Influence of heredity on rate of gain in Poland-China pigs

James Arnold Whatley Jr.

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INFLUENCE OF HEREDITY ON RATE OF GAIN
IN POLAND-CHINA PIGS

by

James Arnold Whatley, Jr.

A Thesis Submitted to the Graduate Faculty
for the Degree of

DOCTOR OF PHILOSOPHY

Major Subject Animal Breeding - Genetics

Iowa State College

1939
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INTRODUCTION

The purpose of this study was to estimate the proportion of the variance in rate of gain in a herd of Poland-China pigs that could be attributed to hereditary differences between the pigs. Weight at 180 days was selected as the measure of rate of gain because it was thought that at this age the faster growing pigs should be approaching a desirable market weight of 200 to 225 pounds. The rate of gain up to an age at which the pig is at an approximate market weight is the factor of most concern to the swine grower interested in finishing his pigs for market at as early an age as possible. The rates of gain at earlier ages such as from conception to birth and from birth to weaning generally are of value only insofar as they are indications of the length of time which will yet be required to attain the desired market weight. In recent years there has been a decrease in the demand for lard. Consequently heavy hogs are not as desirable on the market as those weighing around 200 to 225 pounds. If heavier hogs were desirable, weight at a more advanced age than 180 days would more accurately show the pig's rate of gain to this heavier market weight.

Weight at 180 days is influenced by the interaction
of genetic factors and environmental factors, which affect the growth of the individual pig through all stages of development from fertilization of the egg to 180 days of age. Certain factors such as the nutrition of the embryo and the nursing of the pig from birth to weaning may be partly genetic from the preceding generation (dam's influence) but are environmental as far as the pig itself is concerned.

The meaning of the term heritability as it is heard in every day use may lead to some confusion. The expression is used to describe differences between individuals (with respect to whether the differences had their origin in differences in the genes which those individuals had or in differences in the environments under which they developed) and not absolute magnitudes of a characteristic. The statement that a certain characteristic is forty per cent hereditary means that forty per cent of the total variance in that characteristic among the individuals of a certain population is caused by differences between them in their genetic constitution. It does not mean (as it may often appear to mean) that for one individual, forty per cent of that individual's development in the characteristic in question is caused by his inheritance and the remainder by non-hereditary factors. This point should be borne in mind when considering a study of the kind reported here.

In the narrowest sense of the word "hereditary"
may be restricted to include only the average effects of the genes, excluding as not hereditary the effects which genes have in some gene combinations but not in others.

If the substitution of a gene for its allele always produced the same effect regardless of what other genes were present, the characteristics of the genotype as a whole would be simply the sum of the average effects of the constituent genes. If the effect of a gene is sometimes more and sometimes less than average, according to the nature of the other gene associated with it in that pair of alleles, there is some degree of dominance; that is, there are dominance deviations from the additive scheme. If the magnitude of the effect of a gene depends on the nature of the genes in the other allelic series with which it is present, then there are epistatic deviations from the additive scheme. That dominance deviations and epistatic deviations exist for many characteristics is known, but little is known as to whether they are very important or comparatively unimportant compared to the gene effects described by supposing that the gene has in all combinations the same effect as its average effect in that particular population. In many respects the dominance deviations and epistatic deviations may be likened to environmental factors since they act in much the same way by making the phenotype unlike the genotype. However, it is also logical to consider them as genetic because they are
dependent on the interactions of the genes with each other rather than with the environment. Some of these gene combinations will from time to time be transmitted from one generation to the next and will therefore give rise to some resemblance between relatives.

The animal breeder attempts to improve his animals by increasing the proportion of individuals possessing more of the desired genes and fewer of the undesired ones. To estimate the amount of success that will accompany his selection it is important to know what portion of the variance in the characteristic or characteristics in question is hereditary, because it is only through the selection of hereditary differences that permanent improvement can be made. The selection of environmental differences has no effect on the next generation.
REVIEW OF LITERATURE

Quantitative studies on the influence of heredity on rate of growth of pigs have not been very extensive. There is an abundance of literature showing that environmental factors affect the rate of gain, but such genetic studies as have been made of this subject have been mainly of a qualitative nature. Differences between litters in the length of time required to attain a certain weight have indicated that the rate of gain is influenced to some extent at least by genetic factors.

Heuser and Streeter (1929) have observed differences in the size of pig embryos as early as the first week after pregnancy. At the age of seven days a study of 41 fertilized eggs showed different rates of cell division and a varying number of cells in eggs of the same age. It is impossible to say what proportion of this variation is of genetic origin, although it seems likely that genetic factors have some influence on growth even at this early age.

Differences between litters in average daily gain were reported by Culbertson et al (1931). In 44 litters (of four pigs each) fed under as near standard conditions as possible from 65 days of age to 225 pounds average weight there was a range of 1.13 to 1.68 pounds in average daily
gain during this period. It is evident that the gaining abilities of the pigs in different litters were quite different.

Ferrin (1932) also observed similar variations in the average rate of gain of groups of pigs from different litters. These pigs were fed under identical conditions in the Minnesota Record of Performance tests.

Læthge (1933) studied the variability in weight among 4,351 Improved Landrace and Berkshire pigs. Family differences were observed in the amount of variability present. Litters from some families tended to be relatively more uniform in weight than litters from other families. The author believes that this tendency is hereditary.

Mohler in a Report by the Bureau of Animal Industry (1935) indicated that there was a direct relation between birth weight and daily gain. Pigs weighing more than three pounds at birth averaged 4.7 pounds heavier at weaning than pigs weighing less than three pounds at birth.

Further evidence on the relation between weights at different ages was given by Menzies-Kitchen (1937) who reported a definite negative correlation between the weight of pigs at six weeks and the age at which they attained bacon weight. The actual correlation was not given but pigs in the heavy weight groups at six weeks were younger when slaughter weight was reached than pigs in the light weight
groups.

Lush et al (1934) have made a detailed analysis of the factors affecting birth weight. In their data six per cent of the total variance in birth weight was attributed to the heredity of the pig, 47 per cent to the environment common to litter mates, and 47 per cent to the environment not common to litter mates. These results indicate that heredity plays a small role in determining birth weight. The authors state, however, that most of the variance caused by dominance and epistasis was not segregated from the two environmental sources. If a quantitative estimate of this source of variance could have been made from the data, the genetic portion of the variance would have been increased slightly and both environmental portions decreased. Differences between dams included in the "environment common to litter mates" might have been in large part genetic. There was also the possibility that some of the variance from year to year was genetic since only one litter from each sow was included in this study. All of these points indicate that the figure of six per cent is probably an underestimation of the total genetic portion of the variance.

Bywaters (1937) concluded that the hereditary portion of the variance in 60-day weaning weight of Poland-China pigs was moderately small. The data taken from an inbreeding experiment included 1635 pigs from 271 litters.
An estimate of the hereditary portion of the variance was obtained by the use of the following correlations between relatives: litter mates, .46; parent-offspring, .05; maternal half-sibs, .11; and paternal half-sibs, .02. From these correlations it was concluded that one-fifth of the variance in weaning weight was determined by the heredity of the pig. Of this amount four per cent was attributed to additive genetic effects, one per cent to dominance deviations, 13 per cent to epistatic interactions, and a trace to sex.

From data taken from Danish testing stations Lush (1936) concluded that one-fifth of the variance in daily gain while the pigs were on test was influenced by additive genetic effects. Although this genetic portion of the variance may seem small, the author thinks that it is large enough for selection to make marked changes in the population for at least several more generations.

Smith and Donald (1937) found a correlation of only .15 between the post weaning growth rates of pigs of the same weaning weight. This indicated to the authors that weight at weaning is not of much value in estimating the pig's subsequent gain. In litter sizes of eight and nine they found that the correlation between growth rates of litter mates was .3 and .5, respectively. From their study the conclusion was drawn that at least a fifth of the
individual variance in growth rate was due to additive genetic factors.

Lush and Molln (1937) analyzed a large group of data taken from several different experiment stations. Among contemporary sows of the same breed and at the same station they found that the average correlation between weaning weights of litters from the same sow was .12. Variations in weaning weight of the litter were affected by variations in the number of pigs in the litter and by variations in the average weight per pig. No statement was made as to what part of the permanent differences between sows was genetic.

Carroll and Roberts (1933) attempted to produce rapidly and slowly gaining pigs by selection. The fifth generation of the selected pigs showed no significant evidence that selection within the stocks used had been effective. This was only a brief summary given in an annual report. The details of the experiment such as the breeding plan followed, the number of animals involved, and the size of the selection differential were not given. Without some knowledge of these points the results cannot be accepted as conclusive evidence that there is no hereditary basis for rate of gain.

It is generally believed that inbreeding decreases rate of growth. Craft (1932) compared the growth of inbred
and outbred Duroc-Jersey pigs. The inbreds consisted of five generations of half brother-sister matings and included 54 litters. The outbreds were 22 per cent heavier than the inbreds at birth and their average rate of growth up to market weight was 16 per cent higher.

Mohler in a Report by the Bureau of Animal Industry (1936) also showed that outbred pigs gained faster than inbred pigs. Chester White outbred litters gained ten per cent faster than litters inbred five and six generations by brother-sister matings.

