1965

Genetic analysis of behavior traits in swine

Rolf George Beilharz
Iowa State University

Follow this and additional works at: https://lib.dr.iastate.edu/rtd

Part of the Agriculture Commons, and the Animal Sciences Commons

Recommended Citation
Beilharz, Rolf George, "Genetic analysis of behavior traits in swine " (1965). Retrospective Theses and Dissertations. 3903.
https://lib.dr.iastate.edu/rtd/3903

This Dissertation is brought to you for free and open access by the Iowa State University Capstones, Theses and Dissertations at Iowa State University Digital Repository. It has been accepted for inclusion in Retrospective Theses and Dissertations by an authorized administrator of Iowa State University Digital Repository. For more information, please contact digirep@iastate.edu.
GENETIC ANALYSIS OF BEHAVIOR TRAITS IN SWINE

by

Rolf George Beilharz

A Dissertation Submitted to the
Graduate Faculty in Partial Fulfillment of
The Requirements for the Degree of
DOCTOR OF PHILOSOPHY

Major Subject: Animal Breeding

Approved:

Signature was redacted for privacy.

In Charge of Major Work

Signature was redacted for privacy.

Head of Major Department

Signature was redacted for privacy.

Dean of Graduate College

Iowa State University
Of Science and Technology
Ames, Iowa

1965
# TABLE OF CONTENTS

<table>
<thead>
<tr>
<th>Section</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>INTRODUCTION</td>
<td>1</td>
</tr>
<tr>
<td>REVIEW OF LITERATURE</td>
<td>4</td>
</tr>
<tr>
<td>MATERIALS AND METHODS</td>
<td>14</td>
</tr>
<tr>
<td>STATISTICAL ANALYSIS</td>
<td>22</td>
</tr>
<tr>
<td>RESULTS</td>
<td>28</td>
</tr>
<tr>
<td>DISCUSSION OF RESULTS</td>
<td>40</td>
</tr>
<tr>
<td>SUMMARY</td>
<td>52</td>
</tr>
<tr>
<td>ACKNOWLEDGMENTS</td>
<td>54</td>
</tr>
<tr>
<td>REFERENCES</td>
<td>55</td>
</tr>
<tr>
<td>APPENDIX</td>
<td>59</td>
</tr>
</tbody>
</table>
INTRODUCTION

Much has been written about the behavior of animals including man. At times different groups have taken widely different approaches to the study of behavior. Different backgrounds and training of the workers involved have helped to keep some of these groups apart to the present day. Thus, for example, animal behavior is currently studied by two such distinct groups as psychologists who use animals mainly in studies of learning, and ethologists who study comparative behavior of wild species from taxonomic and evolutionary aspects.

Scott (1958), in his preface, sketches the history of the study of animal behavior. The stress placed on progressively improved adaptation by Darwin's theory of evolution stimulated scientific thought about behavior. Until after 1900, important biologists including T.H. Morgan, R. Pearl and H.S. Jennings were interested in behavior. Interest was distracted from this field by the rediscovery of Mendel's work. Pavlov's discovery of conditioned reflexes also occurred shortly after 1900. The latter heightened the preoccupation of psychologists with learning theory. Study of behavior as related to adaptation decreased. Schjelderup-Ebbe's (1922) description of social dominance in poultry, and
an understanding of the meaning of song and territory in birds shifted the emphasis in the problem of adaptation from individuals to groups of animals. Allee et al. (1949) greatly furthered the knowledge of animal sociology and steady progress in this field has continued to the present day. Lorenz, Tinbergen and others in Europe and Britain are studying instinctive behavior. One group of American biologists including Guhl, is working on social organization of wild and domestic species. Another group, including Scott, is studying behavior genetics.

K. Lashley and N. Tinbergen in introducing an English translation of European behavior studies (Schiller 1957) comment on the differences in approach still so obvious between the ethologists of Europe (Lorenz, Tinbergen, etc.) and American psychologists, as distinct from biologists. The ethologists are zoologists by training and they study the largely instinctive behavior patterns of wild animals. Psychologists interested in learning use caged animals and apparatus such as a maze in non-natural situations. Two reasons for the apparent lack of communication between these two groups are given. Animals suitable for caged conditions have behavior patterns modified from those present in the wild state, and
much of the European work has been published in German.

With such a diversity of attitudes in the field of animal behavior, it is not surprising that the role of heredity in behavior traits should have been controversial. The so-called nature-nurture controversy in relation to behavior traits was argued in black and white, presence or absence terms. The idea that heredity excluded environment, and vice versa, was also prevalent. This controversy has waned since the nineteen twenties but still papers appear (Hirsch 1962) in which concepts long accepted in genetics of quantitative traits are recommended to psychologists.

In the present work methods of quantitative genetics were used to study inheritance of two behavior traits of swine and their relation to production characters.
REVIEW OF LITERATURE

No attempt was made to review the complete field of behavior, or even of behavior genetics. Instead, pertinent work in which the contribution of hereditary variation to phenotypic variation in behavior traits of animals has been estimated, will be considered. The literature related to the traits studied in the present work must also be examined.

Most genetic studies of behavior traits in animals have been attempts to demonstrate merely that statistically significant strain differences existed or could be produced by selection. This is understandable from the vigor of the nature-nurture controversy among psychologists. The following quotation from Broadhurst (1960, p. 5) illustrates a psychologist's point of view.

"Psychological authorities are agreed that there are two main approaches to the study of the inherited determinants of behavior in animal subjects. The first is by selection and the second by the analysis of the characteristics displayed by different, preferably pure, strains."

The studies of behavior genetics in animals have been done mainly with mice, rats and Drosophila. There has been some work with dogs but little in other species. The genetic hypotheses underlying much of the work on
strain difference have been in terms of single or small numbers of Mendelian pairs. Such hypotheses have been verified for many traits including waltzing, shaking and susceptibility to seizures in mice (Grüneberg 1952), some personality traits in dogs (Scott 1958), mating behavior in Drosophila (Sturtevant 1915, Bastock 1956) and others. But in many traits a quantitative approach is more suitable. Fuller and Thompson (1960) have reviewed the work on behavior genetics fully and ably, and the reader may look there for more details of the vast amount of work on strain differences.

Broadhurst (1960) described a selection experiment and a diallel cross in rats. The traits considered were defecation and ambulation in the open field. They will be described more fully later, as they are related to the present work. In the selection experiment he used the method of Jinks and Jones (1958), assuming the selected lines homozygous, and obtained estimates of heritability of 0.95 for defecation and 0.80 for ambulation. In the diallel cross he used the method of the Birmingham group (Hayman 1960) on six purebred strains of rats to obtain heritability estimates of 0.62 for defecation and 0.89 for ambulation. These methods depend on rather restrictive assumptions (Hayman 1954) and seem inappropriate.
Hirsch and Erlenmeyer-Kimling (1962) studied geotaxis (response to gravity) in Drosophila by treating the response as a multifactorial trait and examining the effect of individual chromosomes in selected and unselected populations. They found that selection for positive and negative geotaxis produced changes in the effects of the individual chromosomes. This approach should eventually lead to estimates of the proportion of variance due to each chromosome. It seems to lead to a natural extension of the heritability concept.

Hirsch and Boudreau (1958) did a selection experiment with Drosophila for high and low phototaxis (response to light). The variance within strain \( \sigma^2 \) pooled over the 28th and 29th generations in both high and low strains was taken as an upper limit of the variance of an isogenic line (i.e. environmental variance). Heritability was calculated as \( h^2 = \frac{\sigma^2 - \sigma_o^2}{\sigma_o^2} \) where \( \sigma_o^2 \) was the variance of the unselected flies. The estimate of \( h^2 \) was 0.57. The authors considered it conservative as \( \sigma^2 \) may be greater than the true environmental variance, and it was supposedly free of dominance and epistasis. This is clearly not so, as variance due to dominance and epistasis, if present, must occur in \( \sigma_o^2 \) and would be absent from \( \sigma^2 \) if the selected lines were truly isogenic. The formula takes no account of the
possible difference in variance between isogenic and non-isogenic lines.

Komai, et al. (1959) studied social rank of pullets. As ranks have a uniform distribution, the distribution-free method which has been attributed to Schwartz and Wearden (1959) was used to estimate heritability as follows

\[ h^2 = \frac{(\text{Mean rank, daughters of high dams}) - (\text{Mean rank, high dams})}{2} - \frac{(\text{Mean rank, daughters of low dams}) - (\text{Mean rank, low dams})}{2} \]

Average heritability within strain was 0.30 and 0.34 for two different ways of treating social rank.

Guhl, et al. (1960) selected for increased and reduced aggressiveness in chickens. The trait was measured by percentage of flock dominated and by performance in paired encounters. They found a realized heritability (actual gain/selection differential) of 0.18 and 0.22 for the two measures, respectively.

Tindell and Craig (1960) studied the correlation between competition effects on production and mean social rank of sire groups. Competition effects were measured as the difference in performance of daughters of a sire group when mixed with hens of other sire groups.
and when unmixed. Submissive families were later matur-
ing and laid fewer eggs when in competition, but the
correlations were small and not statistically signif-
icant.

Siegel (1960) measured aggressiveness of poultry by
dividing his flocks in half and matching each bird from
one half with eight birds randomly chosen from the other
half. The arc sin of the proportion of wins was used as
the measure of aggressiveness. Realized heritability
from selection was 0.57.

In swine Willham, et al. (1963) studied variation
in avoidance of electric shock announced by a buzzer.
Such avoidance is an indication of learning. A hier-
archical analysis of variance of avoidance responses
in the third ten trials gave a heritability estimate
of 0.45 ± 0.12 and indicated that there was little var-
iation due to non-additive gene effects or to common en-
vironment.

