NS} = 0.81 \); \( r_{S,MS} \) is imaginary.

The additive genetic variance on the logarithmic scale is expected to be twice as great in the small selected as in the large selected line, since \( D_L : D_S :: 1 : 2 \).

Using
Using the recorded values of \( F_{LN} = 0.3 = F_{SN} \), one expects \( D_L = 3.16 \) (c.f. 2.30 ± 1.08), and \( D_S = 4.23 \) (c.f. 4.72 ± 1.75). For these expected values of \( D_L, D_S \), the heterosis in the N-stock crosses is given by:

\[
2H_{LN} = 20.29 \left(1 - \frac{F_{LN}}{F_{LN} + F_{LN}}\right) - 14.32
\]

\[
2H_{LS} = 22.68 \left(1 - \frac{F_{LN} + F_{SN}}{F_{LN} + F_{SN} + F_{SN}}\right) - 14.48
\]

\[
2H_{NS} = 23.65 \left(1 - \frac{F_{SN}}{F_{SN} + F_{SN}}\right) - 19.46
\]

Maximum, minimum, and probable values can be given to the inbreeding coefficients if the recorded values of \( F_{LN} \), \( F_{SN} \), and \( F_{NO} \) are used in the relation given on page 60, connecting the inbreeding coefficients in parent and offspring. Substituting values thereby obtained in the three equations given above, one gets approximate limits and expected values for the heterosis, which are shown in Table 23.

The value of \( F_{MS,0} \) is not fully recorded, but by tracing the line back to its origin a value of not less than 0.57 was obtained. \( D_{MS} = 5.91 \left(1 - F_{MS,0}\right) \), so that the expected value will be 3.42, slightly less perhaps, and this value is to be compared with the observed value of 7.47 ± 1.62.

The expected value of the heterosis in the cross of /
of the two small lines is

\[ 2H_{5,15} = 24.07 \left( 1 - \frac{1}{15 + 15} \right) - 15.30 \]
giving a maximum of 4.20, provided the lines are not negatively correlated, a minimum of 0.38, and a probable of 4.08, to be compared with the observed values of 5.95 ± 0.52 in the F₁ - generation and 4.93 ± 0.80 in the F₂ - generation of the cross.
The hypothesis of dominance has proved adequate to only a limited extent in accounting for the changes in the mean six week weight on inbreeding and crossing lines of widely differing mean. It has been shown in the previous section that the observed estimates of inbreeding depression and heterosis were somewhat less than expected for the lines at a higher level of mean six week weight, and were considerably greater than expected for lines at low levels of mean six week weight. Several possible explanations of these systematic deviations, some of which have already been mentioned in the introduction, are now considered.

(i) The deviations may be errors of estimation.

(ii) The logarithmic scale may be inadequate.

(iii) The assumption of no correlation between gene frequencies and gene effects may be invalidated by the effects of selection.

(iv) The degree of dominance of genes may have been changed by selection.

(v) There may be natural selection for heterozygosity in the small lines.

(vi) Maternal hybrid vigour and maternal inbreeding depression may have little effect on the offspring of the larger lines where maternal performance is already high, but may make considerable difference to the sometimes very poor mothering qualities in the smaller lines.

Can it be decided which of these causes, if any, is in operation?
(i) In the one case where equivalent estimates from two different sources were obtained, the agreement was good (page 76). The solutions in the previous section also indicate that there is good agreement between the estimates of inbreeding depression and the estimates of heterosis for corresponding lines. Although it is difficult to attach standard errors directly to the deviations measured in terms of the inbreeding coefficient, substitution of the estimates of inbreeding depression and heterosis with twice their standard error added or removed, indicate that all but two of the deviations (MS and S x MS) can individually be attributed to chance (See Fig. 15). The probability, however, of random errors showing the observed systematic trend is very small indeed ($P = .008$), and this explanation can be discarded.

(ii) The scale must certainly be brought into question. One might imagine that a contraction of the lower part of the logarithmic scale and an expansion of the higher part would remove the overestimation for the large lines and the underestimation for the small lines. The values of the inbreeding depression would indeed be altered in the desired manner, but the heterosis in the N-stock crosses would tend to be removed. In fact, the change suggested tends to return the data to the arithmetic scale which was shown to be quite inadequate. The nature of the difficulty has already been
been expressed (page 85), and any contraction of the lower part of the logarithmic scale to improve the values of the inbreeding depression would have the effect of reducing the mean gene frequency in the unselected reference line, which merely reintroduces the feature one is trying to remove. An expansion of the upper part of the scale has the same effect. It is thus far from obvious that the logarithmic scale is at fault. Two further transformations of data have been carried out, one in the growth curve form and the other in the arcsinh form, but neither brought about the desired improvement; and the conclusion seems to be that the choice of a superior scale, if such exists, is a matter of extreme delicacy. The form of the transformation must first be decided on theoretical considerations, and thereafter some means evolved for determining the constants of transformation. The only really satisfactory means would be to determine the constants by substituting in all the observational equations, so as to obtain the agreement desired; but, apart from being excessively laborious, this procedure would require considerable justification. Since no scale was found to be superior to the logarithmic, and since the logarithmic scale has many theoretical justifications which have been given earlier,
earlier, and since the overall results on this scale are not
unsatisfactory, it may be that the logarithmic scale is
adequate, and that the feature under discussion is one
superimposed on the multiplicative effects of the genes, with
a ready explanation in one of the other possibilities listed.

(iii) Inequality of gene effects can apply either to the
additive gene effect, \( a_r \), or to the degree of dominance, \( d_r \).
Correlation between the gene frequencies and either or both of
these gene effects may be set up by different rates of change
of gene frequency due to selection. In the notation
previously used the additive term in the expression for the
phenotypic mean is given by

\[
\sum_{r=1}^{n} a_r (p_r - \bar{q}_r) = n \bar{a} (p - \bar{q}) + n \text{cov} \{ a_r, (p - \bar{q}_r) \},
\]

and it has been assumed up till now that the covariance term
was zero. If the additive gene effects were unequal, it
would be those genes with the greater mean effect which would
have been selected first, whatever the direction of selection.
There would therefore be set up a positive correlation between
\( a_r \) and \( (p_r - \bar{q}_r) \) in lines selected for large size, and a
negative correlation in those lines selected for small size.
Experimental estimates of the additive term measure

\[
\sum_{r=1}^{n} a_r (p_r - \bar{q}_r),
\]

so that a somewhat smaller value than
that directly calculated should have been given to \( \bar{a}(p - \bar{q}) \)
in
in the case of large lines, and a somewhat greater value in the case of small lines. The mean gene frequency would therefore be overestimated in the larger lines, and underestimated in the smaller lines. This might account for the discrepancy in connection with the upper limit to the range mentioned in the previous section, but it was shown at the time that the systematic trend in the dominance term would not be reduced but only altered in origin by increasing the upper limit to the range.

The effect of correlations between gene effects and gene frequencies on the dominance term of the phenotypic mean is much more difficult to see. The dominance term estimated by inbreeding is

$$\sum_{r=1}^{n} 2a_r d_r (p_{x} - p_{y})^2$$

and the heterosis measures

$$\sum_{r=1}^{n} 2a_r d_r (p_{x} - p_{y})^2$$

Now

$$\sum_{r=1}^{n} 2a_r d_r p_{x} = 2 \bar{a}_d \bar{p}_{x} + 2 n \text{cov}(a_r d_r, p_{x})$$

and

$$\sum_{r=1}^{n} a_r d_r (p_{x} - p_{y})^2 = n \bar{a} \bar{d} (\bar{p}_{x} - \bar{p}_{y})^2 + n \text{cov}\{a_r d_r, (p_{x} - p_{y})^2\}$$

and in the theory, the covariance terms have been taken as zero, so that \(\bar{a}_d \bar{p}_{x}\) and \(\bar{a} \bar{d} (\bar{p}_{x} - \bar{p}_{y})^2\) represent the expected values. The case of unequal additive effects, \(a_{x}\), and unequal degrees of dominance, \(d_{x}\), must be considered separately. Suppose first that the degrees of dominance are equal,
equal, or at least distributed over the additive effects. In lines selected in either direction the genes with greater additive effects are expected to be at more extreme frequencies than those with the same degree of dominance but with smaller additive effects. The value of \( p_rq_r \) would therefore be relatively less for those genes with the greater additive effects. This would imply (1) a negative correlation between \( a_r \) and \( p_rq_r \), in both the large selected line and the small selected line; (2) no correlation between \( a_r \) and \( (p_{xr} - p_{yr})^2 \) provided the lines X and Y were both selected in the same direction; and (3) a positive correlation between \( a_r \) and \( (p_{xr} - p_{yr})^2 \) for lines selected in opposite directions.

Therefore (1) the inbreeding depression would be less than expected for both large and small selected lines; (2) the heterosis on crossing lines at the same phenotypic level would not differ from the expected value; and (3) the heterosis on crossing lines selected in opposite directions would be greater than expected. This certainly does not agree with the present experimental observations, and in the case of (3) is quite the reverse of the situation observed in experiments by several others. Johansson and Venge (1953), and Pease (1928) have published results showing negative heterosis in such crosses.