In a previous study of 106 litters which make up a part of the present study, Whatley (1937) observed a negative correlation of .41 between the inbreeding coefficient and the average rate of gain to approximately 180 days of age. The average inbreeding of the litters was 12.8 per cent and the range was only from zero to 32.9 per cent. Correlations of .38 between the rates of gain of litter mates and .02 between paternal half-sibs were also obtained. These correlations although small indicate a genetic basis for rate of gain.
SOURCE OF DATA

The data for the present investigation were taken from an inbreeding experiment with Poland-China swine begun at the Iowa Agricultural Experiment Station in 1930. The object of this experiment was to study the effect of inbreeding, especially when accompanied by selection, and the possibility of improving the herd by selecting animals produced within it. No outside blood was introduced into the herd after its foundation in 1930. Each year breeding replacements were selected from pigs farrowed in the spring.

A brief history of the foundation animals in this herd is given by Bywaters (1937). Twenty-seven sows and three boars purchased from various breeders were used to form the foundation of the herd. Some of the sows were bred when purchased. These bred sows introduced other blood into the herd by producing pigs sired by three boars other than the three boars purchased. Twelve of the foundation animals were inbred, but all of these had inbreeding coefficients of less than four per cent. (All inbreeding coefficients are relative to a base date of about 1925 when the American Poland-China Record Association began issuing numbers preceded by the letter A.)

The general breeding plan was to use four boars
each season, but certain deviations from this plan were necessary at intervals because of injury to a boar, refusal to breed, sterility, or some other cause that rendered a boar unserviceable. Each season the boars were mated to groups of sows that were comparable in age, production, type and relationship to the boar to which they were bred. Although the average relationship between each boar and his mates was about the same for all boars used in the same season, an attempt was made to get some closely inbred litters and some outbred litters from each boar.

The original breeding plan was changed for the 1936 spring farrow. A two-sire herd and three one-sire herds were started from the original four-sire herd, which was continued on the original plan. This splitting of the original herd into non-interbreeding lines within which there are different rates of inbreeding would eventually lead to the establishment of lines quite different in their genetic constitution. In this study, however, these lines cannot be considered as having yet diverged much from the four-sire herd from which they were derived, because the present data include only the first crop of pigs produced after the separation of these lines from the rest of the herd.

First selections for herd replacements were made at weaning. These selections were based mainly on the
The parents consisted of a blue, and a proportion supplemented of tan and red. The period the sows were self-feed corn, a mixture of two in a house for each sow and her litter. During the stockmanship period, the sows were placed in one pasture with an plot of hay a couple of weeks of age (1). From four to eight plots were from one to two weeks of age when the sows and their litters were moved to pasture as soon as the sows and their litters were moved to a central confinement house, the received supplemented food of the same kind of treatment. In the receiving the gestation and stockmanship period all sows need to be vaccinated of the dam in comparison to other sows in the average type score and rate of growth of the litter mates and most emphatically. Some considerations were also given to the the individual and productive aptitude of the dam were given the those that selected the type score and rate of growth of time to start breeding for the next spring season. In not made until about October or early November just before fall. Plant selections of both females and boars were utilized. Groups were done once or twice during the summer and some were first selected at weaning and some cutting of this general type and weight of the litter mates. Poor this of the pit, with some consideration of feed given to the production of the dam and the type and weight-for-age.
some other small grain crop. Fall farrowed pigs were handled in much the same way except that the sows were not farrowed in the farrowing house. Because of weather conditions farrowing was done either in the individual houses on pasture or under an open shed.

Pigs were weaned at 60 days in the first years of the experiment. Beginning with the 1937 fall pigs the weaning age was advanced to 56 days. The spring farrowed pigs received different treatments after weaning. Usually about seventy to a hundred of them were used in feeding experiments. Others were used to follow cattle in the feed lots. Groups of four litter mates from certain selected litters were fed under standard conditions to determine the difference between litters from certain sows and boars in rate of gain, cost of gain, and carcass quality. Each spring a group of boar pigs were fed together and a group of selected gilts were also fed together. Those pigs not in one of the above groups were self-fed the usual ration of corn, mineral mixture, and protein supplement. These latter pigs usually consisted of late pigs and cull pigs not suitable for feeding experiments. As a rule no feeding experiments were conducted with fall farrowed pigs. Those not used in the feed lots to follow cattle or used in the litter testing experiment were self-fed in dry lots.

The fact that the pigs were not all treated in
exactly the same manner from weaning to 180 days requires consideration in any genetic analysis of the weight at this age. It was not possible to control all environmental variations completely and to study only variations of a genetic nature. Such a perfect control of all variables except the one in question is seldom if ever obtained with biological material. In these data a pig may have a low weight because he received a ration that was below average or perhaps because he was sick part of the time. On the other hand a very heavy pig may have been heavy largely because he received a good ration and (more than the average pig) was not affected by sickness or any other detrimental environmental factor. Treatment differences can influence the weight of the pigs and some of them are present in the data, but nearly all the treatments used here were reasonably good ones and the range of their effects on 180-day weights was rather small, as shown by the averages. There was little tendency for all pigs from the same litter, from the same sire, or same dam to be handled alike. They were distributed more or less at random in the different treatments. If truly random these effects of treatment should have little influence on a genetic analysis if the data are of sufficient volume for the plus and minus effects to cancel out. Their major effect would be to reduce the correlations between relatives through introducing some
additional random variation in the 180-day weights. The data available consist of 1394 pigs from 267 litters. This amount should be ample to allow the plus and minus treatment effects to cancel each other out.

The data included in the present study were collected over a period from the spring farrow of 1934 through the spring farrow of 1938. (Most of the sows produced crossbred litters in the fall of 1936. The three purebred litters that were produced were not included in this study.) They include five spring seasons and three fall seasons. Birth weights, weaning weights, and weights at approximately 180 days were taken on all pigs. The reason for taking a final weight at 180 days was to get an index of the pig's rate of gain up to the time when he should be around 200 to 225 pounds weight. This weight at 180 days is the subject of this study, and the other weights are included only insofar as they are related to the 180-day weight.

It was not convenient to weigh all pigs at exactly 180 days. Weights obtained before or after 180 days were age-corrected using the method derived in a previous study (Whatley, 1937). The estimated 180-day weight is equal to the actual weight times \( \frac{180 - 60}{\text{actual age} - 60} \).

In any closed population the inbreeding increases
at least a little with each generation. In a four-sire-herd, such as the one from which the material for this study came, there is an average increase of about three per cent in inbreeding per generation. Actually the inbreeding increased from an average of 11.8 per cent in 1934 to 19.5 per cent in 1938 (Table 1). The average inbreeding of all the pigs studied was 14.7 per cent, which is slightly higher than the equivalent of one generation of half brother-sister mating (12.5 per cent). The average weight and average inbreeding for both seasons of each year are given in Table 1. These averages are plotted in Figure 1 and show that the average weight decreased slightly over the five year period while the average inbreeding increased. From Table 1 the average weight of all the pigs was 180.3 pounds and the intra-farrow standard deviation was 31.3 pounds.

Figure 2 shows the distribution of the 180-day weights of the 1394 pigs. The pigs were grouped in classes with limits of ten pounds. The number of pigs in each class is shown in the diagram. The distribution was not exactly normal but was skewed slightly in the direction of the heavier classes.
Table 1.

Average 180-Day Weight and Percentage Inbreeding by Years

<table>
<thead>
<tr>
<th>Year</th>
<th>Number of pigs</th>
<th>Spring Average inbreeding</th>
<th>Average 180-day weight</th>
<th>Fall Number of pigs</th>
<th>Average inbreeding</th>
<th>Average 180-day weight</th>
</tr>
</thead>
<tbody>
<tr>
<td>1934</td>
<td>206</td>
<td>11.8</td>
<td>198.1</td>
<td>87</td>
<td>9.9</td>
<td>205.3</td>
</tr>
<tr>
<td>1935</td>
<td>207</td>
<td>12.3</td>
<td>178.4</td>
<td>55</td>
<td>8.2</td>
<td>188.5</td>
</tr>
<tr>
<td>1936</td>
<td>187</td>
<td>13.3</td>
<td>167.0</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1937</td>
<td>189</td>
<td>15.5</td>
<td>178.9</td>
<td>62</td>
<td>15.7</td>
<td>184.5</td>
</tr>
<tr>
<td>1938</td>
<td>401</td>
<td>19.5</td>
<td>171.2</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>1190</td>
<td>15.3</td>
<td>177.9</td>
<td>204</td>
<td>11.2</td>
<td>194.5</td>
</tr>
</tbody>
</table>

Grand Total 1394 14.7 180.3

Intra-farrow standard deviation for the 180-day weights was 31.3 pounds.
Figure 1. Average 180-Day Weight and Percentage Inbreeding by Years.
Figure 2. Distribution of the 180-Day Weights of 1394 Pigs.
ANALYSIS OF DATA

Correlation of 180-Day Weight as Dependent on Birth
Weight and Weaning Weight.

Although the multiple correlation of 180-day
weight as dependent on birth weight and weaning weight has
no direct bearing on the question of heritability of 180-
day weight, it is interesting to explore the relations
between the weights at younger ages and the 180-day weight.
One point of special interest is how much value birth weight
and weaning weight have in the prediction of weight at 180
days.