The heritability estimates reported for behavior
traits are medium to high and one could predict at least
short term responses to selection for the traits inves-
tigated so far.

To be able to determine variance components of
traits, one needs large numbers of animals. Thus the be-
behavior traits studied must be defined so that they can readily
be measured on a large number of animals. The traits studied in the present work were "open field score" (OF) and "social dominance value" (DV).

"Open field score" is derived from work on rats and mice. The typical open field in laboratory animal studies consists of a flat enclosed area, either square or round, with uniform, solid walls, and with the floor marked off into smaller areas. This is generally a strange environment for the animal being tested. Usually a bright light, and sometimes noise, is present to increase the tension or anxiety produced by the strange environment. Defecation score is the number of boluses produced by the animal in the test time. Ambulatory activity is measured by the number of squares, or other defined areas, entered by the animal during the test.

Developed initially to study exploratory drive in rats, the open field was also used to record defecation. Since then it has been used with laboratory animals mainly to study defecation, but also ambulation. Psychologists have used at least the defecation score as an index of "emotionality" (Hall 1934; Broadhurst 1960, Tobach and Schneirla 1962). Denenberg and Morton (1962) concluded that both defecation and ambulation measured the same component of "emotionality" although others are
less certain. For example, Broadhurst (1960) mentions the concept "exploratory drive", as well as "emotionality", in relation to ambulatory activity.

The "open field score" for swine used in this study was a count of the number of squares marked on the floor over which a pig moved in two minutes when in an enclosed strange situation for the first time. This is analogous to the ambulatory behavior of laboratory animals. Although pigs defecate in the test situation they do not leave neat boluses and defecation would thus be hard to score.

For the present work "dominance value" was found from observations of social dominance between animals, in two ways. The details of the methods are described in the next chapter.

Methods in which social dominance has been evaluated in the past are of two main types, ranks and quantitative scores. Previous work seems to agree that the dominance/submission relationship between any two animals can usually be observed quite accurately. The relationship may be unidirectional, as when one animal always submits to another, once the relationship has been determined. Or both animals may submit at different times with one animal submitting more often than the other. The latter
situation has been called bidirectional dominance (Guhl 1962). Opinions differ as to what one does with many such observations on pairs of animals.

Most research on social dominance has been done with poultry. Guhl (1953) and Wood-Gush (1955) reviewed the poultry literature to that time. Both stated that in small flocks peck orders tend to be transitive (i.e. the dominant bird may peck all others, the second bird all but the top bird, and so on), while in large flocks this transitivity is rare, there occurring pecking circles such as $A \rightarrow B \rightarrow C \rightarrow A$. Such relations seem to hold in other species also.

The Kansas group of workers (Guhl 1953, 1964, Guhl et al. 1960, Komai et al. 1959) has used ranks to measure social order based on either the number of birds pecked in established flocks, or on the results of initial paired encounters of birds of the same sex across flocks.

The group in Queensland (McBride 1958) has developed a measure of aggressiveness in which individual birds are matched against a standard panel of birds and scored from 0 to 8 depending on the number of birds in the standard panel that they defeat. The measure of aggressiveness was taken as an indication of social dominance. For the special case of measuring social dominance in cages,
James and Foenander (1961) scored the birds from 0 to 3 depending on the numbers of neighbors they dominated in paired encounters. The scoring systems used by this group classified social dominance into several classes and may thus be called quantitative, although the underlying distribution is unspecified.

The work of Siegel (1960) has already been cited. He also used a measure of aggressiveness to indicate social dominance. The measure was the arc sin of the proportion of opponents that a bird defeated. The opponents were selected at random from the other half of a divided flock.

In cattle Schein and Fohrman (1955) used a transitive rank dominance order, subsequently normalized for statistical treatment. Guhl and Atkeson (1959), Kilgour and Scott (1959) and McPhee et al. (1964) also used rank orders. The latter seem to have had the most justification for doing so as their groups of cattle were small. The only work with cattle in which ranks were not used was that of Beilharz and Mylrea (1963), who used the arc sin of the fraction of the group that a cow dominated.

Rasmussen et al. (1962) found rank dominance orders in pens of seven gilts when feed was restricted. McBride et al. (1964) used dominance ranks, subsequently normal-
ized, for pigs. They pointed out that ranks, even if normalized arbitrarily, restrict differences between animals regardless of the true difference in social dominance between them.

Ranks can readily be normalized for correlating with production traits. One can also use rank correlations with suitable production data. Yet, the objection that ranks arbitrarily define differences between animals, is serious enough for us to look at methods that do not have this drawback. A little reflection reveals also that it is hard to accommodate dominance circles such as A → B → C → A into a rank order. Guhl (1953) and Wood-Gush (1955) indicate that such circles are common in larger flocks of poultry. Beilharz and Mylrea (1963) found many in their group of heifers, and the data of the present study also show many in litter groups of growing pigs.

The alternative to ranking has been to use the proportion of wins an animal had, either against panels of opponents or against its groupmates. This proportion tends to become a continuous variable if sufficient opponents are used. Even with large discontinuities, proportions seem to estimate the true differences in dominance between animals more correctly than ranks do. The arc sin of the proportion equalizes variance of errors
of estimation if the number of opponents is constant. It also gives the data a more normal distribution than the proportions have. Siegel's division of the flock into two halves seems unnecessary, one may just as well find dominance relationships of any bird with all members of its flock. Thus, of the measures of dominance discussed, the arc sin of the proportion of groupmates dominated appears the most suitable. This measure has been called raw dominance value in the present study.

Kaiser (1959) described a least squares solution for finding underlying values from observed differences between pairs of values. This suggests another method of estimating dominance from the observations of differences in dominance between animals. Values found in this way were called least squares dominance value in the present study. The details of this method are in the next chapter.
MATERIALS AND METHODS

The data were obtained from Iowa State University's swine irradiation project (A.E.C. contract number AT(11-1)-707) at Bilsland Memorial Farm near Madrid, Iowa. About 300 litters of Duroc and Hampshire pigs were produced in each of two farrowing seasons each year. The sires of the pigs were purchased from purebred breeders as pairs of full brothers born in the same litter. Sires were used for one season only. One out of each pair was subjected to scrotal X-irradiation of 300 r at approximately six months of age. The sires were not used for breeding until just over one year of age to ensure that the sperm used were exposed to radiation in the gonial stage (Willham and Cox 1961). The dams were raised from litters in the herd.

The animals used for open field test were pigs born in the second season of 1963 and the first season of 1964. The animals used for dominance value determinations were pigs born in the first season of 1964.

An attempt was made to use in the open field test only litters with at least two males and two females that had not been subjected to avoidance learning (Karas et al. 1962). Only females had been used for the latter.
The attempt was not completely successful and some litters with less than two pigs of either sex available were used. But no pig tested for OF had been tested for avoidance learning. The numbers used were 938 pigs from 240 litters in fall of 1963 and 915 pigs from 217 litters in spring of 1964.

The litters observed for dominance values were those already used in the open field test, that had a total of 5 or more pigs at the time of testing. Dominance was difficult to observe in small groups under our conditions. Two hundred and one litters with 1629 pigs were observed.

Determining the Open Field Score

Pigs were tested when from 48 to 52 days old, inclusive. The males had been castrated before they were 21 days old, and weaning occurred at 42 days of age. At weaning the sow was taken from the pen. Until they reached 154 days of age, the pigs remained as litter groups in the single pens eight feet by sixteen feet where they were born. They had not been isolated from littermates except briefly for routine weighings.

The open field, definitely a misnomer as it resembled a prison much more than a field, was a pen, ten feet square, with solid grey wooden walls four feet high. The
only unevenness in the walls resulted from two sliding doors used as entrance and exit. The concrete floor was marked off in units two feet square. A fluorescent white light about ten feet above the floor provided normal working light. The pen was inside an enclosed building. The observer watched the pigs from behind a Venetian glass screen.

The pig to be tested was picked up, usually by a hind leg, and placed inside the pen through the entrance door. Simultaneously a stop watch was started and the door shut. After ten seconds the number of squares into which it stepped with the right front foot in one minute and in two minutes was counted. The square where the animal was standing at the start of the count was included. The open field score (OF) is the count of squares stepped into in the relevant period and ranges from one to over 100 for two minutes.

Preliminary testing showed that pigs should never be left, either before or after the test, alone in a pen. A pig by itself, apparently becomes anxious. The OF probably measures something related to anxiety, expressed as movement, on the first occasion the pig is isolated from the litter in a strange situation. Obviously, if a pig is alone before the test, he is prematurely exposed to
something like the test situation. This may well affect his subsequent behavior. If an anxious pig is left isolated after the test, often he becomes highly vocal and disturbs the pig in the test pen.

In the fall of 1963 a sample of 47 pigs was subjected to the procedure of the open field test with another pig present in the pen. The scores obtained were compared with standard open field scores to obtain possible clues about what the open field test measures.

Determining the Dominance Value

Pigs between 90 and 130 days of age were used for dominance study. They were observed in litter groups in the pens in which they had been since birth. As young animals that grow up together tend to develop peaceful habits towards each other (Scott 1962), it was necessary to withhold feed temporarily to get observations of dominance relationships in a reasonably short time. Accordingly, the feeder openings were closed either overnight, for pigs observed before noon, or at 7 a.m. for pigs observed on the same afternoon. The feeders used were rectangular hoppers holding 600 pounds of pelleted feed normally available all the time. The
front of the feeders was four feet wide with four D shaped holes, each nearly one foot wide, giving access to the feed. The feeders stood near one side of the pen. They could be approached from the front and the two outside holes could also be reached from the side. Only one pig could eat from a hole at one time.