The /
The case of unequal degrees of dominance is now considered, assuming that the additive effects are equal. The dominance term \( \sum \frac{1}{2} 2a_x d_x p_rq_r \), can be split into two components, one in which the values of \( d_x \) are positive, \( D(+) \), and one in which the values of \( d_x \) are negative, \( D(-) \). In an initial population with the degrees of dominance symmetrically distributed about a zero mean, \( D(+) = D(-) \), and inbreeding will produce no change in the mean phenotypic value. Under selection, both \( D(+) \) and \( D(-) \) change in value, but if selection is for large size, \( D(+) \) will be greater than \( D(-) \) to the extent of differential selection for dominants (see page 6), so that \( D(+) + D(-) > 0 \), and inbreeding will cause depression of the phenotypic mean. If selection is for small size, the reverse will be true, namely \( D(+) + D(-) < 0 \), so that inbreeding will increase the phenotypic mean. If the dominance in the unselected population is directionally distributed, these effects would be superimposed on the major trend. In terms of correlations, selection for large size would set up a positive correlation between \( d_x \) and \( p_rq_r \), and selection for small size a negative correlation, so that the inbreeding depression would be greater than otherwise expected for large selected lines, and less for small selected lines.

Correlations /
Correlations between $d_x$ and $(p_{xx} - p_{yy})^2$ would be very small if not zero, so that heterosis will not in general be affected by differential selection for dominants. A slightly less than expected value of the heterosis would result from the cross between an unselected line and a line selected therefrom in either direction, provided the value of the mean gene frequency in the unselected line was about one half.

Such deviations from expectation are again quite unlike the observed deviations, and are the exact reverse in the case of inbreeding depression.

An explanation of the present observed deviations in terms of differential selection on unequal gene effects would require negative correlations between $a_xd_x$ and $pq_{x}$ and also between $a_xd_x$ and $(p_{xx} - p_{yy})^2$ for large selected lines, and equivalent negative correlations for the small selected lines. There is no evidence whatsoever for such a situation.

One might imagine that overdominance ought to be more fully considered, but this is unnecessary since there is no restriction placed on the value of $d$, which may well be numerically greater than one. If there were any overdominant genes, those with $d > 1$ would be maintained heterozygous in large selected lines, and those with $d < -1$ fixed in the recessive phase. Inbreeding would thus be expected to cause a marked depression in the phenotypic mean of large selected lines. Similarly inbreeding would have an almost beneficial effect on small selected lines. Thus overdominance is merely a particular case of the general conclusion reached above.
(iv) The question of selection causing changes in the actual degree of dominance was discussed in the introduction to this thesis, where arguments advanced by Fisher (1930a) and Mather (1943a) in accordance with the Theory of Evolution of Dominance were given. The conclusions were that as the frequency of an allele was increased by selection, the degree of dominance of that allele was increased also; that therefore a cross between two lines both selected in the same direction would show heterosis in the direction of selection; and that the inbreeding of a selected line would cause its phenotypic mean to approach the mean of the initial unselected population. This is again exactly the reverse of the present observed situation, where the inbreeding depression in the small selected lines was very marked; where the heterosis on crossing two small selected lines was considerable; and where inbreeding depression in the large selected line was comparatively small. If, then, the genes have a variety of different degrees of dominance, both positive and negative, there seems to be no present support, but, if anything, rather contradiction of the conclusions drawn therefrom by Fisher and Mather.

(v) The highly detrimental effect of inbreeding on the small lines, and the consequent strong natural selection for fertility and survivability which was unquestionably in operation, might together seem to point to the small lines having been resisting an increase in inbreeding coefficient, thereby accounting for their excess inbreeding depression. No amount /
amount of heterozygosity, however, can give the negative inbreeding coefficients required for agreement with expectation, and, further, such heterozygosity in both small lines would imply that the heterosis in their cross would be much less than expected, which is not the case. The conclusion therefore is that the natural selection was operating in the usual way against deleterious genes. (vi) It might be thought that the mothering qualities, which are themselves genetically controlled and which differ in the various lines as a result of correlated response to selection for 6 week weight, would only serve to reinforce the expected deviations in 6 week weight due to differential selection for dominants or to changes in the degrees of dominance, but the reinforcing effect would be slight and of little importance compared with those main 1st order changes in 6 week weight caused by maternal effects if those 1st order changes were not proportional to the changes in 6 week weight caused by direct genetic control.

If weights prior to 6 weeks, taken before, at, and after weaning, are used as an indication of the maternal effect (and the fact that these earlier weights scarcely changed till the 2nd inbred generation and showed only half as much heterosis in the F_1 of the small cross as in the F_2 suggest that they can be), then evidence provided in the section on observed results (especially Table 9 (2) ) indicates that in the larger lines a much smaller proportion of the inbreeding depression/
depression and heterosis in mean 6 week weight is due to maternal effect than in the smaller lines, where the maternal effect is relatively important.

An explanation of the deviations of the observed estimates of inbreeding depression and heterosis in 6 week weight from their expected values can therefore be taken as due to the relative unproportionality of changes in 6 week weight caused by maternal effect as compared to the direct genetic effect.

Such unproportionality, in turn, yields to two possible explanations. The first is that the maternal effect on 6 week weight changes much more rapidly with change in mean gene frequency than does 6 week weight itself. The second is that the mean frequency, \( \bar{p} \), for genes controlling mothering qualities is much greater in the unselected line than the mean frequency for genes controlling 6 week weight, so that a smaller change in the mean frequency of genes controlling mothering qualities would give a relatively much greater change in \( \bar{p} \), \( \bar{q} \), and consequently a relatively greater amount of maternal inbreeding depression and heterosis in the smaller lines (see page 62).

Although both explanations are probably true to some extent, the second is favoured since, in the light of natural selection, the optimum for the character, 6 week weight, is probably intermediate, while the character, maternal qualities, almost certainly has a high optimum.

Summarily,
Summarily, the conclusions are:

(1) that the hypothesis of dominance for equal gene effects gives some but not full quantitative agreement with the observed changes in mean 6 week weight on crossing and inbreeding the present lines;

(2) that the observed estimates of inbreeding depression and heterosis deviate systematically from their expected values, the observed estimates being somewhat less than expected for the lines at a higher level of mean 6 week weight and considerably greater than expected for the lines at lower levels of mean 6 week weight;

(3) that a ready explanation of the systematic deviations can be found in terms of the maternal effect on 6 week weight; and

(4) - perhaps the main conclusion - that the expected differential changes in the genetic constitution of the various lines, caused by differential selection for genes dominant in the direction of selection or by the evolution of dominance in the direction of selection, are not found; in fact the calculated deviations of the observed dominance terms from their expected values not only disagreed with the deviations expected, but were in general opposed to them. Conversely, genetic changes caused by selection acting differentially on unequal gene effects or by selection changing the degree of dominance of genes cannot provide the explanation for the observed deviations, so that if such differential/
differential genetic changes have occurred they are certainly undetectable. It follows that correlations between gene frequencies and gene effects can, in this case at least, be neglected in the theoretical treatment of crossing and inbreeding. The absence of such correlations may further be taken as implying more or less equal excess of individual heterozygous effects over the corresponding mid-homozygous effects, or, even more generally, more or less equal mean gene effects and degrees of dominance.
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### TABLE 1

Mean six week weight in gm. for sexes combined in the Inbred Lines and their Control Lines.

<table>
<thead>
<tr>
<th>Line</th>
<th>0</th>
<th>GENERATION</th>
<th>Mean of Generations</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td></td>
<td>24.01</td>
<td>23.60</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>LC</td>
<td>25.46</td>
<td>24.25</td>
<td>23.67</td>
</tr>
<tr>
<td>LI</td>
<td>23.96</td>
<td>23.03</td>
<td>23.81</td>
</tr>
<tr>
<td>Depression</td>
<td>0.29 ± 0.36</td>
<td>0.64 ± 0.37</td>
<td>0.30 ± 0.27</td>
</tr>
<tr>
<td>NC</td>
<td>22.07</td>
<td>20.92</td>
<td>20.06</td>
</tr>
<tr>
<td>NI</td>
<td>21.06</td>
<td>19.32</td>
<td>19.09</td>
</tr>
<tr>
<td>Depression</td>
<td>-0.14 ± 0.19</td>
<td>0.74 ± 0.30</td>
<td>2.16 ± 0.27</td>
</tr>
<tr>
<td>SC</td>
<td>14.44</td>
<td>15.06</td>
<td>14.60</td>
</tr>
<tr>
<td>SI</td>
<td>14.99</td>
<td>13.74</td>
<td>13.50</td>
</tr>
<tr>
<td>Depression</td>
<td>0.07 ± 0.35</td>
<td>0.86 ± 0.31</td>
<td>0.62 ± 0.40</td>
</tr>
<tr>
<td>MSC</td>
<td>13.05</td>
<td>12.71</td>
<td>13.10</td>
</tr>
<tr>
<td>MSI</td>
<td>12.54</td>
<td>12.23</td>
<td>11.37</td>
</tr>
<tr>
<td>Depression</td>
<td>0.17 ± 0.20</td>
<td>0.87 ± 0.32</td>
<td>1.15 ± 0.37</td>
</tr>
<tr>
<td>Mean Depression of lines</td>
<td>-</td>
<td>0.10 ± 0.14</td>
<td>0.78 ± 0.16</td>
</tr>
</tbody>
</table>