The simple correlations between the three weights
are given in Table 2. The correlations were computed for
each farrow, i.e. each season of each year, and the total
intra-farrow correlations are given in the bottom row of
the table. All of the correlations were positive and sig-
nificant, except the gross correlation between 180-day
weight and weaning weight and the gross and intra-litter
correlations between 180-day weight and birth weight for the
1937 fall pigs. There were few pigs in this group of data
and the negative correlations between 180-day weight and
birth weight and the non-significant positive gross correla-
tion between 180-day weight and weaning weight may be only
Table 2.

Correlations between Weights at Different Ages

\[ W = 180\text{-Day Weight} \quad Y = \text{Weaning Weight} \quad Z = \text{Birth Weight} \]

<table>
<thead>
<tr>
<th>Farrow</th>
<th>D/f</th>
<th>WY Intra-litter</th>
<th>Gross</th>
<th>WZ Intra-litter</th>
<th>Gross</th>
<th>YZ Intra-litter</th>
<th>Gross</th>
<th>Intra-farrow</th>
</tr>
</thead>
<tbody>
<tr>
<td>1934 spring</td>
<td>204</td>
<td>170</td>
<td>.550</td>
<td>.492</td>
<td>.369</td>
<td>.253</td>
<td>.423</td>
<td>.463</td>
</tr>
<tr>
<td>1934 fall</td>
<td>85</td>
<td>73</td>
<td>.1300</td>
<td>.510</td>
<td>.296</td>
<td>.445</td>
<td>.646</td>
<td>.551</td>
</tr>
<tr>
<td>1935 spring</td>
<td>205</td>
<td>170</td>
<td>.529</td>
<td>.517</td>
<td>.324</td>
<td>.390</td>
<td>.524</td>
<td>.580</td>
</tr>
<tr>
<td>1935 fall</td>
<td>53</td>
<td>43</td>
<td>.393</td>
<td>.424</td>
<td>.305</td>
<td>.456</td>
<td>.342</td>
<td>.361</td>
</tr>
<tr>
<td>1936 spring</td>
<td>185</td>
<td>147</td>
<td>.452</td>
<td>.479</td>
<td>.277</td>
<td>.620</td>
<td>.576</td>
<td>.448</td>
</tr>
<tr>
<td>1937 spring</td>
<td>187</td>
<td>146</td>
<td>.718</td>
<td>.619</td>
<td>.435</td>
<td>.332</td>
<td>.574</td>
<td>.479</td>
</tr>
<tr>
<td>1937 fall</td>
<td>60</td>
<td>49</td>
<td>.234</td>
<td>.474</td>
<td>-.163</td>
<td>-.237</td>
<td>.502</td>
<td>.523</td>
</tr>
<tr>
<td>1938 spring</td>
<td>399</td>
<td>321</td>
<td>.492</td>
<td>.640</td>
<td>.369</td>
<td>.550</td>
<td>.481</td>
<td>.484</td>
</tr>
</tbody>
</table>

Intra-farrow 1385 1126 ±.020** ±.021 ±.024 ±.024 ±.020 ±.023

*For this farrow the age at weaning was 56 days rather than 60 days as in former years. Although the weights were not age-corrected this slight discrepancy in age should not disturb the general relation between weaning weight and the other two weights.

**The figures following the ± signs in this paper are standard errors, which were computed according to the formula \( \frac{1-r^2}{n-2} \). With extremely high values for \( r \) Fisher's standard error of \( z \) is more accurate.
sampling variations. In all of the data the correlation between 180-day weight and birth weight was the smallest of the three correlations. This was to be expected as 180-day weight and birth weight were further apart in time than either 180-day weight and weaning weight or weaning weight and birth weight.

The intra-litter correlations were computed to free the correlations from possible effects of environmental conditions which might have been alike for litter mates but varied from litter to litter as well as from farrow to farrow. A summary of the intra-litter correlations is shown in the bottom line of Table 2. The intra-litter correlations were slightly higher than the intra-farrow correlations for 180-day weight with weaning weight and 180-day weight with birth weight but lower for weaning weight with birth weight. On the whole the intra-litter and the intra-farrow correlations are not very different. Heterogeneity of litter means evidently contributed little to the intra-farrow correlation.

From the intra-litter correlations the betas were computed according to the method given by Snedecor (1937). In Figure 3 a diagram of the relations between the three variables is shown. As in Table 2 \( W, Y, \) and \( Z \) are symbols used for 180-day weight, weaning weight, and birth weight, respectively.
Figure 3. Intra-Litter Correlations Involved in Predicting 180-Day Weight (W) from Weaning Weight (Y) and Birth Weight (Z).

\[ R_{WYZ}^2 = \beta_{WY}^2 + \beta_{WZ}^2 + 2(\beta_{WY} \cdot \beta_{WZ} \cdot r_{YZ}) \]

\[ = .449^2 + .208^2 + 2(.449 \cdot .208 \cdot .485) \]

\[ = .202 + .043 + .091 = .336 \]

\[ R_{WYZ} = .579 \]
The multiple correlation coefficient of 180-day weight as dependent on birth weight and weaning weight was .579, as compared with a correlation coefficient of .550 between 180-day weight and weaning weight. A comparison of the two correlations shows that birth weight added very little information to the multiple correlation that was not already included in the weaning weight. The portion of variance in 180-day weight ($r^2$) that would have disappeared if both birth weight and weaning weight had been held constant was 33.6 per cent. Weaning weight accounted for 20.2 per cent of this 33.6 per cent, birth weight 4.3 per cent, and the joint effect of weaning weight and birth weight working together 9.1 per cent. A comparison of the betas in the regression equation indicates that weaning weight would be more than twice as important as birth weight in predicting 180-day weight.

Influence of Certain Environmental Factors on 180-Day Weight.

Analysis of variance as given by Fisher (1936) is a useful statistical tool for segregating the causes of variation in a group of data. By its use the total variance in the dependent variable may be broken up into its component parts; that is, the effect of different variables on the dependent variable may be compared. This form of
analysis will be used in this section and certain other sections of this study.

Season

The 1394 pigs included in these data were farrowed in the spring and fall seasons over a five year period. During this five year period, data were obtained for five spring seasons and three fall seasons. It is very likely that the season of year has an influence on the rate at which pigs gain up to 180 days of age, especially since the ration varies at least a little in accordance with the pig’s ability to get green feed. To answer this question an analysis of variance of 180-day weights as between fall and spring seasons was made. The original breeding plan was to have most of the pigs farrowed in the spring and only a few pigs farrowed in the fall, all from sows two years of age or older. For this reason there were more spring farrowed pigs than fall farrowed pigs. The actual numbers were 1190 spring pigs and 204 fall pigs.

The results of the analysis of variance due to season are given in Table 3. There was a highly significant difference between the mean square between seasons and the mean square between litters farrowed in the same season, showing that the difference between the weight of the spring pigs and the weight of the fall pigs could not have been
Table 3.
Analysis of Variance due to Season of Year

<table>
<thead>
<tr>
<th>Source of variance</th>
<th>D/f</th>
<th>Sum of squares</th>
<th>Mean square</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total</td>
<td>1393</td>
<td>1,543,958</td>
<td>1,108.4</td>
</tr>
<tr>
<td>Between seasons</td>
<td>1</td>
<td>47,981</td>
<td>47,981.0</td>
</tr>
<tr>
<td>Within seasons</td>
<td>1392</td>
<td>1,495,977</td>
<td>1,074.7</td>
</tr>
<tr>
<td>Between litters</td>
<td>265</td>
<td>755,634</td>
<td>2,851.4</td>
</tr>
<tr>
<td>in the same season</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Within litters</td>
<td>1127</td>
<td>740,343</td>
<td>656.9</td>
</tr>
</tbody>
</table>

\[
\frac{1,108.4 - 1,074.7}{1,108.4} = .030
\]

expected to be a chance result. The average weight of the 1,190 spring farrowed pigs was 177.9 pounds as compared with an average weight of 194.5 pounds for the fall farrowed pigs. The difference of 16.6 pounds is very large and it may be worth economic consideration. In this herd Bywaters (1937) found that the fall pigs were also significantly heavier at weaning.

The ratio of the difference between the total variance and the residual variance to the total variance expresses the correlation between members of a certain group. In these data .03 of the variance would have been lost if
all pigs had been born in the same season (Table 3).

The intraclass correlation between pigs farrowed in the same season can be found according to the method given by Fisher (1936). This method of analysis is valid when the different sources of variance are independent of each other. To be perfectly correct the intraclass correlation should be computed on data in which the groups are equal in size, but ordinarily the use of an average group size will not affect the size of the correlation much. When the number of groups is small and especially if the groups are very unequal in size the discrepancy may be serious enough that the average group size needs correction before it is used in computing a correlation by this method. In place of the average group size should be used:

\[ \frac{L}{n} - \frac{V_k}{L^2} \]

L is the number of individual items, n is the number of groups, and \( V_k \) is the variance in the size of the groups. \( \frac{L}{n} \) is the average group size and naturally \( \frac{V_k}{L} \), the correction to it, is small if the groups do not vary much in size; that is, if \( V_k \) is small.