When the feeder cover was removed the pigs typically strove to get their heads into a hole to feed and to stay there until other pigs pushed them away. There was much pushing and any hole was rarely occupied by one pig for more than a few minutes. All four holes were opened for large litters. For litters of five or six pigs, one or two of the holes were left covered to ensure competition for the open holes.

Pigs were observed until the first signs that any one pig was no longer hungry. These usually came between 30 to 60 minutes after the cover was removed. Every occasion on which one pig took over a hole from another pig was recorded, provided this did not happen during a generalized movement, the result of several pigs pushing at once. In other words only reasonably clear take-overs involving just two pigs, were recorded. Successful defenses of a hole (biting and pushing by the pig already feeding) were also recorded. Both types of observation
were recorded on litter cards with winner and loser identified.

Each litter was observed twice, usually on successive days. Most of the work was done by two observers, each observing a litter once. An effort was made to note all possible comparisons at least once. At times the observer removed dominant pigs from the feeder to allow more observations to be made. If for any reason only a small proportion of the possible pairs had been recorded after two periods, the litter was observed for a third or even a fourth time. This happened in about 30 percent of the litters. All observations recorded during all periods were transferred to one litter card.

The observations were evaluated in two ways to give the variables raw dominance value (DV1) and least squares dominance value (DV2).

For DV1, relative dominance for the two pigs of any pair was given by the proportion of wins by each pig. These proportions could range from 0 to 1. For each pig the dominance it showed relative to all other pigs with which it was compared, was averaged. This average proportion is identical with the proportion of animals dominated, in a species where dominance is usually unidirectional. Raw DV was the arc sin, of the root of this aver-
age relative dominance. The reasons for using arc sin were given in the previous chapter. As most litters had pigs near the extremes of average relative dominance (0 or 1), the transformation seemed useful. Raw DV thus ranged from 0 to 90. The expectation of each litter mean was 45 as in these data the number of wins equaled the number of losses in each pair, and hence, in each litter.

Least squares DV (DV2) was obtained with Kaiser's (1959) method of solving for effects from observations of differences between pairs. Estimates of DV2 were obtained from least squares minimization of $d_{ij} - (DV2_i - DV2_j)$, where $d_{ij}$ is the observed difference in relative dominance between pigs $i$ and $j$. The $d_{ij}$ were calculated from the proportions of wins by each pig thus, $d_{ij} = \frac{p}{n} - \frac{n-p}{n} = -d_{ji}$, where $\frac{p}{n}$ was the proportion of wins by pig $i$ and $\frac{n-p}{n}$ was the proportion of wins by pig $j$. The denominator of the proportions ($n$) varied from 1 to 10 or more. Thus the $d_{ij}$ did not have equal variances. Any transformation of the proportions within pairs of animals, would be tedious without giving much practical benefit. DV2 had an expectation of 0 for each litter mean.

Both variables in which DV was expressed gave a pig's dominance status relative to its litter only. With litter means constant, there was no variation between whole
litters. This followed necessarily from the fact that pigs were raised as litter groups. Yet, the effect of social competition must be studied in the conditions of management that are present in any particular situation.
STATISTICAL ANALYSIS

The aim of analyzing the data was to find out as much as possible about the inheritance of both open field score and dominance value. For OF, heritability was obtained from the variance component due to sire. The effects of several factors, both genetic and environmental, on OF and on its variance, were examined. It was possible only to study the effect of sex and its interactions on DV. However, the effects of several genetic factors on variance of DV were examined. The correlations of the behavior traits with production traits were also studied.

OF was analyzed within subclasses which were the 16 combination of 2 seasons, 2 breeds, 2 irradiation treatments of sires and two sexes. Sex was included as a subclass factor to detect trends in variance due to sex chromosomes, if present. The model used to interpret OF within subclasses was \( y_{ijk} = u + s_i + d_{ij} + e_{ijk} \), where \( y_{ijk} \) was OF of a single pig,

- \( u \) was the mean of the subclass,
- \( s_i \) was the effect of the \( i \)th sire,
- \( d_{ij} \) was the effect of the \( j \)th dam mated to sire \( i \), pen being completely confounded with \( d_{ij} \).
$e_{ijk}$ was the effect peculiar to pig $ijk$.

The following assumptions were made:

\[
E(s_i) = E(d_{ij}) = E(e_{ijk}) = 0;
\]
\[
E(s_i^2) = \sigma^2_s, E(d_{ij}^2) = \sigma^2_d, E(e_{ijk}^2) = \sigma^2_e;
\]
\[
E(s_is'_i) = E(d_{ij}d_{ij'}) = E(e_{ijk}e_{ijk'}) = E(d_{ij}d_{ij'}) = 0;
\]
\[
E(s_id_{ij}) = E(s_i e_{ijk}) = E(d_{ij} e_{ijk}) = 0.
\]

In the above description, primes indicate $i \neq i'$, $j \neq j'$ and $k \neq k'$.

A hierarchical analysis of variance was used to estimate $\sigma^2_s$, $\sigma^2_d$ and $\sigma^2_e$. Trends in these variance components from subclass to subclass were examined (Table 1). As no evidence of non-homogeneity was found, it was assumed that these variances were constant over all subclasses. Hence the pooled variance components were used to estimate heritability from intraclass correlations.

Identical models were adopted for the six production traits, 1) average backfat at shoulder, back and loin, and 2-6) weights at birth, 21 days, 42 days, 98 days and 154 days of age, respectively. Both phenotypic and genetic correlations of OP with these production traits, were found from pooled variances and covariances within subclasses.
The subclass means of OF were also examined. The model used for this analysis was 

\[ y_{ijkl} = u + a_i + b_j + c_k + d_l + (ab)_{ij} + (ac)_{ik} + (ad)_{il} + (bc)_{jk} + (bd)_{jl} + (cd)_{kl} + e_{ijkl}, \]

where \( a_i \) is the effect of the \( i \)th season,
\( b_j \) is the effect of the \( j \)th sire treatment,
\( c_k \) is the effect of the \( k \)th breed,
\( d_l \) is the effect of the \( l \)th sex, the other terms, except \( e_{ijkl} \), are effects of interactions, and \( e_{ijkl} \) is the effect peculiar to the mean \( ijkl \). With the exception of the \( e \)'s, the effects were considered fixed and hence each was defined to sum to 0. For the interactions this summation to zero occurred for each factor at all levels of the other factor. The \( e \)'s were assumed to have \( E(e_{ijkl}) = 0, E(e_{ijkl}^2) = \sigma e^2 \) and covariances between non-identical \( e \)'s = 0. Interactions of second or third order were assumed to be absent. Thus \( \sigma e^2 \) was estimated with 5 degrees of freedom from the variances which would otherwise be attributed to these interactions.

One could have considered breed a random factor. This would change the tests for seasons, treatments and sex, if the interactions of breed with seasons, treatment and sex respectively, were real. Table 2 shows that these
interactions were negligible or absent. Thus the testing procedure, and the conclusions, were similar, whether breed was considered fixed or random.

DV data were obtained in one season only. The data were analysed within subclasses which were the 4 possible combinations of 2 sire treatments and 2 breeds. Analysis of variation between litters in DV was meaningless. Hence one could study only variation within litters. The possible sources of variation within litters were sex, interaction of sex and litter, and error. Interaction of sex and litter could be divided into the interactions of sex with sire, and sex with dam, within sire. Thus the model suitable for interpreting DV within subclasses was $y_{ijkl} = u + s_i + d_{ij} + m_k + (s\!m)_{ik} + (d\!m)_{ijk} + e_{ijkl}$, where $u$ was the mean of the subclass,

$s_i$ was the effect of the $i$th sire,

$d_{ij}$ was the effect of the $j$th dam mated to sire $i$,

$(s\!m)_{ik}$ was the effect of the interaction of sire $i$ with sex $k$,

$(d\!m)_{ijk}$ was the effect of the interaction of dam $ij$ with sex $k$,

$e_{ijkl}$ was the effect peculiar to pig $ijkl$, with $s_i$ and $d_{ij}$ having no genetic meaning in these data.
The following assumptions were made:

\[
E(s_i) = E(d_{ij}) = E(e_{ijk}) = 0;
E(s_i^2) = \sigma s^2, E(d_{ij}^2) = \sigma d^2, E(e_{ijk}^2) = \sigma e^2;
\]

All covariances within and between the effects \(s, d\) and \(e = 0\), except, of course, the variances already described;

\[
\sum_{k} N_{ik} m_{ik} = \sum_{k} N_{ik} (sm)_{ik} = \sum_{k} N_{ijk} (dm)_{ijk} = 0, \text{ for all } \ i \text{ and } i j, \text{ respectively, in the case of the interactions.}
\]

N indicates the number of individuals in the class indicated by the subscripts.

\[
E \left[ (lm)^2_{ak} \right] = \frac{1}{2} \sigma lm^2, E \left[ (lm)_{ak} (lm)_{ak'} \right] = 0,
E \left[ (lm)_{ak} (lm)_{ak'} \right] = -\frac{1}{2} \sigma lm^2, \text{ where } l \text{ stands for } s \text{ or } d \text{ and } a \text{ stands for } i \text{ or } ij.
\]

The data did not entirely fit this description. With respect to \(\sigma e^2\), Table 3 shows that variance within sex within litter in both DV variables decreased as litter size increased. It can also be shown that differences between groups of individuals in a litter, such as sex difference, depend on litter size. The statistical shortcomings of DV analysis will be discussed again later.

Fortunately, there was no association of litter size with subclass \(X^2 = 13.73 \text{ with } 18 \text{ degrees of freedom, } 0.7 < p < 0.8\). There were not enough litters per sire to test independence of litter size and sire in this
way. It was felt that errors introduced through variation in litter size were not systematic. Thus, although the results must be interpreted with caution, the model above was accepted as a reasonable attempt to describe DV in the available data.