### PERCENTAGE DEPRESSION

<table>
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</thead>
<tbody>
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<td>2</td>
<td>3</td>
</tr>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>L</td>
<td>1.2</td>
<td>2.7</td>
</tr>
<tr>
<td>N</td>
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<td>3.7</td>
</tr>
<tr>
<td>S</td>
<td>0.5</td>
<td>5.9</td>
</tr>
<tr>
<td>MS</td>
<td>1.3</td>
<td>6.6</td>
</tr>
<tr>
<td>Mean of Lines</td>
<td>0.6</td>
<td>4.7</td>
</tr>
</tbody>
</table>
TABLE 2

Ratio of mean weight of females to that of males in a litter averaged over litters in the generation for Inbred Lines and their Control Lines

<table>
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<tr>
<th>Line</th>
<th>Generation</th>
<th>Mean of Generations</th>
</tr>
</thead>
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<tr>
<td>LC</td>
<td>.813</td>
<td>.858</td>
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<td>LI</td>
<td>.855</td>
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<tr>
<td>NC</td>
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<td>.853</td>
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<tr>
<td>NI</td>
<td>.842</td>
<td>.848</td>
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<tr>
<td>SC</td>
<td>.833</td>
<td>.846</td>
</tr>
<tr>
<td>SI</td>
<td>.853</td>
<td>.877</td>
</tr>
<tr>
<td>MSC</td>
<td>.887</td>
<td>.901</td>
</tr>
<tr>
<td>MSI</td>
<td>.846</td>
<td>.850</td>
</tr>
<tr>
<td>C</td>
<td>.842</td>
<td>.865</td>
</tr>
<tr>
<td>T</td>
<td>.849</td>
<td>.854</td>
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<tr>
<td>Line</td>
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<td>Mean of Generations</td>
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<td>------</td>
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</tr>
<tr>
<td></td>
<td>1 df.</td>
<td>2 df.</td>
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<td>LC</td>
<td>within litters</td>
<td>4.8</td>
</tr>
<tr>
<td></td>
<td>between litters</td>
<td>7.5</td>
</tr>
<tr>
<td>LI</td>
<td>within litters</td>
<td>4.8</td>
</tr>
<tr>
<td></td>
<td>between litters</td>
<td>10.5</td>
</tr>
<tr>
<td>NC</td>
<td>within litters</td>
<td>5.4</td>
</tr>
<tr>
<td></td>
<td>between litters</td>
<td>6.0</td>
</tr>
<tr>
<td>NI</td>
<td>within litters</td>
<td>6.3</td>
</tr>
<tr>
<td></td>
<td>between litters</td>
<td>4.5</td>
</tr>
<tr>
<td>SC</td>
<td>within litters</td>
<td>10.7</td>
</tr>
<tr>
<td></td>
<td>between litters</td>
<td>6.7</td>
</tr>
<tr>
<td>SI</td>
<td>within litters</td>
<td>7.7</td>
</tr>
<tr>
<td></td>
<td>between litters</td>
<td>8.3</td>
</tr>
<tr>
<td>MSC</td>
<td>within litters</td>
<td>9.2</td>
</tr>
<tr>
<td></td>
<td>between litters</td>
<td>4.5</td>
</tr>
<tr>
<td>MSI</td>
<td>within litters</td>
<td>10.9</td>
</tr>
<tr>
<td></td>
<td>between litters</td>
<td>2.2</td>
</tr>
</tbody>
</table>
# Table 4

Mean 4 week weight for sexes combined in the Inbred Lines and their Control Lines

<table>
<thead>
<tr>
<th>Line</th>
<th>Generation 1</th>
<th>Generation 2</th>
<th>Generation 3</th>
<th>Mean of Generations</th>
</tr>
</thead>
<tbody>
<tr>
<td>LC</td>
<td>16.46</td>
<td>15.91</td>
<td>16.94</td>
<td>16.44</td>
</tr>
<tr>
<td>LI</td>
<td>16.62</td>
<td>15.75</td>
<td>16.35</td>
<td>16.21</td>
</tr>
<tr>
<td>Depression</td>
<td>-0.16</td>
<td>0.16</td>
<td>0.59</td>
<td>0.20</td>
</tr>
<tr>
<td>NC</td>
<td>15.18</td>
<td>14.30</td>
<td>15.42</td>
<td>14.97</td>
</tr>
<tr>
<td>NI</td>
<td>15.22</td>
<td>13.63</td>
<td>13.63</td>
<td>14.16</td>
</tr>
<tr>
<td>Depression</td>
<td>-0.04</td>
<td>0.67</td>
<td>1.79</td>
<td>0.81</td>
</tr>
<tr>
<td>SC</td>
<td>10.47</td>
<td>9.84</td>
<td>8.92</td>
<td>9.74</td>
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<tr>
<td>SI</td>
<td>10.52</td>
<td>8.55</td>
<td>8.50</td>
<td>9.19</td>
</tr>
<tr>
<td>Depression</td>
<td>-0.05</td>
<td>1.29</td>
<td>0.42</td>
<td>0.55</td>
</tr>
<tr>
<td>MSC</td>
<td>9.70</td>
<td>10.11</td>
<td>9.25</td>
<td>9.78</td>
</tr>
<tr>
<td>MSI</td>
<td>9.38</td>
<td>8.96</td>
<td>7.18</td>
<td>8.50</td>
</tr>
<tr>
<td>Depression</td>
<td>0.32</td>
<td>1.15</td>
<td>2.07</td>
<td>1.18</td>
</tr>
</tbody>
</table>

**Percentage Depression**

<table>
<thead>
<tr>
<th>Line</th>
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<th>Generation 2</th>
<th>Generation 3</th>
<th>Mean of Generations</th>
</tr>
</thead>
<tbody>
<tr>
<td>L</td>
<td>-1.0</td>
<td>1.0</td>
<td>3.5</td>
<td>1.2</td>
</tr>
<tr>
<td>N</td>
<td>-0.3</td>
<td>4.7</td>
<td>11.6</td>
<td>5.3</td>
</tr>
<tr>
<td>S</td>
<td>-0.5</td>
<td>13.1</td>
<td>4.7</td>
<td>5.8</td>
</tr>
<tr>
<td>MS</td>
<td>3.3</td>
<td>11.4</td>
<td>22.4</td>
<td>12.4</td>
</tr>
<tr>
<td>Mean of Lines</td>
<td>0.4</td>
<td>7.6</td>
<td>10.6</td>
<td>6.2</td>
</tr>
<tr>
<td>Line</td>
<td>1</td>
<td>2</td>
<td>3</td>
<td>Mean of Generations</td>
</tr>
<tr>
<td>------</td>
<td>-------</td>
<td>-------</td>
<td>-------</td>
<td>---------------------</td>
</tr>
<tr>
<td>IC</td>
<td>10.36</td>
<td>9.45</td>
<td>10.07</td>
<td>9.96</td>
</tr>
<tr>
<td>LI</td>
<td>10.23</td>
<td>9.39</td>
<td>9.84</td>
<td>9.82</td>
</tr>
<tr>
<td>Depression</td>
<td>0.13</td>
<td>0.06</td>
<td>0.23</td>
<td>0.14</td>
</tr>
<tr>
<td>NC</td>
<td>10.19</td>
<td>8.70</td>
<td>9.61</td>
<td>9.50</td>
</tr>
<tr>
<td>NI</td>
<td>10.14</td>
<td>8.66</td>
<td>8.93</td>
<td>9.24</td>
</tr>
<tr>
<td>Depression</td>
<td>0.05</td>
<td>0.04</td>
<td>0.68</td>
<td>0.26</td>
</tr>
<tr>
<td>SC</td>
<td>7.71</td>
<td>7.33</td>
<td>6.68</td>
<td>7.24</td>
</tr>
<tr>
<td>SI</td>
<td>7.88</td>
<td>6.61</td>
<td>6.09</td>
<td>6.86</td>
</tr>
<tr>
<td>Depression</td>
<td>-0.17</td>
<td>0.72</td>
<td>0.59</td>
<td>0.38</td>
</tr>
<tr>
<td>MSC</td>
<td>6.85</td>
<td>7.05</td>
<td>6.53</td>
<td>6.81</td>
</tr>
<tr>
<td>MSI</td>
<td>6.64</td>
<td>6.32</td>
<td>5.49</td>
<td>6.15</td>
</tr>
<tr>
<td>Depression</td>
<td>0.21</td>
<td>0.73</td>
<td>1.04</td>
<td>0.66</td>
</tr>
</tbody>
</table>

**PERCENTAGE DEPRESSION**

<table>
<thead>
<tr>
<th>Line</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>Mean of Generations</th>
</tr>
</thead>
<tbody>
<tr>
<td>L</td>
<td>1.3</td>
<td>0.6</td>
<td>2.3</td>
<td>1.4</td>
</tr>
<tr>
<td>N</td>
<td>0.5</td>
<td>0.5</td>
<td>7.1</td>
<td>2.7</td>
</tr>
<tr>
<td>S</td>
<td>-2.2</td>
<td>9.8</td>
<td>8.8</td>
<td>5.5</td>
</tr>
<tr>
<td>MS</td>
<td>3.1</td>
<td>10.4</td>
<td>15.9</td>
<td>9.8</td>
</tr>
<tr>
<td>Mean of Lines</td>
<td>0.7</td>
<td>5.3</td>
<td>8.3</td>
<td>4.8</td>
</tr>
</tbody>
</table>
### TABLE 6

Mean 12 day weight of litters for the Inbred Lines and their Controls.