The variance in Table 3 comes from three sources: the intra-litter variance (A), the increase in variance for pigs born in the same season but from different litters (P), and the increase in variance for pigs born in different

*Unpublished material furnished by Dr. J. L. Lush.*
seasons (S). A is 656.9 and the mean square between litters in the same season (2,851.4) contains A plus kP. k corrected for unequal group sizes (using the above formula) is \( \left( \frac{1394}{287} - \frac{4.73}{1394} \right) \) or 5.22.

\[
5.22 \cdot P + 656.9 = 2,851.4
P = 223.8
\]

The mean square between seasons is composed of the mean square between litters in the same season plus

\[
\left( \frac{1394}{2} - \frac{486.098}{1394} \right) S.
\]

\[
348.3 \cdot S + 2,851.4 = 47,981.0
S = 128.6
\]

A + P + S is the variance which would be found in pairs of pigs of which one is a fall pig and the other is a spring pig. S as a fraction of A + P + S is a way of expressing the importance of the average seasonal difference relative to all sources of variance. This fraction as derived from the present data is .128. That the .03 in Table 3 is so much smaller than this, results solely from the fact that in these data there were many more spring pigs than fall pigs. Thus in only about one fourth of the cases when two pigs were picked at random from the present data would there be a spring-fall difference in the pair.

Although the question of why fall pigs were heavier than spring pigs cannot be answered definitely,
there were several differences in the treatment of spring and fall pigs, in addition to changes in weather conditions, which are likely responsible for the differences in weight. The fact that the growing period for fall pigs occurred during colder weather than the growing period for spring pigs may have been conducive to a better appetite and a greater tendency toward fattening. The fall pigs were used in only a few feeding experiments and consequently their rations may have been better balanced on the whole than spring pigs. However, the fact that most of the spring pigs were fed on pasture and the fall pigs were fed in dry lot may have made the rations fed in the two seasons about equal in nutritive properties.

The dams of fall pigs were nearly all at least two years old while many of the dams of spring pigs were gilts. The fact that their dams were older, and thus were probably better nurses and mothers than gilts, may have been to the advantage of the fall pigs. Prior to fall farrowing the sows all had access to pasture but of course there was none of that during the winter while the spring pigs were undergoing their pre-natal development. Just how much influence green feed in the ration of sows during pregnancy has on the subsequent growth of the pigs is not known, but it seems likely that there could be some advantageous effect. Most of the sows farrowing in the fall had not suckled
litters for a longer period prior to farrowling than the sows farrowing spring pigs. For this reason they were in better physical condition for nourishing their pigs. Older sows (the average age of the dams of fall litters was higher than the dams of spring litters) in this herd had also been subjected to severer culling than gilts and their ability as mothers (aside from the age effect) very likely was above that of the dams of spring pigs.

Table 1 shows that the average inbreeding of the fall pigs was less than the average inbreeding of the spring pigs. However a negative regression coefficient of .76 pounds in weight for each one per cent of inbreeding (given in a later section of this report) indicates that the difference in inbreeding of 4.1 per cent between fall and spring pigs could have accounted for only about three pounds of the difference in weight.

Year

The effect of year-to-year differences on the 180-day weight is shown in Table 4. Only pigs farrowed in the five spring seasons were included in this analysis. In two of the years (1936 and 1938) there were no fall pigs, and in the other years the proportion of spring pigs to fall pigs varied. The large disproportionate frequencies
Table 4.

Analysis of Variance due to Year,
Spring Seasons Only.

<table>
<thead>
<tr>
<th>Source of variance</th>
<th>D/f</th>
<th>Sum of squares</th>
<th>Mean square</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total</td>
<td>1189</td>
<td>1,312,510</td>
<td>1,103.9</td>
</tr>
<tr>
<td>Between years</td>
<td>4</td>
<td>124,972</td>
<td>31,242.9</td>
</tr>
<tr>
<td>Within years</td>
<td>1185</td>
<td>1,187,538</td>
<td>1,002.1</td>
</tr>
<tr>
<td>Between litters in the same year</td>
<td>226</td>
<td>542,988</td>
<td>2,402.7</td>
</tr>
<tr>
<td>Within litters</td>
<td>959</td>
<td>644,550</td>
<td>672.1</td>
</tr>
</tbody>
</table>

\[
\frac{1,103.9 - 1,002.1}{1,103.9} = 0.092
\]

between the spring pigs and fall pigs in the different years would confuse seasonal differences in weight with the yearly differences. To eliminate this effect the fall pigs were excluded from this particular analysis.

The mean square between years was significantly larger than the mean square between litters in the same year. The amount of variance that year to year differences accounted for in Table 4 was 9.2 per cent.

The total variance is composed of the intra-litter variance (A or 672.1), the increase in variance between pigs
born in the same year but from different litters (Q), and the increase in variance between pigs born in different years (T).

The mean square between litters in the same year contains A plus \( \frac{1190 - 4.73}{231} \) Q.

\[
5.15 \times Q + 672.1 = 2,402.7
\]

\[
Q = 336.0
\]

The mean square between years is made up of the mean square between litters in the same year plus

\[
\frac{1190 - 3.389}{1190} \) T.
\]

\[
230.9 \times T + 2,402.7 = 31,242.9
\]

\[
T = 124.9
\]

T divided by A + Q + T is .11. Pigs born in different years have between them a variance 11 per cent above that between pigs born in the same year.

**Age of dam**

In Table 5 is shown an analysis of variance due to age of dam. There was a greater difference between litters from dams of different ages than between litters from dams of the same age, although the difference was not significant. If all pigs had been from dams of the same age the total variance would have been reduced only 1.3 per cent.
Table 5.

Analysis of Variance due to Age of Dam,
Spring Seasons Only.

<table>
<thead>
<tr>
<th>Source of variance</th>
<th>D/f</th>
<th>Sum of squares</th>
<th>Mean square</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total</td>
<td>1189</td>
<td>1,312,510</td>
<td>1,103.9</td>
</tr>
<tr>
<td>Between ages of dams</td>
<td>5</td>
<td>22,482</td>
<td>4,492.4</td>
</tr>
<tr>
<td>Within ages of dams</td>
<td>1184</td>
<td>1,290,948</td>
<td>1,089.6</td>
</tr>
<tr>
<td>Between litters from</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>dams of the same age</td>
<td>225</td>
<td>645,498</td>
<td>2,868.9</td>
</tr>
<tr>
<td>Within litters</td>
<td>959</td>
<td>644,550</td>
<td>672.1</td>
</tr>
</tbody>
</table>

\[
\frac{1,103.9 - 1,089.6}{1,103.9} = .013
\]

To obtain the increase in variance between pairs of pigs from dams of different ages, the total variance (spring pigs only) was broken down into the intra-litter variance (A) which was 672.1, the increase in variance between pigs from dams of the same age (R), and the increase in variance between pigs from dams of different ages (U).

The mean square between litters from dams of the same age includes A plus 5.15 R.
5.15 R + 672.1 = 2,868.9
R = 426.6

The mean square between dams includes the mean square between litters from dams of the same age plus
\[
\left( \frac{1190}{6} - \frac{53.231}{1190} \right) U.
\]

\[
153.6 U + 2,868.9 = 4,492.4
U = 10.6
\]

\[
\frac{10.6}{672.1 + 426.6 + 10.6} = .009
\]

The fraction of the variance due to comparisons of pigs from dams of different ages was .009. It is surprising that this figure should be lower than the figure of .013 obtained by the other method which should give an underestimate since many of the differences on which the total mean square (1,103.9) is based do not include a difference between ages of dams. The explanation seems to be that differences between dams (which are important in these data) are not distributed independently of differences between ages of dams. The mean square between ages of dams in Table 5 contained many cases of litters from the same dam (that is, did not always include differences between dams), whereas the mean square between litters from dams of the same age always included a difference between dams. The estimate of .009 is doubtless too low as an expression
of the true importance of age of dam. Even the figure of .013 is probably too low, although not very much.

Table 6 shows the average weights of the pigs from dams of different ages and the number of pigs included in these averages. There was a gradual increase in weight of the spring pigs until the dams were four years old, and then a decrease in the weight of pigs from five and six year old dams. The number of pigs from the six year old dams was so small that it is doubtful if much confidence can be placed in the figure of 163.8 pounds. Because the numbers of fall pigs were small, they were not analyzed in detail. Their average weight, however, showed no consistent increase with an increase in age of dam, as did the average weight of spring pigs. The irregularity might have been due to the small numbers.

Most of the difference in weight in favor of pigs from the older sows could probably be explained by the more intense selection of the older sows. Sows whose first litters were inferior were usually culled after the first or second litter. The average producing ability of the older sows then was above that of the one and two year old sows. There could have been an age effect on the nursing ability of the sow which might have influenced the gain of her pigs. Russell (1936) observed that the weaning weights of pigs from mature sows were higher than those for pigs
Table 6.

Average Weight of Spring and Fall Pigs from Dams of Different Ages.