The appendix shows the expectations of the various sums of squares that arise from this model, for unequal numbers, and for the case in which sexes are balanced in each litter. Clearly, with sexes balanced in each litter, one gets sums of squares which can readily be interpreted. Thus, to estimate $\sigma^{2}_{sm}, \sigma^{2}_{dm}$ and the effect of sex, the data were balanced by random elimination of DV values of pigs of one sex from most litters. The number of pigs available was reduced from 1629 to 1184. The process of balancing changed the means of many litters. Thus the analyses showed some variance between sires and between dams which had no genetic significance.

The correlations of DV and production traits were measured within litters. 1601 pigs having both DV and production information were available to compute these correlations.
RESULTS

Open Field

Pigs tested in pairs

For the sample of 47 pigs tested in pairs in the fall of 1963 the mean open field score for the total period (OFT) was 30.8±2.2. The mean OFT for their 64 littermates tested singly in the routine open field test was 49.0±3.2. Mean score for all pigs tested singly in the fall of 1963 was 46.3±0.7. Obviously, having two pigs in the pen greatly lowered the OF score.

Variance trends in subclasses

Table 1 shows variance components and mean squares within subclasses for total open field score (OFT). No marked consistent trend in the variance components was evident. Bartlett's test of homogeneity of the mean square for individuals gave $X^2$ with 15 degrees of freedom of 23.3. (0.05<p<0.1). For the mean squares between sires $X^2$ was 5.6 (0.98<p<0.99 if 15 degrees of freedom are used). Thus the factors constituting subclasses did not produce heterogeneity of variance within subclasses in total open field score. Mean squares between sires were too uniform for this to have been a chance result.
Table 1. Variance components and mean squares for total open field score within subclasses

<table>
<thead>
<tr>
<th>Subclass</th>
<th>Variance components</th>
<th>Mean squares</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Yr Tmt Br Sex</td>
<td>B. individuals B. dams B. sires</td>
</tr>
<tr>
<td>63 0 1 1</td>
<td>575 96 49</td>
<td>1230 (12)</td>
</tr>
<tr>
<td>63 0 1 2</td>
<td>355 55 80</td>
<td>975 (12)</td>
</tr>
<tr>
<td>63 0 2 1</td>
<td>541 54 24</td>
<td>950 (10)</td>
</tr>
<tr>
<td>63 0 2 2</td>
<td>328 100 67</td>
<td>1169 (10)</td>
</tr>
<tr>
<td>63 1 1 1</td>
<td>396 240 43</td>
<td>1444 (12)</td>
</tr>
<tr>
<td>63 1 1 2</td>
<td>620 41 60</td>
<td>1143 (12)</td>
</tr>
<tr>
<td>63 1 2 1</td>
<td>468 151 --</td>
<td>823 (13)</td>
</tr>
<tr>
<td>63 1 2 2</td>
<td>291 250 --</td>
<td>643 (13)</td>
</tr>
<tr>
<td>64 0 1 1</td>
<td>346 200 36</td>
<td>1173 (10)</td>
</tr>
<tr>
<td>64 0 1 2</td>
<td>534 168 --</td>
<td>959 (10)</td>
</tr>
<tr>
<td>64 0 2 1</td>
<td>429 112 8</td>
<td>773 (11)</td>
</tr>
<tr>
<td>64 0 2 2</td>
<td>398 233 --</td>
<td>716 (11)</td>
</tr>
<tr>
<td>64 1 1 1</td>
<td>457 106 31</td>
<td>1065 (10)</td>
</tr>
<tr>
<td>64 1 1 2</td>
<td>608 -- 10</td>
<td>513 (10)</td>
</tr>
<tr>
<td>64 1 2 1</td>
<td>602 129 16</td>
<td>1129 (10)</td>
</tr>
<tr>
<td>64 1 2 2</td>
<td>492 3 57</td>
<td>971 (10)</td>
</tr>
</tbody>
</table>

^a^Treatment 0 = no sire irradiation, Treatment 1 = 300 r X irradiation of sires; Breed 1 = Duroc, Breed 2 = Hampshire; Sex 1 = Male, Sex 2 = Female.

^b^Negative variance components assumed = 0.
As sex was a subclass factor, pairs of subclasses had the same sires. Also, some of the treated and control sires in both breeds were full brothers. Thus sire effects were not independent from subclass to subclass within a breed and the probability associated with the \( X^2 \) was not correct. There was less independence than 15 degrees of freedom indicate.

Scores for first minute (OF1) and second minute (OF2) also showed no consistent trends. Hence pooling variances over subclasses seemed justified for open field score.

**Heritability of open field score**

Heritabilities were obtained from pooled variance components within subclasses. The estimates, calculated as four times the paternal half sib correlations, were 0.12, 0.14 and 0.16 for OF1, OF2, and OFT, respectively. Those calculated as twice full sib correlation were 0.49, 0.30 and 0.46 for the three variables, respectively. Each estimate had 176 degrees of freedom for sires within subclasses and was derived from 1853 pigs. Variance components for dams within sires were about five times the size of variance components for sires within subclasses.

A phenotypic and a genetic correlation with 1836 and 175 degrees of freedom respectively were obtained
between OF1 and OF2. The phenotypic correlation was 0.550, and the genetic correlation was 0.898. Observers had noticed that pigs in the test pen seemed to move for some time, then pause, and then continue to move until the end of the period. This had led to speculation on possible differences in scores for the first and second minute. Mean scores were 21.9 and 21.1, for first and second minute, respectively. The variances within litters were 138 for OF1 and 181 for OF2, each with 986 degrees of freedom. Mean squares between sires, with 175 degrees of freedom, were 281 for OF1 and 310 for OF2.

Lower variance in the first minute could occur if all pigs tended to move a constant amount as a result of handling. Apparently the second minute was a slightly better indicator of differences between pigs. The high positive correlation between OF1 and OF2, and the similar heritabilities, suggest, however, that scores in both minutes measured substantially the same trait of the pigs.

**Effect of fixed factors on OF scores**

Table 2 shows the factorial analysis of variance of subclass means of total open field score. With the assumption that higher order interactions were absent the appropriate test for all effects was with mean square for error.
Table 2. Factorial analysis of variance of subclass means of OFT

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>Mean square</th>
</tr>
</thead>
<tbody>
<tr>
<td>Seasons</td>
<td>1</td>
<td>178.89**</td>
</tr>
<tr>
<td>Sire treatment</td>
<td>1</td>
<td>9.15</td>
</tr>
<tr>
<td>Breed</td>
<td>1</td>
<td>22.80</td>
</tr>
<tr>
<td>Sex</td>
<td>1</td>
<td>0.18</td>
</tr>
<tr>
<td>Season x Treatment</td>
<td>1</td>
<td>1.89</td>
</tr>
<tr>
<td>Season x Breed</td>
<td>1</td>
<td>0.33</td>
</tr>
<tr>
<td>Season x Sex</td>
<td>1</td>
<td>24.26</td>
</tr>
<tr>
<td>Treatment x Breed</td>
<td>1</td>
<td>2.48</td>
</tr>
<tr>
<td>Treatment x Sex</td>
<td>1</td>
<td>7.43</td>
</tr>
<tr>
<td>Breed x Sex</td>
<td>1</td>
<td>1.76</td>
</tr>
<tr>
<td>Error</td>
<td>5</td>
<td>4.17</td>
</tr>
</tbody>
</table>

**p < 0.01.
Clearly, season was the only significant effect on open field score. There were suggestions of an interaction of season with sex and of a breed difference.

The means for seasons were 46.3 and 39.6 for fall 1963 and spring 1964, respectively. The means for the sexes within seasons were 47.6 for males and 45.0 for females in the fall, and 38.5 for males and 40.7 for females in the spring. The breed means were 44.1 for Durocs and 41.8 for Hampshires. Possibly warmer weather at the time spring pigs were tested (early summer) accounts for the lower scores in the second season. High temperature leads generally to more lethargic behavior in pigs.

**Dominance Value**

**Relations among DV variables**

Dominance value was observed within litters. Thus for comparing raw and least squares DV, only the correlation within litter was meaningful. This correlation was 0.97 with 1228 degrees of freedom. Hence, raw DV and least squares DV evaluated the pigs in any litter almost identically from the same set of observations. There seemed no need to analyze both variables completely.

With raw DV the implicit assumption is that the pigs with which another pig is compared represent the group.
This assumption could lead to extra sampling variation in raw DV if each pig was only compared with a few of its groupmates. Least squares DV is less affected by such sampling variation. For example, suppose that pigs A and B were of equal dominance and at the group mean. Suppose further that A was compared only with animals of higher dominance, and B only with animals of lower dominance. This would give A a much lower raw DV than B. As long as a few comparisons between the pigs in the top and bottom halves of the litter had been made, the least squares procedure would take into account the differences between the pigs used for comparison with A and B. Apparently the present data contained sufficient observations per litter to make errors in raw DV, due to sampling of pigs for comparisons, small.