<table>
<thead>
<tr>
<th>Line</th>
<th>GENERATION</th>
<th>Mean of Generations</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>LC</td>
<td>7.35</td>
<td>6.81</td>
</tr>
<tr>
<td>LI</td>
<td>7.09</td>
<td>6.04</td>
</tr>
<tr>
<td>Depression</td>
<td>-0.28</td>
<td>0.18</td>
</tr>
<tr>
<td>NC</td>
<td>7.25</td>
<td>6.64</td>
</tr>
<tr>
<td>NI</td>
<td>6.46</td>
<td>5.55</td>
</tr>
<tr>
<td>Depression</td>
<td>0.18</td>
<td>-0.27</td>
</tr>
<tr>
<td>SC</td>
<td>5.12</td>
<td>5.69</td>
</tr>
<tr>
<td>SI</td>
<td>5.79</td>
<td>5.23</td>
</tr>
<tr>
<td>Depression</td>
<td>-0.10</td>
<td>0.23</td>
</tr>
<tr>
<td>MSC</td>
<td>5.27</td>
<td>5.15</td>
</tr>
<tr>
<td>MSI</td>
<td>5.15</td>
<td>5.09</td>
</tr>
<tr>
<td>Depression</td>
<td>0.12</td>
<td>0.06</td>
</tr>
</tbody>
</table>

#### PERCENTAGE DEPRESSION

<table>
<thead>
<tr>
<th>Line</th>
<th>GENERATION</th>
<th>Mean of Generations</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>L</td>
<td>-4.1</td>
<td>2.9</td>
</tr>
<tr>
<td>N</td>
<td>2.7</td>
<td>-5.1</td>
</tr>
<tr>
<td>S</td>
<td>-1.8</td>
<td>4.2</td>
</tr>
<tr>
<td>MS</td>
<td>2.3</td>
<td>1.2</td>
</tr>
<tr>
<td>Mean of Lines</td>
<td>-0.2</td>
<td>0.8</td>
</tr>
</tbody>
</table>
### Table 7
Fertility in the Inbred Lines and their Control Lines

<table>
<thead>
<tr>
<th>Line</th>
<th>Generation</th>
<th>Mean of Generations</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>LI</td>
<td>8.0</td>
<td>8.2</td>
</tr>
<tr>
<td>SLI</td>
<td>8.0</td>
<td>8.2</td>
</tr>
<tr>
<td>LC</td>
<td>7.3</td>
<td>7.5</td>
</tr>
<tr>
<td>SLN</td>
<td>7.3</td>
<td>7.5</td>
</tr>
<tr>
<td>SC</td>
<td>3.8</td>
<td>4.7</td>
</tr>
<tr>
<td>SL</td>
<td>4.0</td>
<td>5.5</td>
</tr>
<tr>
<td>SI</td>
<td>4.0</td>
<td>5.5</td>
</tr>
<tr>
<td>SC</td>
<td>5.5</td>
<td>5.8</td>
</tr>
<tr>
<td>SL</td>
<td>3.8</td>
<td>4.9</td>
</tr>
<tr>
<td>MS</td>
<td>5.5</td>
<td>5.8</td>
</tr>
<tr>
<td>SL</td>
<td>3.8</td>
<td>4.9</td>
</tr>
</tbody>
</table>

### Percentage Depression

<table>
<thead>
<tr>
<th>Line</th>
<th>Generation</th>
<th>Mean of Generations</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>L</td>
<td>-2.5</td>
<td>5.8</td>
</tr>
<tr>
<td>N</td>
<td>1.3</td>
<td>8.0</td>
</tr>
<tr>
<td>S</td>
<td>14.9</td>
<td>-10.0</td>
</tr>
<tr>
<td>MS</td>
<td>34.5</td>
<td>-6.5</td>
</tr>
<tr>
<td>Mean of Lines</td>
<td>12.1</td>
<td>1.3</td>
</tr>
</tbody>
</table>
TABLE 8

Average Percentage of Survivors at six weeks per mating set up in the Inbred Lines and in their Control Lines.

<table>
<thead>
<tr>
<th>Line</th>
<th>0</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>Mean of Generations</th>
</tr>
</thead>
<tbody>
<tr>
<td>LC</td>
<td>96</td>
<td>100</td>
<td>95</td>
<td>100</td>
<td>98</td>
</tr>
<tr>
<td>LI</td>
<td>90</td>
<td>77</td>
<td>99</td>
<td>99</td>
<td>89</td>
</tr>
<tr>
<td>NC</td>
<td>100</td>
<td>100</td>
<td>99</td>
<td>99</td>
<td>99</td>
</tr>
<tr>
<td>NI</td>
<td>96</td>
<td>85</td>
<td>79</td>
<td>79</td>
<td>87</td>
</tr>
<tr>
<td>SC</td>
<td>71</td>
<td>90</td>
<td>84</td>
<td>74</td>
<td>83</td>
</tr>
<tr>
<td>SI</td>
<td>87</td>
<td>50</td>
<td>41</td>
<td>41</td>
<td>59</td>
</tr>
<tr>
<td>MSC</td>
<td>99</td>
<td>99</td>
<td>91</td>
<td>91</td>
<td>90</td>
</tr>
<tr>
<td>MSI</td>
<td>87</td>
<td>45</td>
<td>52</td>
<td>52</td>
<td>61</td>
</tr>
</tbody>
</table>

PERCENTAGE DEPRESSION

<table>
<thead>
<tr>
<th>Line</th>
<th>0</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>Mean of Generations</th>
</tr>
</thead>
<tbody>
<tr>
<td>L</td>
<td>10.0</td>
<td>19.0</td>
<td>1.0</td>
<td>10.0</td>
<td></td>
</tr>
<tr>
<td>N</td>
<td>4.0</td>
<td>14.1</td>
<td>20.2</td>
<td>12.8</td>
<td></td>
</tr>
<tr>
<td>S</td>
<td>3.3</td>
<td>40.5</td>
<td>44.6</td>
<td>29.5</td>
<td></td>
</tr>
<tr>
<td>MS</td>
<td>12.1</td>
<td>50.5</td>
<td>35.8</td>
<td>32.8</td>
<td></td>
</tr>
<tr>
<td>Mean of Lines</td>
<td>7.4</td>
<td>31.0</td>
<td>25.4</td>
<td>21.3</td>
<td></td>
</tr>
</tbody>
</table>
### TABLE 9

(1) Mean Weights of certain litter groups in the Small Inbred Line

<table>
<thead>
<tr>
<th>Group</th>
<th>Mean weight of litters in group at:</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>12 days</td>
</tr>
<tr>
<td>for 2 further generations for only one generation no further</td>
<td>6.67</td>
</tr>
<tr>
<td>for one further generation no further</td>
<td>6.08</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Group</th>
<th>Mean weight of litters in group at:</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>12 days</td>
</tr>
<tr>
<td>for 2 further generations for only one generation no further</td>
<td>5.10</td>
</tr>
<tr>
<td>for one further generation no further</td>
<td>5.50</td>
</tr>
</tbody>
</table>

(2) Relative percentage inbreeding depression for Weights prior to six weeks, and at six weeks.