<table>
<thead>
<tr>
<th>Age of dam (years)</th>
<th>Spaing No. pigs</th>
<th>Average weight (pounds)</th>
<th>Spring No. pigs</th>
<th>Average weight (pounds)</th>
<th>Fall No. pigs</th>
<th>Average weight (pounds)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>624</td>
<td>174.1</td>
<td>1.5</td>
<td>35</td>
<td>192.3</td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>293</td>
<td>179.7</td>
<td>2.5</td>
<td>99</td>
<td>194.6</td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>136</td>
<td>182.4</td>
<td>3.5</td>
<td>27</td>
<td>188.7</td>
<td></td>
</tr>
<tr>
<td>4</td>
<td>77</td>
<td>188.8</td>
<td>4.5</td>
<td>27</td>
<td>195.4</td>
<td></td>
</tr>
<tr>
<td>5</td>
<td>49</td>
<td>181.6</td>
<td>5.5</td>
<td>16</td>
<td>206.3</td>
<td></td>
</tr>
<tr>
<td>6</td>
<td>11</td>
<td>163.8</td>
<td>Total 1190</td>
<td>Total 204</td>
<td>194.5</td>
<td></td>
</tr>
</tbody>
</table>

from gilts. This difference was extended throughout the fattening period until the pigs had reached a final weight of approximately 200 pounds, but at this time the difference in favor of pigs from mature sows was smaller than at weaning.

Effect of Sex

In Table 7 is given an analysis of variance of the effect of sex on weight at 180 days. A comparison of the
Table 7.

Influence of Sex on 180-Day Weight.

<table>
<thead>
<tr>
<th>Source of variance</th>
<th>D/f</th>
<th>Sum of squares</th>
<th>Mean square</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total</td>
<td>1393</td>
<td>1,545,958</td>
<td>1,108.4</td>
</tr>
<tr>
<td>Sex</td>
<td>1</td>
<td>17,054</td>
<td>17,053.6</td>
</tr>
<tr>
<td>Within Sex</td>
<td>1392</td>
<td>1,526,904</td>
<td>1,096.9</td>
</tr>
</tbody>
</table>

\[
\frac{1.108.4 - 1.096.9}{1.108.4} = .010
\]

The mean square between sexes with the mean square between pigs of the same sex showed that on the average there was a greater difference between pigs of opposite sex than between pigs of the same sex. The mean square between sexes was composed of the intra-sex error term of 1,096.9 plus 1394/2 times the sex effect. (The number of pigs of each sex was so near equality that the use of the average group size would not introduce much error.)

\[
1394/2 \times \text{sex effect} + 1,096.9 = 17,053.6
\]

The increase in variance which was present only between members of unlike sex was 22.9, which was two per cent of the total variance. In the present data the sex difference would of course be present in only about half of the pairs chosen at random and consequently the total variance was
reduced only one per cent by excluding the sex difference (Table 7).

The average weight of the 694 males (620 barrows
and 74 boars) was 183.8 pounds and the average weight of
the 700 gilts was 176.8 pounds. The males averaged seven
pounds heavier than the females at 180 days. Most of the
males were barrows, but a few of them were not castrated
and were saved as boars, some of which were to be used for
breeding the following year. There were 74 of these boars
that averaged 192.4 pounds and 620 barrows that averaged
182.8 pounds. The boars averaged 9.6 pounds heavier than
the barrows and the barrows themselves averaged six pounds
heavier than the gilts. It is impossible to determine from
these data whether the difference between boars and barrows
has a physiological explanation. The boars represented a
selected group of males. They were selected to be saved as
boars because they were the most promising males among their
contemporaries at sixty days of age (weaning age). For this
reason much of the observed difference between the weight of
boars and barrows could probably be explained by this
selection of the boars. If the heavier weight of the boars
has no physiological explanation it indicates that there
was some success in selecting at sixty days pigs that would
make a faster than average rate of gain up to 180 days.
(Rate of gain was not the only character considered in these
selections but weight-for-age played a large part.)

It is conceivable that there could have been a litter effect on sex difference. The sex difference might have varied from one litter to another more than could be explained by chance and the variation between litter mates of the same sex. Only 225 litters out of the total 267 had members of both sexes in them. In the 225 litters there was a total of 1298 pigs of which 655 were males and 643 were females. The difference between the average weight of all the males and all of the females in each of the 225 litters was computed. The average of the intra-litter sex difference was 6.42 pounds in favor of the males. A straight average of this kind gives equal weight to each litter regardless of the number of pigs in it.

To place more weight on the differences in the larger litters, the difference between the average weight of the two sexes in each litter was multiplied by the square root of the reciprocal of one over the number of males plus one over the number of females. The following example will illustrate the method. In one litter there was one male weighing 133 pounds and four females averaging 176.5 pounds. The difference of 4.5 pounds was multiplied by the reciprocal of $\frac{1}{1} + \frac{1}{4}$. This factor is $\frac{4}{5}$ or .8944. This attaches more weight to litters with a large number of pigs and to those litters in which the sex ratio is approximately equal.
For example, the factor for a litter of five with three males and two females is 1.0954 and the factor for a litter of eight with five males and three females is 1.3893.

The weighted average intra-litter difference was 7.19 pounds, which is only slightly different from the unweighted average litter difference of 6.42 pounds and the difference between the average weight of all males and all females (seven pounds). The differences between the averages found in the three ways are not large enough to be important. Roughly it can be said that there was an average difference of seven pounds between the weight of males and females in these data.

If it were desirable to correct for a sex difference, the difference of seven pounds and the average weight of the males of 183.8 pounds could be used in deriving such a correction.

If \( M = \) average weight of males and \( F = \) average weight of females, then

\[
\frac{M - F}{M} = \frac{7.0}{183.1} = .04
\]

\[
M - F = .04 M
\]

\[
F = .96 M
\]

\[
M = \frac{F}{.96}
\]

\[
M = 1.04 F
\]

The females were four per cent lighter than the
males. The weight of the females could be made comparable to that of the males by multiplying the weight of each female by the factor 1.04.

Effect of Inbreeding

It is generally believed that inbreeding has a deleterious effect on the general characteristics of vigor. Inbreeding increases uniformity within a population bred as a single inbred line by making those factors homozygous that were heterozygous when the inbreeding was first begun. Genes heterozygous in the original population are made homozygous at a rate depending on the intensity of the inbreeding. The ill effects generally associated with inbreeding presumably are the result of making deleterious recessive genes homozygous as well as desirable dominant genes. Some of the undesirable genes are not culled from the population and these tend to lower the average merit. Even when selection of the usual magnitude practical with farm animals is practiced, intense inbreeding systems fix undesirable genes at such a rapid rate that selection cannot possibly eliminate all of them from the population as rapidly as they become fixed.

The inbreeding coefficients were computed on all the pigs using Wright's (1921) formulae for computing
inbreeding and relationship coefficients. The base date for computing these coefficients was 1925 (Bywaters, 1937). The average inbreeding of all the pigs was 14.7 per cent which is only slightly higher than the equivalent of one generation of half brother-sister mating (12.5 per cent). The amount of inbreeding has increased slightly over the five year period (Table 1 and Figure 1). The largest increase for any one year was for 1938 when a two-sire herd and three one-sire herds were begun from the original four-sire herd.

Table 2 shows the correlations between 180-day weight and percentage inbreeding for each farrow. All of the correlations were negative with the exception of the one for the 1934 fall data. This correlation of +.121 has a standard error of .106 and it could easily have resulted from sampling errors. The total intra-farrow correlation was -.171 ± .026. This correlation is highly significant and indicates that as the percentage inbreeding increased there was a tendency for the weight at 180 days to decrease. The regression coefficient of 180-day weight on the percentage inbreeding was -.76 pounds per one per cent increase in inbreeding.

The above correlation of -.171 was computed on individual pigs. A slightly higher correlation of -.190 ± .059 was observed between the average weight of the pigs
Table 8.

Correlations Between the 180-Day Weight of Individual Pigs and Their Per Cent of Inbreeding.

<table>
<thead>
<tr>
<th>Farrow</th>
<th>D/f</th>
<th>r</th>
</tr>
</thead>
<tbody>
<tr>
<td>1934 spring</td>
<td>204</td>
<td>-.297</td>
</tr>
<tr>
<td>1934 fall</td>
<td>85</td>
<td>+.121</td>
</tr>
<tr>
<td>1935 spring</td>
<td>205</td>
<td>-.334</td>
</tr>
<tr>
<td>1935 fall</td>
<td>53</td>
<td>-.192</td>
</tr>
<tr>
<td>1936 spring</td>
<td>185</td>
<td>-.047</td>
</tr>
<tr>
<td>1937 spring</td>
<td>187</td>
<td>-.307</td>
</tr>
<tr>
<td>1937 fall</td>
<td>60</td>
<td>-.178</td>
</tr>
<tr>
<td>1938 spring</td>
<td>399</td>
<td>-.107</td>
</tr>
<tr>
<td><strong>Intra-farrow</strong></td>
<td>1385</td>
<td>±.026</td>
</tr>
</tbody>
</table>

In each litter and the inbreeding of the litter, thus using each litter but once. In the computation of the correlation with individual pigs the inbreeding coefficient is the same for each pig in the litter but the individual weights may vary widely. (Of course the heterozygosis may not be exactly the same for litter mates. The inbreeding coefficient expresses the fraction of the initial heterozygosis.
which has probably been lost by the Mendelian sampling within populations of finite size. Naturally the actual heterozygosis in any one pig may by chance be higher or lower than the probable result which the inbreeding coefficient shows.) It is to be expected that the correlation computed on individual pigs would be smaller than that computed on litter averages, because the variance in weight would be decreased by the averaging while the variance in inbreeding and the covariance of weight and inbreeding would remain unchanged. In these data it is a little surprising that the difference between the two correlations is not greater. The variances in inbreeding were about the same, but the covariance was slightly larger for individual pigs as was the variance in weight. The larger covariance for individual pigs almost compensates for the larger variance in weight, thus making the two correlations almost the same.