Effect of litter size on variance within litter

Litter sizes ranged from five to twelve pigs. The data were partitioned into groups of equal litter size and each group was analyzed. Table 3 shows for each variable variance within sex, within litter, for the eight classes. Bartlett's test of homogeneity of variance over the eight classes gave

\[ X^2 = 23.461 \ (p<0.01) \] for DV1 and
Table 3. Variance within sex, within litter for two DV variables in 8 litter size classes

<table>
<thead>
<tr>
<th>Litter size</th>
<th>df</th>
<th>DV1 (Raw DV)</th>
<th>DV2 (Least squares DV)</th>
</tr>
</thead>
<tbody>
<tr>
<td>5</td>
<td>61</td>
<td>380</td>
<td>0.184</td>
</tr>
<tr>
<td>6</td>
<td>105</td>
<td>266</td>
<td>0.154</td>
</tr>
<tr>
<td>7</td>
<td>176</td>
<td>306</td>
<td>0.173</td>
</tr>
<tr>
<td>8</td>
<td>192</td>
<td>214</td>
<td>0.124</td>
</tr>
<tr>
<td>9</td>
<td>266</td>
<td>197</td>
<td>0.139</td>
</tr>
<tr>
<td>10</td>
<td>232</td>
<td>171</td>
<td>0.107</td>
</tr>
<tr>
<td>11</td>
<td>117</td>
<td>129</td>
<td>0.099</td>
</tr>
<tr>
<td>12</td>
<td>80</td>
<td>102</td>
<td>0.077</td>
</tr>
</tbody>
</table>
\[ X^2 = 30.387 \text{ (p<0.01) for DV2,} \]
each with 7 degrees of freedom. An unweighted linear regression of intra-litter variance on litter size was obtained. The variation in this variance that was attributable to the linear regression was compared with that attributable to deviations from regression in an F test with 1 and 6 degrees of freedom. The proportion of variation due to regression was

92 percent in DV1 (F = 68.6, p<0.01) and
89 percent in DV2 (F = 47.7, p<0.01).

These results clearly show that in both variables the variance within litters depended on litter size. The dependence on litter size seems to be an automatic consequence of the fact, that in larger litters more individuals occur in a range, which is constant in raw DV, and almost so in least squares DV. These results gave us no basis for preferring either of the variables. Least squares DV was chosen for further analysis.

**Variance trends in subclasses**

Table 4 shows the mean squares in least squares DV, for individuals within sex within litter, in each subclass. All 1629 pigs with DV observations were used for these
Table 4. Error mean squares of least squares DV for different subclasses

<table>
<thead>
<tr>
<th>Subclass</th>
<th>Sex</th>
<th>Error mean square</th>
</tr>
</thead>
<tbody>
<tr>
<td>01</td>
<td>1</td>
<td>0.1092</td>
</tr>
<tr>
<td>01</td>
<td>2</td>
<td>0.0936</td>
</tr>
<tr>
<td>02</td>
<td>1</td>
<td>0.1375</td>
</tr>
<tr>
<td>02</td>
<td>2</td>
<td>0.1279</td>
</tr>
<tr>
<td>31</td>
<td>1</td>
<td>0.1202</td>
</tr>
<tr>
<td>31</td>
<td>2</td>
<td>0.1090</td>
</tr>
<tr>
<td>32</td>
<td>1</td>
<td>0.1971</td>
</tr>
<tr>
<td>32</td>
<td>2</td>
<td>0.1564</td>
</tr>
</tbody>
</table>

^a First figure is treatment of sire, second figure is breed.
Treatment 0 = no treatment, 3 = 300 r X irradiation.
Breed l = Duroc, 2 = Hampshire.
^b Sex 1 = male, 2 = female.
mean squares. Bartlett's test of homogeneity of these error variances gave a $X^2 = 18.620$ (p<.01) with 7 degrees of freedom. Variance within litters was not homogeneous over all subclasses.

Table 4 also shows that within every subclass the males tended to be more variable within litters than females. The F ratios (males/females) were

- 1.17 (df 129, 187) in control Durocs,
- 1.08 (df 137, 164) in control Hampshires,
- 1.10 (df 136, 184) in treated Durocs,
- 1.26 (df 155, 137) in treated Hampshires.

None of these values were significant at the 0.05 level. Pooling variances for all males and all females gave an F ratio of 1.20 (df 557, 672) which had a probability of about 0.01 of happening by chance.

As males were not much more variable than the females, and as the F ratios shown for all subclasses were similar, pooling error variance over both sexes seemed reasonable. The pooled variances within sex, within litter, were

- 0.1000 (316 df) for control Durocs,
- 0.1323 (301 df) for control Hampshires,
- 0.1138 (320 df) for treated Durocs,
- 0.1780 (292 df) for treated Hampshires.

Two results are apparent. Hampshires were more variable
than Durocs in both treatment groups and sire treatment increased the variance in both breeds. This increase was statistically significant in Hampshires (p about 0.01). The results suggested that further analysis of DV should be done separately for each subclass.

**Analysis of DV within subclasses**

The further analysis of least squares DV was done within subclasses, and with sexes balanced in each litter. The advantage of balanced sexes for interpreting variance components was discussed in Statistical Analysis. Balanced litters were achieved by random elimination of the DV records of some pigs, in the litters not having equal numbers of each sex. The results of the analysis for all subclasses are given in Table 5.

Sex had a significant effect on DV in each subclass. Differences between mean DV of males and mean DV of females were

- $0.10 \pm 0.04$ in control Durocs,
- $0.25 \pm 0.05$ in control Hampshires,
- $0.13 \pm 0.05$ in treated Durocs,
- $0.17 \pm 0.07$ in treated Hampshires.

The standard errors are only approximate because of unequal numbers of progeny per dam, and dams per sire. On
Table 5. Analyses of least squares DV within subclasses\(^a\)

<table>
<thead>
<tr>
<th>Subclass</th>
<th>Source</th>
<th>df</th>
<th>Mean Square</th>
<th>Approx.F</th>
<th>Component of variance</th>
</tr>
</thead>
<tbody>
<tr>
<td>01</td>
<td>Sex</td>
<td>1</td>
<td>.7912</td>
<td>6.9</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Sex x Sire</td>
<td>10</td>
<td>.0368</td>
<td>&lt;1</td>
<td>-.0044</td>
</tr>
<tr>
<td></td>
<td>Sex x Dam(S)</td>
<td>38</td>
<td>.0970</td>
<td>&lt;1</td>
<td>-.0062</td>
</tr>
<tr>
<td></td>
<td>Error</td>
<td>196</td>
<td>.1147</td>
<td></td>
<td></td>
</tr>
<tr>
<td>02</td>
<td>Sex</td>
<td>1</td>
<td>4.8901</td>
<td>25.7</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Sex x Sire</td>
<td>11</td>
<td>.1303</td>
<td>&lt;1</td>
<td>-.0049</td>
</tr>
<tr>
<td></td>
<td>Sex x Dam(S)</td>
<td>35</td>
<td>.1902</td>
<td>1.5</td>
<td>.0184</td>
</tr>
<tr>
<td></td>
<td>Error</td>
<td>216</td>
<td>.1301</td>
<td></td>
<td></td>
</tr>
<tr>
<td>31</td>
<td>Sex</td>
<td>1</td>
<td>1.2810</td>
<td>7.25</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Sex x Sire</td>
<td>10</td>
<td>.1768</td>
<td>1.55</td>
<td>.0047</td>
</tr>
<tr>
<td></td>
<td>Sex x Dam(S)</td>
<td>42</td>
<td>.1134</td>
<td>&lt;1</td>
<td>-.0003</td>
</tr>
<tr>
<td></td>
<td>Error</td>
<td>192</td>
<td>.1142</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

\(^a\)The mean squares between sires, and between dams within sires, had no genetic meaning; They were omitted.

\(^b\)First figure is sire treatment, second figure is breed.
Treatment 0 = control, 3 = 300 r X irradiation. Breed 1 = Duroc, 2 = Hampshire.
"Table 5 (Continued)".

<table>
<thead>
<tr>
<th>Subclass</th>
<th>Source</th>
<th>df</th>
<th>Mean Square</th>
<th>Approx. F</th>
<th>Component of Variance</th>
</tr>
</thead>
<tbody>
<tr>
<td>32</td>
<td>Sex</td>
<td>1</td>
<td>2.0970</td>
<td>5.98</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Sex x Sire</td>
<td>10</td>
<td>.3508</td>
<td>2.16</td>
<td>.0162</td>
</tr>
<tr>
<td></td>
<td>Sex x Dam(s)</td>
<td>39</td>
<td>.1484</td>
<td>&lt; 1</td>
<td>-.0050</td>
</tr>
<tr>
<td></td>
<td>Error</td>
<td>182</td>
<td>.1622</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
the average males were dominant to females, and sex difference seemed to be greater in Hampshires than in Durocs.

The components of variance for the interaction of sire by sex were negative in control subclasses and positive in irradiated ones. Negative components were not ignored in these calculations. One can obtain approximate standard errors for the variance components following Osborne and Patterson (1952). If the unequal numbers present are ignored, such standard errors for the components of the interaction of sex and sire, are about as large as the variance components.

No reasons were found to explain why the variance component for the interaction of sire by sex should have been negative in the two control groups. Clearly, however, irradiation of sires increased variation of sex difference in DV, from sire to sire.

Relations Among Traits

Behavior traits

Tables 6 and 7 contain the coefficients of correlation calculated from the data. For the pooled data the degrees of freedom available were

452 for correlations between OPT and DV,
Table 6. Simple correlations among traits\(^a\) (pooled data)

<table>
<thead>
<tr>
<th>Trait</th>
<th>Correlated trait ((h^2))</th>
<th>OFT</th>
<th>DV1</th>
<th>DV2</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Genetic</td>
<td>Phenotypic</td>
<td>Within sex</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

\(^a\)Traits are OFT = total open field score, DV1 = raw DV, DV2 = least squares DV, Avg. fat = avg. fat at 3 locations at 154 days, W154 — W0 = weights at 154 — 0 days.