<table>
<thead>
<tr>
<th>Line</th>
<th>PERCENTAGE INBREEDING DEPRESSION</th>
<th>Ratio of depression between 6 wks. to that at 6 wks.</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>12 days</td>
<td>3 weeks</td>
</tr>
<tr>
<td>L</td>
<td>0.5</td>
<td>1.4</td>
</tr>
<tr>
<td>N</td>
<td>1.2</td>
<td>2.7</td>
</tr>
<tr>
<td>S</td>
<td>3.2</td>
<td>5.5</td>
</tr>
<tr>
<td>MS</td>
<td>2.7</td>
<td>9.8</td>
</tr>
</tbody>
</table>
TABLE 10

Mean 6 week weight for sexes combined in the F₁ and F₂ of the N-stock Crosses and their Parental Control Populations

<table>
<thead>
<tr>
<th></th>
<th>F₁</th>
<th>F₂</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>L♀</td>
<td>N♀</td>
</tr>
<tr>
<td>Paternal Line</td>
<td></td>
<td></td>
</tr>
<tr>
<td>L♂</td>
<td>24.00</td>
<td>22.50</td>
</tr>
<tr>
<td>N♂</td>
<td>22.98</td>
<td>20.96</td>
</tr>
<tr>
<td>S♂</td>
<td>20.26</td>
<td>19.16</td>
</tr>
<tr>
<td></td>
<td>Paternal Line</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Maternal Line</td>
<td></td>
</tr>
<tr>
<td></td>
<td>L♀</td>
<td>N♀</td>
</tr>
<tr>
<td>L♂</td>
<td>24.00</td>
<td>22.50</td>
</tr>
<tr>
<td>N♂</td>
<td>22.98</td>
<td>20.96</td>
</tr>
<tr>
<td>S♂</td>
<td>20.26</td>
<td>19.16</td>
</tr>
<tr>
<td></td>
<td>Mothers</td>
<td></td>
</tr>
<tr>
<td></td>
<td>LN♀</td>
<td>NL♀</td>
</tr>
<tr>
<td>LN♂</td>
<td>21.46</td>
<td>23.51</td>
</tr>
<tr>
<td>NL♂</td>
<td>21.55</td>
<td>22.12</td>
</tr>
<tr>
<td>F₂ controls: LC = 24.80 NC = 20.07 SC = 14.12</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

The 1st capital indicates the maternal line

<table>
<thead>
<tr>
<th>CROSS</th>
<th>F₁</th>
<th>F₂</th>
</tr>
</thead>
<tbody>
<tr>
<td>L,N</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mid-parent</td>
<td>22.48</td>
<td>22.44</td>
</tr>
<tr>
<td>Crossbred</td>
<td>22.78</td>
<td>22.16</td>
</tr>
<tr>
<td>Heterosis</td>
<td>0.30 ± 0.16</td>
<td>-0.28 ± 0.18</td>
</tr>
<tr>
<td>L,S</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mid-parent</td>
<td>19.30</td>
<td>19.46</td>
</tr>
<tr>
<td>Crossbred</td>
<td>19.24</td>
<td>19.24</td>
</tr>
<tr>
<td>Heterosis</td>
<td>-0.06 ± 0.18</td>
<td>-0.22 ± 0.21</td>
</tr>
<tr>
<td>N,S</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mid-parent</td>
<td>17.78</td>
<td>17.10</td>
</tr>
<tr>
<td>Crossbred</td>
<td>17.77</td>
<td>17.02</td>
</tr>
<tr>
<td>Heterosis</td>
<td>-0.01 ± 0.20</td>
<td>-0.08 ± 0.19</td>
</tr>
</tbody>
</table>
TABLE 11

Ratio of mean weight of females to that of males in a litter averaged over the litters in the population for the Crossbred populations of the N-stock and their Parental Control populations

<table>
<thead>
<tr>
<th>Maternal Line</th>
<th>L♂</th>
<th>N♂</th>
<th>S♂</th>
</tr>
</thead>
<tbody>
<tr>
<td>L♂</td>
<td>.840</td>
<td>.841</td>
<td>.809</td>
</tr>
<tr>
<td>N♂</td>
<td>.832</td>
<td>.847</td>
<td>.874</td>
</tr>
<tr>
<td>S♂</td>
<td>.862</td>
<td>.860</td>
<td>.836</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Paternal Line</th>
<th>N♂</th>
<th>S♂</th>
</tr>
</thead>
<tbody>
<tr>
<td>N♂</td>
<td>.832</td>
<td>.847</td>
</tr>
<tr>
<td>S♂</td>
<td>.862</td>
<td>.860</td>
</tr>
</tbody>
</table>

| F2 Controls: | LC = .825 | NC = .823 | SC = .841 |

<table>
<thead>
<tr>
<th>Cross</th>
<th>F1</th>
<th>F2</th>
</tr>
</thead>
<tbody>
<tr>
<td>L,N</td>
<td>Mid-parent</td>
<td>.844</td>
</tr>
<tr>
<td></td>
<td>Crossbred</td>
<td>.837</td>
</tr>
<tr>
<td>L,S</td>
<td>Mid-parent</td>
<td>.838</td>
</tr>
<tr>
<td></td>
<td>Crossbred</td>
<td>.836</td>
</tr>
<tr>
<td>N,S</td>
<td>Mid-parent</td>
<td>.842</td>
</tr>
<tr>
<td></td>
<td>Crossbred</td>
<td>.867</td>
</tr>
</tbody>
</table>
### TABLE 12

Variances at 6 weeks for sexes combined, averaged over 1st, 2nd, and 3rd litters, for the F₁ and the F₂ of the N-stock Crosses and their Parental Control Populations

<table>
<thead>
<tr>
<th>Paternal Line</th>
<th>Maternal Line</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>L♂</td>
<td>d.f</td>
<td>N♂</td>
</tr>
<tr>
<td>L♂</td>
<td>2.451</td>
<td>124</td>
<td>3.805</td>
</tr>
<tr>
<td>N♂</td>
<td>3.124</td>
<td>125</td>
<td>3.754</td>
</tr>
<tr>
<td>S♂</td>
<td>3.128</td>
<td>132</td>
<td>3.854</td>
</tr>
</tbody>
</table>

Mean Variance for Crossbred Populations = 3.283
Mean Variance for Parental Control Populations = 3.436

---

#### F₂

<table>
<thead>
<tr>
<th>Cross</th>
<th>Variance</th>
<th>d.f.</th>
<th>Parental Control Population</th>
<th>Variance</th>
<th>d.f.</th>
</tr>
</thead>
<tbody>
<tr>
<td>L,N</td>
<td>2.993</td>
<td>250</td>
<td>LG</td>
<td>3.386</td>
<td>81</td>
</tr>
<tr>
<td>L,S</td>
<td>5.291</td>
<td>214</td>
<td>NC</td>
<td>3.832</td>
<td>95</td>
</tr>
<tr>
<td>N,S</td>
<td>3.383</td>
<td>202</td>
<td>SC</td>
<td>2.349</td>
<td>65</td>
</tr>
</tbody>
</table>

* The component between mothers from reciprocal crosses has been removed.

Mean Variance for Crossbred Populations = 3.889
Mean Variance for Parental Control Populations = 3.189
TABLE 13

Mean 4 week weight for sexes combined in the F<sub>1</sub> and F<sub>2</sub> of the N-stock Crosses and their Parental Control Populations

<table>
<thead>
<tr>
<th>F&lt;sub&gt;1&lt;/sub&gt;</th>
<th>Maternal Line</th>
</tr>
</thead>
<tbody>
<tr>
<td>Paternal Line</td>
<td>L&lt;sup&gt;♂&lt;/sup&gt;</td>
</tr>
<tr>
<td>L&lt;sup&gt;♀&lt;/sup&gt;</td>
<td>16.14 (127)</td>
</tr>
<tr>
<td>N&lt;sup&gt;♀&lt;/sup&gt;</td>
<td>15.97 (128)</td>
</tr>
<tr>
<td>S&lt;sup&gt;♀&lt;/sup&gt;</td>
<td>13.98 (135)</td>
</tr>
</tbody>
</table>

The number of mice entering the mean are given in brackets.

<table>
<thead>
<tr>
<th>F&lt;sub&gt;2&lt;/sub&gt; Cross</th>
<th>Mean</th>
<th>Parental Control Population</th>
</tr>
</thead>
<tbody>
<tr>
<td>L&lt;sup&gt;♀&lt;/sup&gt;N&lt;sup&gt;♂&lt;/sup&gt;</td>
<td>15.16 (256)</td>
<td>LC</td>
</tr>
<tr>
<td>L&lt;sup&gt;♀&lt;/sup&gt;S&lt;sup&gt;♂&lt;/sup&gt;</td>
<td>12.70 (220)</td>
<td>NC</td>
</tr>
<tr>
<td>N&lt;sup&gt;♀&lt;/sup&gt;S&lt;sup&gt;♂&lt;/sup&gt;</td>
<td>11.30 (208)</td>
<td>SC</td>
</tr>
</tbody>
</table>

Percentage Heterosis

<table>
<thead>
<tr>
<th>Cross</th>
<th>F&lt;sub&gt;1&lt;/sub&gt;</th>
<th>F&lt;sub&gt;2&lt;/sub&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td>L&lt;sup&gt;♀&lt;/sup&gt;N&lt;sup&gt;♂&lt;/sup&gt;</td>
<td>3.9</td>
<td>-0.6</td>
</tr>
<tr>
<td>L&lt;sup&gt;♀&lt;/sup&gt;S&lt;sup&gt;♂&lt;/sup&gt;</td>
<td>0.7</td>
<td>-1.4</td>
</tr>
<tr>
<td>N&lt;sup&gt;♀&lt;/sup&gt;S&lt;sup&gt;♂&lt;/sup&gt;</td>
<td>1.3</td>
<td>0.1</td>
</tr>
</tbody>
</table>
### TABLE 14

Mean 3 week weight for sexes combined in the F₁ and the F₂ of the N-stock Crosses and their Parental Control Populations

**F₁**

<table>
<thead>
<tr>
<th>Maternal Line</th>
<th>L♂</th>
<th>N♀</th>
<th>S♀</th>
</tr>
</thead>
<tbody>
<tr>
<td>L♂</td>
<td>9.70 (127)</td>
<td>9.84 (117)</td>
<td>7.98 (88)</td>
</tr>
<tr>
<td>Paternal Line</td>
<td>N♂</td>
<td>9.88 (128)</td>
<td>9.36 (128)</td>
</tr>
<tr>
<td>S♂</td>
<td>9.32 (135)</td>
<td>9.22 (107)</td>
<td>7.33 (77)</td>
</tr>
</tbody>
</table>

The number of mice entering the mean are given in brackets.