It was also possible to analyze the relation between the inbreeding of the dam and the average 180-day weight of the pigs in her litter. The inbred dam might show her decreased vigor in poorer nutrition and care of her litter during pregnancy and the suckling period. This influence on the pig previous to weaning could be large enough still to be noticeable at 180 days. The observed intra-farrow correlation between the average 180-day weight per pig of the litter
and the inbreeding of the dam was $-0.042 \pm 0.061$.

A positive intra-farrow correlation of $0.134 \pm 0.059$ between the inbreeding of the litter and the inbreeding of the dam indicates that the sows with the higher inbreeding coefficients also produced litters that were more highly inbred than the less inbred sows. Although some effort was made to secure a few outcross litters (within the limits of the herd) from each boar, there was a tendency for the more inbred sows to be more closely related to their mates than less inbred sows.

The relations between the three variables are shown in Figure 4. In this figure the beta of $W$ on $L$ is $-0.139$ and the beta of $W$ on $D$ is $-0.007$. The multiple correlation of $0.190$ was obtained in the following manner:

$$R^2_{W \cdot LD} = (-0.139)^2 + (-0.007)^2 + 2(-0.139 \cdot -0.007 \cdot +0.134)$$

$$= 0.03576 + 0.00005 + 0.00046$$

$$= 0.03627$$

$$R_{W \cdot LD} = +0.190$$

The inbreeding of the litter, inbreeding of the dam, and the two factors working together accounted for 3.6 per cent of the variance in average litter weight. Practically all of the 3.6 per cent could be attributed to the inbreeding of the litter. The effect of the dam's inbreeding
was almost negligible as was the joint effect of the litter inbreeding and dam inbreeding working together.

The data were grouped in inbreeding classes with limits of three per cent (Table 9). In each inbreeding class the number of pigs and average weight are given for the three ages, birth, weaning, and 180 days. These averages are plotted in Figure 5.

In Figure 5 it is difficult to detect any decrease in birth weight with an increase in the degree of inbreeding.
Table 9.

Regression of Weight at Different Ages on Percentage Inbreeding.

<table>
<thead>
<tr>
<th>Imbreeding class mark (per cent)</th>
<th>No. litters</th>
<th>Birth Weight (lbs.)</th>
<th>Weaning Weight (lbs.)</th>
<th>180-Day Weight (lbs.)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.5</td>
<td>8</td>
<td>81</td>
<td>3.0</td>
<td>41</td>
</tr>
<tr>
<td>4.5</td>
<td>12</td>
<td>117</td>
<td>3.1</td>
<td>76</td>
</tr>
<tr>
<td>7.5</td>
<td>30</td>
<td>246</td>
<td>3.2</td>
<td>169</td>
</tr>
<tr>
<td>10.5</td>
<td>58</td>
<td>485</td>
<td>3.0</td>
<td>329</td>
</tr>
<tr>
<td>13.5</td>
<td>47</td>
<td>423</td>
<td>2.8</td>
<td>257</td>
</tr>
<tr>
<td>16.5</td>
<td>30</td>
<td>243</td>
<td>3.0</td>
<td>161</td>
</tr>
<tr>
<td>19.5</td>
<td>19</td>
<td>159</td>
<td>2.9</td>
<td>118</td>
</tr>
<tr>
<td>22.5</td>
<td>27</td>
<td>217</td>
<td>2.6</td>
<td>140</td>
</tr>
<tr>
<td>25.5</td>
<td>7</td>
<td>60</td>
<td>3.0</td>
<td>44</td>
</tr>
<tr>
<td>28.5</td>
<td>4</td>
<td>38</td>
<td>3.2</td>
<td>19</td>
</tr>
<tr>
<td>31.5</td>
<td>15</td>
<td>129</td>
<td>3.0</td>
<td>74</td>
</tr>
<tr>
<td>34.5</td>
<td>5</td>
<td>38</td>
<td>2.6</td>
<td>23</td>
</tr>
<tr>
<td>37.5</td>
<td>4</td>
<td>29</td>
<td>2.7</td>
<td>15</td>
</tr>
<tr>
<td>40.5</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>43.5</td>
<td>1</td>
<td>8</td>
<td>2.7</td>
<td>4</td>
</tr>
</tbody>
</table>

Total or Average

<table>
<thead>
<tr>
<th>Birth Weight (lbs.)</th>
<th>Weaning Weight (lbs.)</th>
<th>180-Day Weight (lbs.)</th>
</tr>
</thead>
<tbody>
<tr>
<td>267</td>
<td>2278</td>
<td>2.9</td>
</tr>
<tr>
<td>1470</td>
<td>39.1</td>
<td>1394</td>
</tr>
<tr>
<td>180.3</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Figure 5. Regression of Weights at Different Ages on the Percentage Inbreeding.
Although the weaning weight regression line is erratic it does exhibit a slight downward trend. The 180-day weight regression line shows a more noticeable decrease than either of the other two. This may be because the weights at birth and weaning are very much dependent on the environment created by the dam while after weaning there is more opportunity for the pig's own heredity to express its effects. The deleterious genes brought to light by the inbreeding then would be more noticeable at 180 days than at either birth or weaning.

Regression of the Variance in 180-Day Weights on the Genotypic Correlation Between Pairs of Pigs

As far as hereditary traits are concerned there is a greater resemblance between related individuals, which are likely to have received some of the same genes from common ancestors than between unrelated individuals. If weight at 180 days is influenced to any extent by the pig's inheritance, then there should be a decrease in the variance between pairs of pigs with an increase in the relationship (correlation between genotypes) between the two pigs in these pairs. In other words there should be a greater difference in the weights of unrelated or only slightly related pigs than between pigs which are closely related. Examples of 100 per
cent relationships are unknown in animals, with the exception of identical twins which are exceedingly rare and also difficult to recognize in swine.

Even if it were possible to get two pigs of the same genetic constitution it is not likely that they would weigh the same, because the environmental influences would usually have affected the two pigs in different ways. The residual variance remaining when members of a pair are alike genetically is that portion of the total variance (in a population of unrelated pigs) which can be attributed to environmental factors. By computing the regression of variance on relationship in a population of pigs showing different relationships to each other, it is possible to estimate how much of the variance among the unrelated pigs was caused by differences in their heredity and how much was caused by differences in environment, known and unknown. Besides the sampling errors attendant on such a computation there are complications from the fact that this regression line will be curvilinear (convex upward) to the extent that dominance and epistatic deviations are important, and the exact shape of that curvilinearity is not known clearly.

If the variance due to dominance deviations and epistatic deviations is large relative to the additively genetic variance, then a regression line over the range of relationships included in this study (.07 to .66) would
overestimate the environmental variance and underestimate the hereditary variance. This error would be less if the variance due to dominance and epistatic deviations were small compared to the additively genetic variance. In general the hereditary variance estimated from the regression line would include all of the additively genetic fraction of the variance plus a varying proportion of the dominance and epistatic fraction. On account of the cirvilinearity, if there were much dominance and epistasis, the range of relationships over which the regression line is calculated would also affect the accuracy of the results. A line fitted to data covering the entire range of relationship from zero to 100 per cent would give the least error.

In beginning this analysis the first question is how to select the pairs. The first reaction would probably be to pair the pigs at random. Closer study of the data, however, reveals that random pairing within the entire group of data might introduce environmental differences which could easily be eliminated. Since all pigs included in this part of the study were farrowed in five spring seasons, there were no seasonal differences; unless consideration is given to differences between early and late farrowed pigs, which are not likely to be of great importance. There were, however, yearly differences and treatment differences which could be eliminated by pairing pigs from the same lot.
Pairs consisting of litter mates were not used because they tend to be more alike than non-litter mates; not only because they have some of the same inheritance but also because of the common environmental influence of the dam during pre-natal life and the suckling period. The possibility of a sex difference increasing the difference between pairs was eliminated by multiplying the gilt's weights by 1.04 to make their weights comparable to the weights of the barrows. In order to get information over as wide a range of relationships as possible one pair with the least relationship and one with the highest relationship within each lot were selected. This gave more information on the variance for extreme relationships than would have been secured if pairing had been strictly at random. Such information was useful in obtaining the regression line for each lot.

In summary, the rules used in pairing the pigs were as follows:

1. Both members of the pair were farrowed in the same year and fed in the same lot after weaning. (This also prevented the pairing of maternal half-sibs, since such of necessity could not be contemporaries.)

2. Litter mate pairs were avoided.

3. The most closely related and the least closely related pairs in each lot were selected.
4. The remainder of the pigs in each lot (after the highest and lowest relationships were selected) were paired at random.

In attacking the problem in this manner the question arises as to how many degrees of freedom are available among the relationships. The answer to this question is not entirely clear. In a lot of nine pigs there are \( \frac{9 \times 9}{2} \) or 36 different relationships possible. These are not absolutely independent of each other, yet they are not as closely dependent as are the various differences in weights, for which there are only eight truly independent differences (degrees of freedom). To illustrate: if the differences in weight between A and B and between B and C are known, then the difference in weight between A and C is rigidly determined and can easily be computed. But the correlation between A and B and between B and C may be known and yet \( r_{AC} \) is not determined except within very wide limits. This problem deserves further study. Since a clear answer to this question was not found, the safest plan seemed to be to assume that there are only eight degrees of freedom. At any rate this would be a minimum number.