\(^{**}\)p < 0.01
Table 7. Simple correlations among traits (within subclass and sex)

<table>
<thead>
<tr>
<th>Subclass^</th>
<th>Sex^</th>
<th>Within litter correlations of DV2 with W154 (.05 conf. int.)</th>
<th>W0 (.05 conf. int.)</th>
</tr>
</thead>
<tbody>
<tr>
<td>01</td>
<td>1</td>
<td>0.62 (.50 - .72)</td>
<td>0.43 (.28 - .56)</td>
</tr>
<tr>
<td>01</td>
<td>2</td>
<td>0.43 (.30 - .54)</td>
<td>0.31 (.19 - .43)</td>
</tr>
<tr>
<td>02</td>
<td>1</td>
<td>0.34 (.18 - .47)</td>
<td>0.20 (.03 - .36)</td>
</tr>
<tr>
<td>02</td>
<td>2</td>
<td>0.46 (.35 - .57)</td>
<td>0.39 (.25 - .51)</td>
</tr>
<tr>
<td>31</td>
<td>1</td>
<td>0.61 (.49 - .70)</td>
<td>0.44 (.29 - .57)</td>
</tr>
<tr>
<td>31</td>
<td>2</td>
<td>0.33 (.19 - .45)</td>
<td>0.27 (.13 - .40)</td>
</tr>
<tr>
<td>32</td>
<td>1</td>
<td>0.55 (.43 - .65)</td>
<td>0.37 (.22 - .50)</td>
</tr>
<tr>
<td>32</td>
<td>2</td>
<td>0.43 (.27 - .55)</td>
<td>0.37 (.22 - .51)</td>
</tr>
</tbody>
</table>

^Subclasses and sex as in Table 5.
1768 for phenotypic correlations of OPT and production traits, 176 for genetic correlations of OPT and production traits and 1202 for correlations of DV and production traits.

For individual subclass correlations 5 percent confidence intervals are given. The relation within litters between the two behavior traits was not significant.

**Open field score and production traits**

Phenotypically, the open field score was correlated significantly only with weight at 154 days. The correlation was negative. Thus open field score, which was available at about 50 days of age, was ineffective for predicting the weights before 154 days, or depth of back-fat. When both OF and weight at 154 days were used to predict fat, the partial regression coefficient of fat on OF was small and positive. Thus, pigs, which walked less in the open field pen, grew faster between 98 and 154 days than pigs with high OF scores. The extra growth apparently did not involve excess fat deposition.

Tallis (1959) has given formulas for the standard errors of genetic correlations. Standard errors were not calculated for the genetic correlations of OF and
production traits. But, because the low intra-class correlations in OF and in the weight go in the denominator of the formula, standard errors for these correlations must have been so high that the computed values are unreliable. The estimated genetic correlation between OF and backfat was very low.

**Dominance value and production traits**

Dominance value was significantly and positively correlated with all production traits, within sexes within litters. The simple relation of DV and average fat was significant and positive. But when both DV and weight at 154 days were used to predict backfat, the partial regression coefficient of fat on DV was small and negative. The reduction in sums of squares of backfat was 65.0 percent when weight alone was used as predictor. With both weight and DV, the reduction in sums of squares of backfat was only 65.3 percent.

As the analysis of DV (Tables 4 and 5) disclosed significant variance trends among the subclasses, correlations within litter of least squares DV with birthweight and with weight at 154 days were calculated separately for each sex in each subclass. Trends such as an increase of correlation in Hampshire males after sire treatment, were found. But the 5 percent confidence intervals of the birth weight correlations overlapped in all compar-
isons, and only those of the two highest and the two lowest of the 154 day correlations did not. Thus the evidence that the correlations were different in the different subclasses was not strong.

The pooled regression coefficients of least squares dominance value on weight at 154 days, within sex and within litter, were + .0058 units of DV per pound in Durocs and + .0081 units of DV per pound in Hampshires. Sex difference in weight was expected to result in a sex difference of 0.055 units of DV in Durocs and of 0.100 units of DV in Hampshires, if weight was the only factor causing sex difference of DV. The actual sex differences in DV were 0.098 units in Durocs and 0.192 units in Hampshires. The relation between DV and weight is one of the points to be discussed again later.
DISCUSSION OF RESULTS

The results may be discussed conveniently as answers to questions that have arisen during the course of this work.

What Does Open Field Score Measure?

The evidence presented does not allow more than speculation on the relation of open field score in pigs to psychological concepts, such as emotionality or anxiety. That pigs tested in pairs scored less than pigs tested singly may indicate that greater anxiety leads to higher scores. On the other hand this result may mean no more than that two different test situations exist when another pig is in the pen and when the pig is alone.

Open field score in pigs had a lower heritability than was found for the behavior traits in the studies reviewed earlier. Variation in the trait seems to have been mainly due to environmental variation. Of the fixed factors which differentiated the subclasses, season of the year had by far the greatest effect. The three genetic factors, sire irradiation, breed and sex, had little or no effect. These results suggest that further genetic study may be difficult until the environmental factors affecting
OF score are better known. Investigating the contribution of dams within sire (or litter) may be interesting, since this accounted for 20 percent of variance in OF within subclasses.

Is Open Field Score Useful for Predicting Weight and Fatness?

Open field score was phenotypically correlated significantly only with weight at 154 days. The proportion of the variance in W 154 that could be predicted by OF was only 5 percent. This correlation with W 154 was much too low to justify routine open field testing for the purpose of predicting gain. Simple weighing should be much more effective.

What Does Dominance Value Describe, and What Does Variance in Dominance Value Mean?

Dominance value indicates how much an animal dominates other members of the group. The animal with the highest DV submits in its actions to the fewest groupmates. Probably this animal suffers least from competition. An animal which never submits would occur at the upper extreme
of the possible range of DV. Many groups do not have animals as extreme as this, because of dominance circles \((A \rightarrow B \rightarrow C \rightarrow A)\) and incomplete dominance within individual pairs ("bidirectional dominance" Guhl 1962). Dominance value thus describes an individual's reaction to its social or competitive environment. Social environment is that part of an individual's environment which exists as a result of other animals being in the group. This social environment does not have merely an additive relation with physical environment. Animals probably behave quite differently depending on whether any or no group mates are present. Open field testing of paired pigs illustrated this.

Independently of change in variance with size of group, increased variance of dominance value indicates more definite or more consistent relationships in the group. If a group had no dominance relationships and chance only decided wins and losses, all animals would have an expectation of 50% wins which equals 45 units of raw DV or 0 units of least squares DV. There would be no variance in the limiting case. To the extent that dominance submission relations become real and thus result in consistent observations of directional dominance, the animals would become spread out over the range of DV
possible for that group.

The relation of ill or well defined dominance order to variation in production is a completely independent question. A well defined social order might eliminate fighting and lead to maximum growth in a particular situation. On the other hand a group of placid animals, which do not fight enough to establish a dominance order, may grow faster than under conditions in which more fighting occurred. The relation of sharpness of dominance order and production should be examined empirically in each management situation.

There are clear indications from the data, even though only variation within litter was examined, that DV, or a pig's reaction to its social environment, is affected genetically. These indications are a breed difference in variation of DV within litter, an increase in variation of DV within litter in the irradiated subclasses, and an increased interaction of sex by sire in the irradiated subclasses (see Tables 4 and 5).

If litters are the groups in which dominance is observed, one can examine only interactions of sex with litter, in data covering only one generation. The simplest way to get information on variation between litters also, is to raise the pigs in groups of several litters.
after weaning. Then components of variance for litters, for sex, and for interaction of sex by litter can be obtained. With appropriate mating schemes the component of variance for litters can be partitioned into components for sires and for dams within sires. From such components one can, at least if sexes are balanced in each litter, estimate the proportion of variance due to additive action of genes (sire component) and to maternal effect plus other environment common to litters (dam component minus sire component). The components for the interactions of sex with sire and dam, give information about the effects of sex chromosomes, or other factors, if any, that affect DV unequally in the two sexes.

With more resources, fostering and cross-nursing could be used to separate variance into more components. One could also do selection experiments. Clearly, the progeny of selected parents would need to be compared for dominance in groups larger than single litters, to be able to estimate the results of selection.

The present study of DV had several interesting results. Males, although castrated, were more dominant than females. Within litters in both sexes, Hampshires were more variable in DV than Durocs (Table 4). This indicates that more definite, or more consistent, dominance relation-
ships were present in Hampshire litters than in Duroc litters.

Effects of X-irradiation of sires on DV were detected in two ways. The effects seemed to be present in both breeds although Hampshires showed at least the first result more definitely. Table 4 shows that progeny of irradiated sires were more variable in DV within litters, than progeny of unirradiated sires. Assuming that irradiation produces mutations at random, and thus generally upsets, rather than improves, the interaction of the genes controlling growth and development, this result may be interpreted as follows. Irradiation has caused some changes in the genetic material which certain individuals received through their sire's sperm. These changes had a net result of lowering the individual's dominance value, i.e. his ability to compete. The genetic change could have occurred on any of the chromosomes.

Table 5 shows, for DV in both breeds, an increased variance component for the interaction of sex by sire in the progeny of irradiated sires. Its consistency in both breeds makes this result seem real. An interaction of sex by sire means that the sex difference was not constant from sire to sire. There seem to be three ways in which sex difference in DV can be modified genetically, through
X chromosomes, through Y chromosomes, and through autosomes if these interact with sex in development. The data do not indicate which type of chromosome was affected by irradiation. Unfortunately the data do not allow us to study variation between litters in order to compare the variance components for sires, with that for the interaction of sex by sire.

**Is Dominance Value Useful for Predicting Weight and Fatness?**

Variation in DV could be used in the present data to predict up to 25 percent of variation in weight within sex, within litters. Thus, in studies of weight or growth where effects of competition are undesirable, the use of DV as a covariate should substantially reduce variation within groups.