**F₂**

<table>
<thead>
<tr>
<th>Cross</th>
<th>Parental Control Populations</th>
<th>F₁</th>
<th>F₂</th>
</tr>
</thead>
<tbody>
<tr>
<td>L,N</td>
<td>LC</td>
<td>10.66 (78)</td>
<td></td>
</tr>
<tr>
<td>L,S</td>
<td>NC</td>
<td>8.59 (98)</td>
<td></td>
</tr>
<tr>
<td>N,S</td>
<td>SC</td>
<td>6.68 (68)</td>
<td></td>
</tr>
</tbody>
</table>

**Percentage Heterosis**

<table>
<thead>
<tr>
<th>Cross</th>
<th>F₁</th>
<th>F₂</th>
</tr>
</thead>
<tbody>
<tr>
<td>L,N</td>
<td>3.5</td>
<td>-2.2</td>
</tr>
<tr>
<td>L,S</td>
<td>1.6</td>
<td>-0.7</td>
</tr>
<tr>
<td>N,S</td>
<td>0.8</td>
<td>2.9</td>
</tr>
</tbody>
</table>
Mean 12 day weight of litters in the F₁ and the F₂ of the N-stock Crosses and their Parental Control Populations

<table>
<thead>
<tr>
<th>Maternal Line</th>
<th>L ♂</th>
<th>N ♂</th>
<th>S ♂</th>
<th>Paternal Mean</th>
</tr>
</thead>
<tbody>
<tr>
<td>L ♂</td>
<td>6.60 (17)</td>
<td>6.52 (17)</td>
<td>5.52 (16)</td>
<td>6.21</td>
</tr>
<tr>
<td>N ♂</td>
<td>6.91 (17)</td>
<td>6.29 (18)</td>
<td>5.20 (17)</td>
<td>6.13</td>
</tr>
<tr>
<td>S ♂</td>
<td>6.73 (18)</td>
<td>6.68 (16)</td>
<td>5.47 (17)</td>
<td>6.29</td>
</tr>
<tr>
<td>Maternal Mean</td>
<td>6.75</td>
<td>6.50</td>
<td>5.40</td>
<td>6.21</td>
</tr>
</tbody>
</table>

The number of litters entering the mean are given in the brackets

<table>
<thead>
<tr>
<th>Cross</th>
<th>Parental Control Populations</th>
<th>F₁</th>
<th>F₂</th>
</tr>
</thead>
<tbody>
<tr>
<td>L,N</td>
<td>LC</td>
<td>4.2</td>
<td>-2.2</td>
</tr>
<tr>
<td>L,S</td>
<td>NC</td>
<td>1.7</td>
<td>2.0</td>
</tr>
<tr>
<td>N,S</td>
<td>SC</td>
<td>1.0</td>
<td>1.1</td>
</tr>
<tr>
<td>Mean of Crosses</td>
<td></td>
<td>2.3</td>
<td>0.3</td>
</tr>
</tbody>
</table>

Percentage Heterosis
Average Number of Survivors per mating set up in the F\textsubscript{1} and F\textsubscript{2} of the N-stock Crosses and their Parental Control Populations

<table>
<thead>
<tr>
<th>Parental Control Populations: LC = 77, NS = 92, SC = 74</th>
</tr>
</thead>
</table>

### F\textsubscript{1}

<table>
<thead>
<tr>
<th>Maternal Line</th>
<th>L\textsuperscript{♂}</th>
<th>N\textsuperscript{♀}</th>
<th>S\textsuperscript{♀}</th>
<th>Paternal Mean</th>
</tr>
</thead>
<tbody>
<tr>
<td>L\textsuperscript{♀}</td>
<td>90</td>
<td>89</td>
<td>87</td>
<td>89</td>
</tr>
<tr>
<td>N\textsuperscript{♀}</td>
<td>93</td>
<td>99</td>
<td>86</td>
<td>93</td>
</tr>
<tr>
<td>S\textsuperscript{♀}</td>
<td>100</td>
<td>89</td>
<td>84</td>
<td>91</td>
</tr>
<tr>
<td>Maternal Mean</td>
<td>94</td>
<td>92</td>
<td>86</td>
<td>91</td>
</tr>
</tbody>
</table>

### F\textsubscript{2}

<table>
<thead>
<tr>
<th>Mothers</th>
<th>L\textsuperscript{♀}</th>
<th>N\textsuperscript{♀}</th>
<th>L\textsuperscript{♂}</th>
<th>S\textsuperscript{♂}</th>
<th>Paternal Mean</th>
</tr>
</thead>
<tbody>
<tr>
<td>L\textsuperscript{♀}</td>
<td>100</td>
<td>100</td>
<td>L\textsuperscript{♂}</td>
<td>97</td>
<td>100</td>
</tr>
<tr>
<td>N\textsuperscript{♀}</td>
<td>100</td>
<td>100</td>
<td>S\textsuperscript{♂}</td>
<td>85</td>
<td>100</td>
</tr>
<tr>
<td>L\textsuperscript{♂}</td>
<td>98</td>
<td>99</td>
<td>NS\textsuperscript{♂}</td>
<td>84</td>
<td>94</td>
</tr>
<tr>
<td>S\textsuperscript{♂}</td>
<td>84</td>
<td>94</td>
<td>NS\textsuperscript{♀}</td>
<td>84</td>
<td>94</td>
</tr>
</tbody>
</table>

1st Capital indicates maternal line.

#### Percentage Heterosis

<table>
<thead>
<tr>
<th>Cross</th>
<th>F\textsubscript{1}</th>
<th>F\textsubscript{2}</th>
</tr>
</thead>
<tbody>
<tr>
<td>L,N</td>
<td>-3.7</td>
<td>18.3</td>
</tr>
<tr>
<td>L,S</td>
<td>7.5</td>
<td>26.5</td>
</tr>
<tr>
<td>N,S</td>
<td>-4.4</td>
<td>13.2</td>
</tr>
<tr>
<td>Mean</td>
<td>-0.2</td>
<td>19.3</td>
</tr>
</tbody>
</table>
TABLE 18

Differences in Weight for Reciprocal Crosses for the N-stock

<table>
<thead>
<tr>
<th>Cross</th>
<th>12 days</th>
<th>3 weeks</th>
<th>4 weeks</th>
<th>6 weeks</th>
</tr>
</thead>
<tbody>
<tr>
<td>L,N</td>
<td>0.39</td>
<td>0.04</td>
<td>0.06</td>
<td>0.48 ± 0.24</td>
</tr>
<tr>
<td>L,S</td>
<td>1.21</td>
<td>1.34</td>
<td>1.79</td>
<td>1.85 ± 0.25</td>
</tr>
<tr>
<td>N,S</td>
<td>1.48</td>
<td>1.62</td>
<td>2.70</td>
<td>2.78 ± 0.27</td>
</tr>
</tbody>
</table>

Weight Differences at 6 weeks*

<table>
<thead>
<tr>
<th>Cross</th>
<th>In F2's of the Reciprocal Crosses</th>
<th>In Reciprocal Crosses of the F1 Reciprocal Crosses</th>
</tr>
</thead>
<tbody>
<tr>
<td>L,N</td>
<td>-0.66 ± 0.30</td>
<td>-1.96 ± 0.30</td>
</tr>
<tr>
<td>L,S</td>
<td>-0.64 ± 0.44</td>
<td>+1.10 ± 0.41</td>
</tr>
<tr>
<td>N,S</td>
<td>+0.85 ± 0.36</td>
<td>+1.83 ± 0.38</td>
</tr>
</tbody>
</table>

* The cross with the smaller maternal line is subtracted from the cross with the greater maternal line.