The eight degrees of freedom in a lot of nine pigs may be broken down into four comparisons of one pig with another, one comparison of one pig with two others, one
comparisons of two pigs with three others, and a comparison of four pigs with five others. As the calculation of the relationships for comparisons more complicated than two pigs with two others is tedious, all comparisons of a higher order than this were omitted from the analysis. This involved omitting some information (two comparisons out of the eight in a lot of nine pigs), but the extra information gained was thought not to be worth the calculations necessary. In all of the data about one fourth of the total degrees of freedom were lost by omitting these comparisons of higher order.

According to Wright (1921) the relationship (correlation between genotypes) of two animals is

\[ r_{XY} = \frac{\frac{1}{2} \left[ n + n^f \right] (1 + F_A)}{\sqrt{(1 + F_X)(1 + F_Y)}} \]

In this formula \( n \) and \( n^f \) are number of generations \( X \) and \( Y \) are from the common ancestor \( A \) and the \( F \)'s are inbreeding coefficients. The relationship between one pig and two others may be obtained in the following manner:

Figure 6 shows a diagram of the correlation between the genotypes of pig 82 with \( A \) the average genotype of 121 and 175.
Figure 6. Correlation Between the Genotype of One Pig (82) with the Average of Two (A).

\[ r_{A \cdot 121} = x + cy \]

\[ r_{A \cdot 175} = cx + y \]

\[ x^2 + 2cxy + y^2 = 1.0 \]

If \( x = y \) (as would be the general case, since no distinction is made between which member of the pair is first and which is second), then --
\[ 2x^2 + 2cx^2 = 1.0 \]
\[ 2x^2 (1 + c) = 1.0 \]
\[ x^2 = \frac{1}{2(1 + c)} \]

\[ r_{82A} = bx + ay = \frac{1}{2(1 + c)}(a + b) \]
\[ = \frac{a + b}{2(1 + c)} \]

Substituting the actual values of \( a = .1131, \) \( b = .1926, \)
and \( c = .0957, \)

\[ r_{82A} = \frac{.1131 + .1926}{2(1.0957)} = .206 \]

In a similar way the correlation between genotypes
in a comparison of two pigs with two others (Figure 7) is
as follows:

\( B = 94 + 200 \) and \( C = 323 + 252. \)

\( x = x^i, y = y^i, \) but \( x \neq y \) unless \( i = h. \)

\( i \) and \( h \) may be quite different because some pairs were
selected for the very reason that they were slightly
correlated (genotypically) and others were chosen because
they were highly correlated.

\[ r_{B\cdotC} = xy(d + e + f + g) = \frac{d + e + f + g}{2(1+h)(1+i)} \]
Figure 7. Correlation between the Average Genotypes of Two Pigs (B) with the Average of Two Other Pigs (C).
If $d = .1276$, $e = .1324$, $f = .2557$, $g = .1833$, $h = .4514$, and $i = .1918$,

$$r_{B.C} = \frac{.1276 + .1324 + .2557 + .1833}{2(1 + .4514)(1 + .1918)} = .266$$

The variance in a population is equal to half of the average squared difference between individual items. The squared difference in a one by one comparison is divided by two, by six in a difference between the sum of two pigs with the sum of two others, Snedecor (1937).

Table 10 shows an analysis of covariance for the 843 independent intra-lot comparisons. The pairs were grouped into 87 lots over the five spring seasons. (The fall pigs were not included in this part of the study.) The total and within-lot regression coefficients were both negative, but the within-lot regression was much the larger. The within-lot regression coefficient is desired because it all controllable environment is eliminated. The intra-lot regression equation (using the means from all of the data) is as follows:

$$V = 719.9 - \frac{2.592}{10.302} (r - .340)$$

$$= 301.7 - 240.5 r.$$  

This straight line is plotted in Figure 8. With an increase in relationship there was a decrease in the
Table 10.

Analysis of Covariance of Variance in 180-Day Weight (V) among Lot Mates and Relationship (R), Maternal Sibs Excluded.

<table>
<thead>
<tr>
<th>Source of variance</th>
<th>D/f</th>
<th>$\Sigma r^2$</th>
<th>$\Sigma rv$</th>
<th>$\Sigma v^2$</th>
<th>Regression coefficient</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total</td>
<td>842</td>
<td>12.714</td>
<td>-1,215.8</td>
<td>843,882,344</td>
<td>- 95.6</td>
</tr>
<tr>
<td>Between lots</td>
<td>86</td>
<td>1.912</td>
<td>-1,382.2</td>
<td>209,231,269</td>
<td></td>
</tr>
<tr>
<td>Within lots</td>
<td>756</td>
<td>10.602</td>
<td>-2,598.0</td>
<td>634,651,075</td>
<td>-240.5</td>
</tr>
</tbody>
</table>

Mean $r = .340$  Mean $V = 719.9$

variance between pairs. Table 11 shows the data when grouped in relationship classes with limits of four per cent. The dots in Figure 8 represent these class averages. The dots are erratic but there is a noticeable downward trend with an increase in relationship.

Accepting this regression equation as correct, $V = 801.7$ when $r = zero$. This would be the variance expected between unrelated pigs which were lot mates. That is, 801.7 equals all of the variance due to differences in heredity (within the population which included all the ancestors of this one at the base date to which relationships were computed) plus all of the variance due to environmental variations, known and unknown, within the lots in these
Figure 8: Regression of Intra-Lot Variance in 180-Day Weight on the Genotypic Correlation between Pairs of Pigs.
Table 11.

Regression of the Variance in 180-Day Weight on the Relationship Between Pairs of Pigs.

<table>
<thead>
<tr>
<th>Relationship class mark</th>
<th>Number of pairs</th>
<th>Mean variance</th>
</tr>
</thead>
<tbody>
<tr>
<td>.02</td>
<td>0</td>
<td>--</td>
</tr>
<tr>
<td>.06</td>
<td>2</td>
<td>718.2</td>
</tr>
<tr>
<td>.10</td>
<td>24</td>
<td>1051.3</td>
</tr>
<tr>
<td>.14</td>
<td>32</td>
<td>733.3</td>
</tr>
<tr>
<td>.18</td>
<td>67</td>
<td>685.8</td>
</tr>
<tr>
<td>.22</td>
<td>88</td>
<td>677.7</td>
</tr>
<tr>
<td>.26</td>
<td>94</td>
<td>803.3</td>
</tr>
<tr>
<td>.30</td>
<td>70</td>
<td>570.4</td>
</tr>
<tr>
<td>.34</td>
<td>70</td>
<td>622.6</td>
</tr>
<tr>
<td>.38</td>
<td>81</td>
<td>677.8</td>
</tr>
<tr>
<td>.42</td>
<td>109</td>
<td>776.8</td>
</tr>
<tr>
<td>.46</td>
<td>91</td>
<td>842.0</td>
</tr>
<tr>
<td>.50</td>
<td>68</td>
<td>763.5</td>
</tr>
<tr>
<td>.54</td>
<td>30</td>
<td>451.9</td>
</tr>
<tr>
<td>.58</td>
<td>10</td>
<td>453.9</td>
</tr>
<tr>
<td>.62</td>
<td>4</td>
<td>934.5</td>
</tr>
<tr>
<td>.66</td>
<td>3</td>
<td>428.5</td>
</tr>
</tbody>
</table>

Total or Average 343 719.9

experiments. Substituting \( r = 1.0 \) yields \( V = 561.2 \) as the estimated variance within an isogenic line. Hence

\[
\frac{801.7 - 561.2}{801.7} = .300 = \text{the fraction of the original variance which was due to differences in heredity.}
\]

Because most of the relationships on which this regression line was fitted were low and because the line curves downward with increasing \( r \) if dominance exists and if there are epistatic combination effects among the genes affecting 180-day
weights, this overestimates the variance which would exist in an isogenic line. The amount of this discrepancy cannot be estimated more closely without either postulating something about the prevalence and size of dominance deviations and epistatic effects or securing and analyzing data concerning relationships ranging up to 1.0. All that can be said here is that this estimate of 30 per cent includes all of the additively genetic part of the variance but only an uncertain fraction of that due to dominance and epistasis. Also it should be remembered that the environmental portion is that found within lots.

In a population from many lots and different years there would almost certainly be a larger environmental variance. Some indication of that may be had from the fraction of environmental variance in 180-day weights from all of the present data treated as a single population. The regression coefficient was -95.6 (Table 10), and the regression equation is as follows:

\[ V = 719.9 - 95.6r + (95.6)(.340) \]

\[ = 752.4 - 95.6r \]

\[ \frac{95.6}{752.4} = .127 \], which is the fraction of the original variance that was due to differences in heredity, and .373 is the fraction that was due to environmental differences. This is based on the assumption that the differences in lot means were purely environmental, which is not quite true. For
this reason the fraction of \(0.873\) is too high for the environmental variance, but it does indicate that in a population consisting of a group of heterogenous treatments the environmental variance is higher in proportion to the genetic variance.