**What is the Causal Relationship between DV and Weight?**

The causal relationship of dominance value to weight.
is not clear. Birthweight was appreciably correlated with DV within sex, within litter. Obviously, the DV measured is not a cause of birthweight. However, possibly birthweight influences DV. A more likely explanation is that there was a common cause, probably genetic, acting on both DV and weight. Weight probably is important when dominance relationships are being formed. It is also probable that after dominance relationships are established, DV affects weight, at least if feed were limited. The correlations of DV and weight (Table 6) were quite similar from 21 days to 154 days.

Thus there were no indication that high DV accelerated extra growth under the conditions of unlimited self feeding. McBride et al. (1964) found that initial weight and social rank both influenced growth, with the relative effect of rank compared to initial weight greater in the second month of the experiment.

What Are the Statistical Shortcomings of the DV Analysis?

Analysis of DV would present no problems if each litter had a constant number of males and the same number of females. This does not happen in practice and we
must work with unequal numbers. Table 3 shows how variance in the measures of DV declines with increase in litter size.

This table illustrates the basic problem in the DV analysis. With raw DV the possible range is constant, 0 to 90, for all groups. With least squares DV, if all relationships are observed, the possible range is from 
\[-\frac{n-1}{n}\] to \[\frac{n-1}{n}\], where n is the number in the group. This range is almost constant when n gets to be more than ten. Dominance relationships among farm animals are consistent observable phenomena. Most small groups have an animal dominant or nearly so, over all others, and another animal submissive to all others. The other members of the group are usually not equal in dominance either. Thus whatever the group size, at least in groups up to twenty, DV ranges from near the possible maximum to near the possible minimum. As group size increases the average deviation from the mean must decrease and thus we see a decrease in variance of DV. This dependency naturally affects differences between subgroups, such as sexes, within litters also.

Holding the range of DV constant is not unreasonable. The animals at the top, or at the bottom, in litters of any size probably experience rather similar competitive
environments. It is quite possible that there is a greater difference in the effect of competition, between the animal at the top and the animal submissive to one only, than between the animal submissive to one and the animal submissive to two others. A similar possibility exists at the other end of the dominance order. If this is so, the use of the arc sin of the proportion in raw DV is very reasonable. This transformation makes differences between extreme fractions worth more than differences between less extreme fractions.

Ranked data do not give us the same statistical problem. Here a transformation of the i th rank to the expected deviation of the i th value in a sample of any size taken from a standard normal distribution can be made. In other words we can assume that the DV values are normally distributed. However, much of the information is lost when, in ranking, the observations that the first and second animals were almost identical in dominance while the third one was clearly much inferior and so on are ignored. This ignoring of information to get normality seems as big a fault as the disadvantages of the procedures used in the present work. Both raw and least squares DV indicate approximately how close together in dominance animals actually are.
SUMMARY

Data on open field scores of 1853 pigs, and social dominance value of 1629 pigs were obtained from Iowa State University's swine irradiation project. The pigs were Durocs and Hampshires. Open field score (OF) is the number of squares, marked on the floor of a strange pen, in which a pig stepped in the first two minutes when put into the pen alone. Dominance value (DV) is the average social dominance position of a pig in its group. DV was measured in two ways. OF data were analyzed in a hierarchical analysis of variance with subclasses, sires, dams and individuals as the levels of hierarchy. Factors distinguishing subclasses were sex, breed, X-irradiation of sires and season of the year.

As pigs were raised in litter groups, DV was estimated relative to a pig's litter. This eliminated any meaningful variance analysis of DV between whole litters. The major analysis of DV was done within subclasses differentiated by irradiation treatment of sires, and breeds. Sexes were balanced within each litter by random elimination of some DV records. Components of variance due to sex and its interactions were studied. Heritability of DV could not be found.
Heritability of OF was 16%. OF had a significant phenotypic correlation of $-0.23$ with weight at 154 days. It was uncorrelated with other weights or with backfat thickness on the live animal.

Raw DV (the proportion of animals dominated, expressed as arc sin in degrees) and least squares DV (the result of least squares minimization of $d_{ij} - \left[DV_i - DV_j\right]$ where $d_{ij}$ is observed difference in DV between animals $i$ and $j$) were highly correlated within sex, within litters. Ranking of pigs was practically identical by the two methods.

Barrows were more dominant than gilts. The sex difference was larger in Hampshires than in Durocs. Sire irradiation increased the variance component for interaction of sire by sex in DV, and increased variance within litters.

DV had highly significant positive correlations, within sex, within litter, with weight at all ages. DV was not significantly positively correlated with backfat thickness if weight was held constant.
ACKNOWLEDGMENTS

The help and encouragement of Dr. D. F. Cox, and of the other members of my committee, Drs. J. L. Lush, L. N. Hazel, O. Kempthorne and W. F. Hollander, is gratefully acknowledged. I thank D. Dal Kratzer for his help with the statistical computations.

A Thomas Lawrance Pawlett Travelling Scholarship from the University of Sydney, N.S.W., and a Fulbright Travel Grant, made it possible for me to study and to do this research.
REFERENCES


The model used to analyze DV is \( y_{ijkl} = u + s_i + \)
\( d_{ij} + m_k + (sm)_{ik} + (dm)_{ijk} + \epsilon_{ijkl} \) where
\( u \) is the mean of the subclass,
\( s_i \) is the effect of sire \( i \),
\( d_{ij} \) is the effect of dam \( ij \),
\( m_k \) is the effect of sex \( k \),
\( (sm)_{ik} \) is the effect of the interaction of \( s_i \) and \( m_k \),
\( (dm)_{ijk} \) is the effect of the interaction of \( d_{ij} \) and \( m_k \),
\( \epsilon_{ijkl} \) is the effect peculiar to individual \( ijkl \).

The effects were defined in Statistical Analysis. Briefly, \( s_i, d_{ij} \) and \( \epsilon_{ijkl} \) are considered random, with means of 0 and variances \( \sigma_s^2, \sigma_d^2 \) and \( \sigma_e^2 \) respectively. \( m_k \) is considered fixed. The interaction effects are considered to have the properties \( E[(lm)_{ak}] = 0, E[(lm)_{ak}^2] = \frac{1}{2} \sigma_{lm}^2, E[(lm)_{ak}(lm)_{ak'}] = 0, E[(lm)_{ak}(lm)_{ak'}] = -\frac{1}{2} \sigma_{lm}^2 \), where \( l \) may be \( s \) or \( d \) and \( a \) may be \( i \) or \( ij \).

The following expectations of sums of squares were obtained when there were unequal numbers in all subclasses. The dot notation (e.g. \( N_{ij}, N_i, N \)) was used to indicate the number of individuals in the subclasses corresponding to the subscripts. The symbol \( Y \) with sub-
scripts and dots was used to indicate summation over all individual \( y_{ijkl} \) within the subclass indicated by the subscripts.

\[
E \text{ (Sum of Squares for sires)}
\]

\[
= E \left( \sum_{i} \frac{Y_{i...}^2}{N_{i...}} - \frac{Y_{...}^2}{N_{...}} \right)
\]

\[
= \left( N_{...} - \sum_{i} \frac{N_{i...}^2}{N_{...}} \right) \sigma_s^2 + \left( \sum_{ij} \frac{N_{ij...}^2}{N_{ij...}} - \sum_{ij} \frac{N_{ij...}^2}{N_{...}} \right) \sigma_d^2
\]

\[
+ \sum_{k} \left( \sum_{i} \frac{N_{ik...}^2}{N_{ik...}} - \frac{N_{ik...}^2}{N_{...}} \right) m_k^2
\]

\[
+ 2 \left( \sum_{i} \frac{N_{i12...}^2}{N_{i12...}} - \frac{N_{i12...}^2}{N_{...}} \right) m_1 m_2
\]

\[
+ \left( \sum_{ik} \frac{N_{ik...}^2}{N_{ik...}} - \sum_{ik} \frac{N_{ik...}^2}{N_{...}} \right) + 2 \sum_{i} \frac{N_{i12...}}{N_{i...}}
\]

\[
- 2 \sum_{i} \frac{N_{i12...}}{N_{i...}} \frac{1}{2} \sigma_{sm}^2
\]
\[ + \left( \sum_{ijk} \frac{N_{ijk}}{N_{i...}} \right)^2 - \sum_{ijk} \frac{N_{ijk}}{N_{i...}} + 2 \sum_{ij} \frac{N_{i1l} N_{i12}}{N_{i...}} \]

\[- 2 \sum_{ij} \frac{N_{i1l} N_{i12}}{N_{i...}} \frac{1}{2} \sigma_{dm}^2 + (s - 1) \sigma_e^2, \]

where \( s = \sum_{i} l \).

\[ \mathcal{E} \text{ (Sums of Squares for dams within sires)} \]

\[ = \mathcal{E} \left( \sum_{ij} \frac{Y_{ijl}}{N_{ij...}}^2 - \sum_{i} \frac{Y_{i...}}{N_{i...}}^2 \right) \]

\[ = (N_{...} - \sum_{ij} \frac{N_{ijl}}{N_{i...}}^2) \sigma_a^2 + \sum_{k} \left( \sum_{ij} \frac{N_{ijl}}{N_{i...}}^2 - \sum_{i} \frac{N_{i1k}}{N_{i...}}^2 \right) m_k^2 \]

\[ + 2 \left( \sum_{ij} \frac{N_{i1l} N_{i12}}{N_{i...}} - \sum_{i} \frac{N_{i1l} N_{i2}}{N_{i...}} \right) m_1 m_2 \]

\[ + \left( \sum_{ijk} \frac{N_{ijk}}{N_{ij...}} - \sum_{ik} \frac{N_{i1k}}{N_{i...}} + 2 \sum_{i} \frac{N_{i1l} N_{i12}}{N_{i...}} \right) \]
\[ -2 \sum_{ij} \frac{N_{111} \cdot N_{112}}{N_{1j}} \frac{1}{2} \sigma_{sm}^2 + \left( \sum_{ijk} \frac{N_{1jk}}{N_{1j}} \right)^2 \]

\[ - \sum_{ijk} \frac{N_{1jk}^2}{N_{1j}} + 2 \sum_{ij} \frac{N_{11j} \cdot N_{1j2}}{N_{1j}} \]

\[ - 2 \sum_{ij} \frac{N_{11j} \cdot N_{1j2}}{N_{1j}} \frac{1}{2} \sigma_{dm}^2 + (d - s) \sigma_e^2, \]

where \( d = \sum_{ij} 1 \).