Weight differences at 6 weeks due to maternal effects and sex effects in the F2's of the N-stock Crosses

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>LS♀</td>
<td>17.50</td>
<td>SL♂</td>
<td>20.84</td>
</tr>
<tr>
<td>SL♀</td>
<td>18.29</td>
<td></td>
<td>20.50</td>
</tr>
<tr>
<td>LS♂</td>
<td>17.50</td>
<td></td>
<td>20.84</td>
</tr>
<tr>
<td>SL♂</td>
<td>18.29</td>
<td></td>
<td>20.50</td>
</tr>
</tbody>
</table>

| NS♀     | 16.40           | SN♂   | 18.60           |
| SN♀     | 16.85           |        | 18.60           |

* = significant differences below 5% level
\(\pm\) = S.E. about .3 to 0.4
Mean Weight at 12, 21, 28, and 42 days after birth in the F₁ and the F₂ of the Cross of the two small Lines and in their Parental Control Populations

**F₁**

<table>
<thead>
<tr>
<th>Cross</th>
<th>6 wk. wt</th>
<th>4 wk. wt</th>
<th>3 wk. wt</th>
<th>12 day wt</th>
</tr>
</thead>
<tbody>
<tr>
<td>S X S</td>
<td>14.44</td>
<td>10.06</td>
<td>7.34</td>
<td>5.12</td>
</tr>
<tr>
<td>S X MS</td>
<td>15.45</td>
<td>10.36</td>
<td>7.50</td>
<td>4.79</td>
</tr>
<tr>
<td>MS X S</td>
<td>16.09</td>
<td>11.51</td>
<td>8.05</td>
<td>5.51</td>
</tr>
<tr>
<td>MS X MS</td>
<td>13.10</td>
<td>10.11</td>
<td>7.05</td>
<td>5.15</td>
</tr>
<tr>
<td>Heterosis</td>
<td>2.0 ± 0.17</td>
<td>0.85</td>
<td>0.58</td>
<td>0.02</td>
</tr>
</tbody>
</table>

**F₂**

<table>
<thead>
<tr>
<th>Population</th>
<th>6 wk. wt</th>
<th>4 wk. wt</th>
<th>3 wk. wt</th>
<th>12 day wt</th>
</tr>
</thead>
<tbody>
<tr>
<td>S - Parental Control</td>
<td>15.06</td>
<td>10.47</td>
<td>7.71</td>
<td>5.69</td>
</tr>
<tr>
<td>Crossbred S, MS</td>
<td>15.72</td>
<td>11.17</td>
<td>7.63</td>
<td>6.01</td>
</tr>
<tr>
<td>MS - Parental Control</td>
<td>12.52</td>
<td>9.25</td>
<td>6.53</td>
<td>5.18</td>
</tr>
<tr>
<td>Heterosis</td>
<td>1.93 ± 0.28</td>
<td>1.31</td>
<td>0.51</td>
<td>0.58</td>
</tr>
</tbody>
</table>
TABLE 20

Total Variance, and the components within and between litters for Weight in the F1 and the F2 of the Cross of the two Small Lines and in their Parental Control Populations

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>♀♀ ♂♂</td>
<td>2.28 (65)</td>
<td>2.14 (65)</td>
<td>0.80 (65)</td>
<td>3.80 (54)</td>
<td>2.54 (54)</td>
<td>1.23 (54)</td>
</tr>
<tr>
<td>S X S</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>S X MS</td>
<td>1.23 (40)</td>
<td>1.92 (40)</td>
<td>0.54 (40)</td>
<td>2.76 (59)</td>
<td>2.94 (59)</td>
<td>1.50 (59)</td>
</tr>
<tr>
<td>MS X S</td>
<td>0.92 (50)</td>
<td>1.08 (50)</td>
<td>0.36 (50)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>MS X MS</td>
<td>1.66 (42)</td>
<td>2.05 (42)</td>
<td>1.00 (42)</td>
<td>2.34 (51)</td>
<td>2.48 (51)</td>
<td>1.21 (51)</td>
</tr>
</tbody>
</table>

Probability of Variance of Crossbreds being intermediate

<table>
<thead>
<tr>
<th>Cross</th>
<th>F1</th>
<th>F2</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>0.005</td>
<td>0.050</td>
</tr>
</tbody>
</table>

The degrees of freedom are entered in brackets after the Variance.

Variance Within Litters for 6 wk. wt.

<table>
<thead>
<tr>
<th>Cross</th>
<th>F1</th>
<th>F2</th>
</tr>
</thead>
<tbody>
<tr>
<td>♀♀ ♂♂</td>
<td>1.03 (54)</td>
<td>2.64 (43)</td>
</tr>
<tr>
<td>S X S</td>
<td>0.63 (31)</td>
<td>1.70 (47)</td>
</tr>
<tr>
<td>S X MS</td>
<td>0.71 (41)</td>
<td></td>
</tr>
<tr>
<td>MS X S</td>
<td>1.20 (32)</td>
<td>1.32 (41)</td>
</tr>
</tbody>
</table>

Variance Between Litters for 6 wk. wt.

<table>
<thead>
<tr>
<th>Cross</th>
<th>F1</th>
<th>F2</th>
</tr>
</thead>
<tbody>
<tr>
<td>♀♀ ♂♂</td>
<td>1.36 (11)</td>
<td>1.28 (10)</td>
</tr>
<tr>
<td>S X S</td>
<td>0.70 (9)</td>
<td>1.14 (12)</td>
</tr>
<tr>
<td>S X MS</td>
<td>0.23 (9)</td>
<td></td>
</tr>
<tr>
<td>MS X S</td>
<td>0.50 (10)</td>
<td>1.11 (10)</td>
</tr>
</tbody>
</table>

Prob. of variance of crossbreds being intermediate

|                   | 0.025  | not. sig |
|                   |        |          |
TABLE 21

Ratio of Sex Weights at 6 weeks, Fertility, Average Number of Survivors per mating set up, and "Producing Speed" in the F₁ and the F₂ of the Cross of the two Small Lines and in their Parental Control Populations

Ratio of mean weight of females in a litter to that of males, averaged over the litters in the populations

<table>
<thead>
<tr>
<th>Cross</th>
<th>F₁</th>
<th>F₂</th>
</tr>
</thead>
<tbody>
<tr>
<td>♂♂ ♂♂</td>
<td>0.833</td>
<td>0.846</td>
</tr>
<tr>
<td>S X S</td>
<td>0.890</td>
<td>0.846</td>
</tr>
<tr>
<td>S X MS</td>
<td>0.840</td>
<td></td>
</tr>
<tr>
<td>MS X S</td>
<td>0.906</td>
<td>0.924</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Cross</th>
<th>Fertility</th>
<th>F₁</th>
<th>F₂</th>
<th>Producing Speed*</th>
</tr>
</thead>
<tbody>
<tr>
<td>♂♂ ♂♂</td>
<td>3.8</td>
<td>71</td>
<td>90</td>
<td>0.81</td>
</tr>
<tr>
<td>S X S</td>
<td>4.4</td>
<td>100</td>
<td>94</td>
<td>0.96</td>
</tr>
<tr>
<td>S X MS</td>
<td>6.3</td>
<td>88</td>
<td>81</td>
<td>0.84</td>
</tr>
<tr>
<td>MS X S</td>
<td>4.6</td>
<td>89</td>
<td>81</td>
<td>0.84</td>
</tr>
<tr>
<td>MS X MS</td>
<td>7.7%</td>
<td>17.5%</td>
<td>10.0%</td>
<td>7.9%</td>
</tr>
</tbody>
</table>

* See page
TABLE 22

The Logarithmic Additive Terms of the Mean 6 week weight of the Parental Lines and their Crossbred Populations and the corresponding Values of the Inbreeding Coefficients given by the Least Squares Solution and by the Most Consistent Solution for the Genetical Constants (See page )

<table>
<thead>
<tr>
<th>Logarithmic Additive Term</th>
<th>Recorded Values or Values deduced therefrom</th>
<th>Values required by Least Squares Solution</th>
<th>Deviation</th>
<th>Values required by most consistent solution</th>
<th>Deviation</th>
</tr>
</thead>
<tbody>
<tr>
<td>L)</td>
<td>136.06</td>
<td>40.5</td>
<td>+ 10.5</td>
<td>49.0</td>
<td>+19.0</td>
</tr>
<tr>
<td>X N)</td>
<td>130.99</td>
<td>14.7</td>
<td>+ 6.7</td>
<td>19.0</td>
<td>+11.0</td>
</tr>
<tr>
<td>X S)</td>
<td>123.76</td>
<td>27.5</td>
<td>+ 9.5</td>
<td>26.6</td>
<td>+ 9.0</td>
</tr>
<tr>
<td>X S)</td>
<td>118.68</td>
<td>9.5</td>
<td>+ 1.7</td>
<td>8.0</td>
<td>0</td>
</tr>
<tr>
<td>X S)</td>
<td>111.45</td>
<td>20.0</td>
<td>- 10.0</td>
<td>22.0</td>
<td>-8.0</td>
</tr>
<tr>
<td>X MS)</td>
<td>107.37</td>
<td>-65.5</td>
<td>- 68.0</td>
<td>-57.2</td>
<td>-59.7</td>
</tr>
<tr>
<td>S)</td>
<td>-3.29</td>
<td>-42.1</td>
<td>-84.1</td>
<td>-26.5</td>
<td>-68.5</td>
</tr>
</tbody>
</table>
### TABLE 23