\[ E (\text{Sums of Squares for sex}) \]

\[ = E \left( \frac{\sum Y_{i..k}^2}{N_{i..k}} - \frac{Y_{i..}^2}{N_{i..}} \right) \]

\[ = \left( \sum \frac{N_{i..k} \cdot N_{i..}^2}{N_{i..k}} - \sum \frac{N_{i..}^2}{N_{i..}} \right) \sigma_s^2 + \left( \sum \frac{N_{i..k} \cdot N_{i..}^2}{N_{i..k}} - \sum \frac{N_{i..} \cdot N_{i..}^2}{N_{i..}} \right) \sigma_d^2 \]

\[ + \sum_k \left( \frac{N_{i..k} \cdot N_{i..}^2}{N_{i..}} \right) m_k^2 - 2 \left( \frac{N_{i..} \cdot N_{i..}^2}{N_{i..}} \right) m_1 m_2 \]
\[ + \left( \sum_{ik} \frac{N_{ik}}{N} \right) - \left( \sum_{ik} \frac{N_{ik}}{N} \right) + 2 \left( \sum_{i} \frac{N_{i1} \cdot N_{i2}}{N} \right) \frac{1}{2} \sigma_{sm}^2 \]

\[ + \left( \sum_{ijk} \frac{N_{ijk}}{N} \right) - \left( \sum_{ijk} \frac{N_{ijk}}{N} \right) + 2 \left( \sum_{ij} \frac{N_{i1} \cdot N_{i2}}{N} \right) \frac{1}{2} \sigma_{dm}^2 \]

\[ + \sigma_e^2. \]

\[ E \text{ (Sums of Squares for interaction of sex by sire)} \]

\[ = E \left( \sum_{ik} \frac{Y_{ik}}{N_{ik}} - \sum_{i} \frac{Y_{i}}{N_{i}} \right) \left( \sum_{ij} \frac{Y_{ij}}{N_{ij}} + \sum_{i} \frac{Y_{i}}{N_{i}} \right) \]

\[ = \left( \sum_{i} \frac{N_{i}}{N} - \sum_{ik} \frac{N_{ik}}{N} \right) \sigma_s^2 \]

\[ + \left( \sum_{ijk} \frac{N_{ijk}}{N} \right) - \left( \sum_{ijk} \frac{N_{ijk}}{N} \right) + \sum_{ij} \frac{N_{i1} \cdot N_{i2}}{N_{ij}} + \sum_{ij} \frac{N_{i1} \cdot N_{i2}}{N_{ij}} \sigma_d^2 \]

\[ + \sum_{k} \left( \sum_{i} \frac{N_{ik}}{N} - \sum_{i} \frac{N_{ik}}{N} \right) \sigma_k^2 \]
\[
+ 2\left(\frac{N_{1.1}N_{1.2}}{N} - \frac{N_{1.1}N_{1.2}}{N}\right) m_1 m_2 + (N_{1...})
\]

\[
- \sum_{i} \frac{N_{1.k}^2}{N_{1.}} - \sum_{i} \frac{N_{1.k}^2}{N_{1.}} + \sum_{i} \frac{N_{1.k}^2}{N_{1.}} + 2 \sum_{i} \frac{N_{1.1}N_{1.2}}{N_{1.}}
\]

\[
- 2\left(\frac{N_{1.1}N_{1.2}}{N_{1...}}\right) \frac{1}{2} \sigma_m^2 + \left(\frac{\sum N_{i.k}^2}{N_{i.k}} - \frac{\sum N_{i.k}^2}{N_{i.}}\right)
\]

\[
- \sum_{i} \frac{N_{1.k}^2}{N_{1.}} + \sum_{i} \frac{N_{1.k}^2}{N_{1.}} + 2 \sum_{i} \frac{N_{i.1}N_{i.2}}{N_{i.}}
\]

\[
- 2\left(\frac{N_{i.1}N_{i.2}}{N_{i...}}\right) \frac{1}{2} \sigma_m^2 + \left(\frac{\sum N_{i.1}N_{i.2}}{N_{i.}} - (s - 1)\sigma_e^2\right)
\]

\[E (\text{Sums of Squares for interaction of sex by dams within sires})\]

\[
= E\left(\sum_{i} \frac{Y_{i.k}^2}{N_{i.k}} - \sum_{i} \frac{Y_{i.k}^2}{N_{1.}} - \sum_{i} \frac{Y_{i.j}^2}{N_{i.}} + \sum_{i} \frac{Y_{i..}^2}{N_{1...}}\right)
\]

\[
= \left(\sum_{i} \frac{N_{i.1}N_{i.2}}{N_{i...}} - \sum_{i} \frac{N_{i.k}^2}{N_{i.}}\right)\sigma_e^2
\]
\[\begin{align*}
  &+ \sum_{k} \left( \sum_{i} \frac{N_{i,k}}{N_{i,j}} \right)^2 - \sum_{i,j} \frac{N_{i,j}}{N_{i,j}} \cdot m_1 \cdot m_2 + 2 \left( \sum_{i} \frac{N_{i,k}}{N_{i,j}} \right)^2 \\
  &- \sum_{i,j} \frac{N_{i,j} \cdot N_{i,j}}{N_{i,j}} \cdot m_1 \cdot m_2 + \left( \sum_{i} \frac{N_{i,k}}{N_{i,j}} \right)^2 - \sum_{i,j,k} \frac{N_{i,k}}{N_{i,j}} \\
  &+ 2 \sum_{i,j} \frac{N_{i,j}}{N_{i,j}} \cdot N_{i,j} \cdot N_{i,j} \cdot N_{i,j} \cdot N_{i,j} \cdot N_{i,j} \cdot N_{i,j} \cdot N_{i,j} \cdot N_{i,j} \cdot N_{i,j} \\
  &\cdot \frac{1}{2} \sigma^2_{sm} \\
  &+ (N_{i,j})^2 - \sum_{i,j,k} \frac{N_{i,j,k}}{N_{i,j,k}} - \sum_{i,j,k} \frac{N_{i,j,k}}{N_{i,j,k}} + \sum_{i,j,k} \frac{N_{i,j,k}}{N_{i,j,k}} \\
  &+ 2 \sum_{i,j} \frac{N_{i,j}}{N_{i,j}} \cdot N_{i,j} \cdot N_{i,j} \cdot N_{i,j} \cdot N_{i,j} \cdot N_{i,j} \cdot N_{i,j} \cdot N_{i,j} \cdot N_{i,j} \cdot N_{i,j} \\
  &\cdot \frac{1}{2} \sigma^2_{dm} \\
  &+ (\sum_{i,j,k} 1 - \sum_{i,k} 1 - d + s)\sigma^2_e
\end{align*}\]

\[E \quad \text{(Sums of Squares for error)}\]

\[E(y_{ijkl} - \sum \frac{Y_{i,j,k}}{N_{i,j,k}})^2\]
When sexes are balanced in each litter, i.e.

\[ N_{ij1} = N_{ij2} \text{ for all } ij, \text{ we also get} \]

\[ N_{i1.} = N_{i2.} \text{ for all } i, \]

\[ N_{..1} = N_{..2} \text{ and we can put} \]

\[ m_1 = -m_2 = m. \] We can use these relationships to find the expectations of the sums of squares, given that sexes are balanced, as follows.

\[ E(\text{Sums of Squares for sires}) = (N_{..} - \sum_{i} N_{ii..}) \sigma_s^2 + \left( \sum_{ij} \frac{N_{ij1}}{N_{i1..}} - \sum_{ij} \frac{N_{ij2}}{N_{i2..}} \right) \sigma_d^2 \]

\[ + (s - 1) \sigma_e^2. \]
E (Sums of Squares for dams within sires)

\[ = (N \ldots - \sum \frac{N_{i.j.}}{N_{i..}})^2 \sigma_d^2 + (d - s) \sigma_e^2 \]

E (Sums of Squares for sex)

\[ = N \ldots m^2 + \sum \frac{N_{i.k.}}{N_{i..}} \frac{1}{2} \sigma_{sm}^2 + \sum \frac{N_{i.j.k.}}{N_{i..k.}} \frac{1}{2} \sigma_{dm}^2 + \sigma_e^2 \]

E (Sums of Squares for interaction of sex by sires)

\[ = (N \ldots - \sum \frac{N_{i.k.}}{N_{i..k.}})^2 \frac{1}{2} \sigma_{sm}^2 + (\sum \frac{N_{i.j.k.}}{N_{i..k.}})^2 \]

\[ - \sum \frac{N_{i.j.k.}}{N_{i..k.}} \frac{1}{2} \sigma_{dm}^2 + (\sum \frac{N_{i.k.}}{N_{i..k.}} - (s - l - 1)) \sigma_e^2 \]

E (Sums of Squares for interaction of sex by dams within sires)

\[ = (N \ldots - \sum \frac{N_{i.j.}}{N_{i..}})^2 \frac{1}{2} \sigma_{dm}^2 + (\sum \frac{N_{i.j.k.}}{N_{i..k.}} - (l - d + s)) \sigma_e^2 \]
\[ E \text{(Sums of Squares for error)} \]

\[ = (N \ldots - \sum_{ijk} 1) \sigma_e^2 \]