(1) **Expected values for the Heterosis in the N-stock Crosses and the corresponding observed values on the Logarithmic Scale**

<table>
<thead>
<tr>
<th>Cross</th>
<th>Observed</th>
<th>Expected</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Probable</td>
</tr>
<tr>
<td>(L,N)</td>
<td>(0.66 \pm 0.31)</td>
<td>0.64</td>
</tr>
<tr>
<td>(L,S)</td>
<td>(1.16 \pm 0.39)</td>
<td>1.91</td>
</tr>
<tr>
<td>(N,S)</td>
<td>(0.58 \pm 0.47)</td>
<td>1.12</td>
</tr>
<tr>
<td>Mean of Crosses</td>
<td>(0.80 \pm 0.34)</td>
<td>1.22</td>
</tr>
<tr>
<td>(L,N)</td>
<td>(-0.31 \pm 0.34)</td>
<td>0.32</td>
</tr>
<tr>
<td>(L,S)</td>
<td>(0.94 \pm 0.47)</td>
<td>0.96</td>
</tr>
<tr>
<td>(N,S)</td>
<td>(0.42 \pm 0.48)</td>
<td>0.56</td>
</tr>
<tr>
<td>Mean of Crosses</td>
<td>(0.35 \pm 0.29)</td>
<td>0.61</td>
</tr>
</tbody>
</table>

(2) **Estimates of Heterosis in the Cross of the two Small Lines**

<table>
<thead>
<tr>
<th>Cross</th>
<th>Observed</th>
<th>Expected in (F_1)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>(\frac{F_1}{F_2})</td>
<td>Probable</td>
</tr>
<tr>
<td>(S, MS)</td>
<td>(5.93 \pm 0.52)</td>
<td>4.93 (\pm 0.80)</td>
</tr>
</tbody>
</table>

(3) **Best estimates of heterosis**

<table>
<thead>
<tr>
<th>Cross</th>
<th>(\frac{2}{5} \left(2H_{F_1} + H_{F_2}\right))</th>
</tr>
</thead>
<tbody>
<tr>
<td>(L,N)</td>
<td>(0.40 \pm 0.28)</td>
</tr>
<tr>
<td>(L,S)</td>
<td>(1.30 \pm 0.36)</td>
</tr>
<tr>
<td>(N,S)</td>
<td>(0.63 \pm 0.42)</td>
</tr>
<tr>
<td>(S, MS)</td>
<td>(6.72 \pm 0.53)</td>
</tr>
</tbody>
</table>
N-stock:
- $N_1 =$ original foundation population of the N-stock
- $N_2 =$ reconstituted ""
- $NF =$ line selected for large size
- $NS =$ line selected for small size
- $LC =$ large control line
- $L_1 =$ large inbred line
- $NC =$ unselected control line
- $NI =$ unselected inbred line
- $SC =$ small control line
- $SI =$ small inbred line

$L \times N =$ large $X$ unselected
$L \times S =$ large $X$ small
$S \times N =$ small $X$ unselected

MacArthur's stock:
- $MSC =$ small control line
- $MSI =$ small inbred line

$S \times MS =$ N-stock $X$ MacArthur's small
Fig. 1 Hourly weights of four mice (a, b, c, d) at 42 days (full lines) and 43 days (broken lines) after birth (See page 17).
Fig. 2 Frequency distribution of the ratio of mean female to mean male weight for 460 litters.  
(See page 21)
Fig. 3 Mean 6 week weights (full lines) for successive generations of the control lines (L, N, S, MS), with corresponding 12 day weights (broken lines) inset. (See page 30)
Fig. 4. Growth curves for several generations of the control lines (L, N, S, MS).

(See page 32)
Fig. 5a Mean 6 week weight for the four inbred (I) lines (full circles) and their control (d) lines (open circles).
(See page 33)
Fig. 5b Mean 6 week weights on the logarithmic scale for the four inbred (I) lines (full circles) and their control (C) lines (open circles) (See page 33)
Fig. 6 The ratio of female to male weight for the four inbred (I) lines (full circles) and their control (d) lines (open circles) (See page 33)
Fig. 7 Fertility in the four inbred (I) lines (full circles) and their control (d) lines (open circles). (See page 33)
Fig. 8 The average percentage of mice born alive per mating set up that survive to 6 weeks in the inbred (I) lines (full circles) and their control (o) lines (open circles) (See page 35)
Fig. 9 Percentage in breeding depression in weight averaged over all lines for successive weighings continuing through the first 3 inbred generations. (See page 36)
Fig. 10 Percentage inbreeding depression averaged over the 3 inbred generations for weight at 12, 21, 28, and 42 days in the large (L) line, in the unselected (N) line, in the small (S) line, and in MacArthur's small (MS) line. (See page 37)
Fig. 10 (a)(b)(c)(d) Percentage deviation (from control population) in weight at 12, 21, 28, and 42 days after birth for the 1st (full lines), 2nd (broken dotted lines), and 3rd (broken lines) inbred generations of the large (L) line (top left), of the unselected (N) line (top right), of the small (S) line (bottom left), and of MacArthur's small (MS) line (bottom right). (See page 37)
Fig. 11 Mean 6 week weight in the F1 and F2 of the N-stock crosses in relation to the parental and parental control populations on the arithmetic scale (left) and the logarithmic scale (right). (See page 38)
Fig. 12a. (bottom) Percentage heterosis in weight in the F₁ (full lines) and F₂ (broken lines) of the 3 N-stock crosses

b. (top) Percentage heterosis in weight for all N-stock crosses at successive weighings continuing through the F₁ and F₂.

(See page 41)
Fig. 13 Mean 6 week weight in the $F_1$ and $F_2$ of the cross of the two small lines in relation to the parental and parental control populations on the arithmetic scale (top) and the logarithmic scale (bottom) (See page 43)
Fig. 14. Deviations from recorded values of the inbreeding coefficient of values calculated from the "least squares" solution (broken line) and from the "most consistent" solution (full line). Deviations based on estimates of inbreeding depression are represented by open circles, those based on estimates of heterosis by full circles. (See pages 84, 86, 87)
Fig. 15 Dominance terms (experimentally determined as inbreeding depression or heterosis) plotted against the additive terms for 6 week weight (on the logarithmic scale) in parental and crossbred populations. The paraboles indicate the expected values of dominance terms (based on the genetical constants from the "most consistent" solution) for different values of the inbreeding coefficient of a line, X, referred to the foundation population of the N-stock, N, as origin of inbreeding. Alternatively, the inbreeding coefficient required to give the observed dominance term can be read off. Interpolation for the inbreeding coefficient is direct at any single value of the additive term. (See page 83)
ABSTRACT OF THESIS

Name of Candidate St. Clair Shearer Taylor

Degree M.A. Date June, 1950

Title of Thesis A Study of Directional Dominance in Quantitative Inheritance

with Special Reference to Size in the House Mouse

Crossing and inbreeding experiments were carried out with a variety of lines of house mouse, all but one of which had previously been selected for weight at 6 weeks after birth; and fairly accurate estimates of heterosis and inbreeding depression were obtained.

The hypothesis of dominance was developed in a theoretical form (involving mean gene effects, degrees of dominance, and gene frequencies) that would be suitable for assessing the extent of the quantitative agreement over the array of observed estimates. Inadequacy of agreement was anticipated from (i) possible differential changes, due to selection, in the frequency of dominant and recessive alleles in the various strains, and (ii) the possible alteration by selection of the degree of dominance of genes (in accordance with Fisher's Theory of Evolution of Dominance).

The direct experimental results were:

1. Significant inbreeding depression in mean 6 week weight occurred in all lines, with the depression much greater in the smaller lines than in the larger lines.
2. The mean 6 week weights on the arithmetic scale of both F₁ and F₂ of crosses with the N-stock (large X unselected, large X small, unselected X small) fell with exception accuracy on their mid-parental means.
3. The cross of two small lines showed considerable heterosis in almost every character. The variance of weights at 3, 4, and 6 weeks in the F₁, however, were all significantly less than the corresponding mean parental variances.
4. There were strong indications that changes in 6 week weight due to maternal effects are relatively much greater in the smaller lines.

The main conclusions are:

1. that the hypothesis of dominance gives some but not full quantitative agreement with the observed changes in mean 6 week weight on crossing and inbreeding;
2. that the observed estimates of inbreeding depression and heterosis deviate systematically from their expected values, the observed estimates being somewhat less than expected for the lines at a higher level of mean 6 week weight and considerably greater.
greater than expected for the lines at lower levels;

(3) that a ready explanation of the systematic deviations can be found in terms of the maternal effect on 6 week weight; and

(4) that the expected differential changes in the genetic constitution of the various lines, caused by differential selection for genes dominant in the direction of selection, or by the evolution of dominance in the direction of selection, are not found, being obscured, if they have occurred, by maternal effects.

It seems that the hypothesis of dominance will therefore be adequate either until maternal effects are understood and capable of quantitative evaluation or until similar experiments can be carried out with a long selected, non-maternally affected character.