**Regression of Offspring Weight on Dam's Weight**

In animal breeding it is usually observed that when selection is practiced in a herd there is a regression of the average merit of the offspring from the average of their selected parents toward the herd average. Although the offspring do not average as high as their selected parents, yet they do not average as low as the generation from which the parents came. The principle is that in selecting for any characteristic not completely determined by heredity some gain in the average merit of the population is made but not as much as was attained in the selected parents themselves. The gain in merit depends on the strictness of selection (how much the selected parents are above the population average) and the degree to which the characteristic in question is influenced by the action of genetic factors that combine additively. Dominance and epistatic interactions of genes act chiefly to reduce the accuracy of selection by making phenotypes appear different from genotypes, although
some of the epistatic effects are gained temporarily by selection.

If selection for a characteristic not completely determined by heredity were made in both a plus direction and a minus direction in a previously unselected population, the first generation produced from the two groups would show regression toward the population average from both directions. The offspring from the high group although above average would not be as good as their parents, whereas the offspring from the low group although below average would not be as poor as their parents. This can be explained by the fact that the parents are selected on the basis of their outward (phenotypic) appearance, which is the result not only of their genetic make-up but is also the result of the action of environmental factors which may make an individual appear better or worse than his actual genetic constitution. Selection is for the outward appearance and for this reason environmental differences as well as genetic differences are selected. Since the offspring from the selected parents are not themselves selected, the environmental differences between these offspring tend to cancel out. So also do the dominance deviations and most of the epistatic deviations. Good and bad environments tend to be equally distributed as between the offspring from parents above average and those from parents below average. The
difference between the offspring from the two selected groups is a genetic difference. A comparison of this difference with the difference between the selected parental groups would give the proportion of the total difference that is genetic in that population at that time. A change in gene frequency might change this proportion as between the parental and offspring generations but as a rule it would require several generations for such a change to become important.

The data for this study were of such a nature as to permit the division of the dams into a high group and a low group on the basis of their weight at 180 days. This permitted comparing the difference between the average weights of the progeny from these groups with the difference between the average weights of the parental groups.

In arranging the data for this analysis the mates of each sire were divided equally into a high group and a low group. The grouping was done on an intra-sire basis to eliminate any effect that the sire might have on the weight of the pigs. Thus any genetic difference between the progeny from the two groups must come from genetic differences in the dams only. In order to give equal weight to both groups it was necessary to discard the information on a few sows and their progeny. This was necessary because some sires had an odd number of mates. To be equally weighted
there must be an equal number of mates in each group. The
general rule followed was to discard the sow whose weight
was nearest the average of all the mates, for the reason
that the sow nearest the average would give the least informa-
tion about the regression. In the initial grouping if there
were one more sow in the high group than in the low group the
lowest sow in the high group was discarded, and vice versa
if the extra sow were in the low group the highest sow in
that group was discarded.

The average weight of all her offspring from one
boar was used for the weight of the dam's offspring. This
was done in order to give equal weight to each dam.

After the division of the dams and their offspring
in the intra-sire groups into a high half and a low half on
the basis of the dam's weight at 180 days, all of the intra-
sire groups were combined and averages calculated. There
were 15 of these intra-sire groups including a total of 101
sows and 728 pigs. Some of the sows were mated to more than
one boar. Such sows were included in more than one intra-
sire group. There were 145 litters in all, but since several
sows produced more than one litter by the same boar there
were only 140 full-sib groups (five groups were each composed
of two full-sib litters). With the 140 mates divided equally
into a high half and a low half there were 70 dam and off-
spring weights in each half.
The results are shown in Figure 9. The average weight of the high mates was 201.9 pounds as compared to 177.9 pounds for the low mates. The difference was 24.0 pounds. The progeny from the high mates averaged 175.3 pounds and were 5.6 pounds heavier than the 169.7 pound average for the progeny from the low mates.

Figure 9 shows that the range between the two groups of dams was not as great as it would have been in an unselected population. The sows with the lowest weights were culled from the herd and were never allowed to produce any offspring. The average weight (188.2 pounds) of all the dams was 7.1 pounds above the 181.1 pound average of the generation from which they came. If there had been no selection of sows the average weight of the dams would have been the same as that of the generation in which they were farrowed. The same point is brought out in another way. The average of the low group of mates was only 3.2 pounds less than the generation average, whereas the average of the high group of mates was 20.8 pounds above the generation average. That the range between the dams was reduced by culling the lightest females in the parental generation is also shown by the fact that the intra-sire standard deviation for the dams was only 16.0 pounds as compared to 32.5 pounds for the intra-sire standard deviation of their offspring.
Figure 9. Regression of the 180-Day Weight of the Offspring on the 180-Day Weights of the High and Low Mates of 15 Sires.
Selection of the independent variable (weight of dam) as in these data might have some effect on the correlation between dam and offspring but it would have little or no effect on the regression. The regression of the offspring weight on the dams weight was 5.6/24.0 or .233. This fraction must be multiplied by two in order to obtain the hereditary fraction of the difference in 180-day weight because the sire influence was eliminated when the high and low groups of mates were selected on an intra-sire basis. The difference between the averages of the progeny of these groups was due to the heredity of the dams. Since the pig only gets half of his heredity from his dam, the intra-sire regression of .233 is doubled, yielding .466 for the hereditary fraction of the difference in 180-day weight. A correlation between the environments of dam and offspring would make this an overestimate, but since the dams and their offspring were farrowed in the same herd and raised under practically the same conditions there should have been no noticeable environmental correlation. Certainly there was no conscious effort to give better-than-average treatment to the offspring of better-than-average dams or the reverse.

Some other interesting points are brought out in Figure 9. The average weight of all the offspring was 7.9 pounds less than that of their parental generation, in spite of the fact that their dams were selected 7.1 pounds above
the average of the generation from which they came. Even though selection (taking the herd as a whole) was for heavier weight, the herd average decreased almost eight pounds in one generation. The increase in inbreeding was 4.3 per cent, but this could not account for all of the decrease in weight. In these data there was a decrease in weight of .76 pounds for each increase in inbreeding of one per cent. The 4.3 per cent increase in inbreeding then could only account for a decrease of about 3.3 pounds in weight. The remainder was due to some cause or causes at present unknown.

The original plan in this part of the study was to use the dam-offspring correlation for estimating the hereditary variance in 180-day weight. In a population in which the standard deviations for the dam's weight and weight of the offspring are the same (as would occur in an unselected population) and the distribution of both variables is normal, the correlation between the weight of the dam and the weight of the offspring would serve as a reliable basis for estimating the hereditary variance. In these data, however, the weight of the dam (the independent variable) was selected (Figure 9). The sows with very low

\*Wright (1921a) has given the biometric relations between parent and offspring in terms of path coefficients.
weights at 180 days never were allowed to produce any offspring. The intra-sire standard deviation of the offspring (32.5 pounds) was twice as large as the intra-sire standard deviation for the dams (16.0 pounds).

The scatter diagram in Figure 10 brings out clearly the lower variability of the dams as compared to that of the offspring. In this figure the weight of the offspring, expressed as a deviation from the average of all the offspring from one sire, is plotted against the weight of the dam, expressed as a deviation from the average of all the dams mated to that sire. This eliminates the differences between the sire groups and makes the dam-offspring pairs from different groups comparable. The graph does not bring out the effect of selection on the distribution or the average weight of the dams. That the selection increased the average weight of the dams over their generation average is brought out in Figure 9.

The type of selection practiced on the dams resulted in cutting off the lower end of the frequency curve, and thus the curve was skewed in the direction of the heavy weights. This selection tends to lower the correlation between dam and offspring in comparison to what this correlation would have been in an unselected population. The regression line, however, should not be either consistently raised or lowered by the selection. The only way in which
the type of selection practiced affects the regression line is to reduce the range of dam's weights over which it extends, and thus there is more chance for the fitted line to be either too high or too low, as compared to a true regression line over an entire range of unselected dams.

The observed correlations and regression coefficients for all of the 15 sire groups of dams and their offspring are given in Table 12. All in all there were 150 different matings and 756 offspring. Certain sows occurred in more than one of the 150 matings because they were mated to different sires. The intra-sire regression coefficient for the 15 groups was .307. Within the limits of the dams mated to the same sire, for each pound increase in weight of the dams there was a corresponding increase in the weight of the offspring of .307 pounds. This regression line is plotted in Figure 10 as are the individual deviations from this line.

On these same groups of dams and offspring the intra-sire regression of the average weight of the progeny from high and low mates was .233. This regression was computed in such a manner as to give equal weight to all dams regardless of the number of offspring produced. Much of the difference between the two regression coefficients is probably explained by one litter of four pigs which were all between 30 and 50 pounds below average weight and whose
Table 12.

Intra-Sire Correlation (r) and Regression Coefficients (b) for 180-Day Weight of Offspring as Dependent on 180-Day Weight of Dam.

<table>
<thead>
<tr>
<th>Sire</th>
<th>Number mates</th>
<th>Number offspring</th>
<th>r</th>
<th>b</th>
</tr>
</thead>
<tbody>
<tr>
<td>3125</td>
<td>7</td>
<td>30</td>
<td>.469</td>
<td>1.771</td>
</tr>
<tr>
<td>3195</td>
<td>4</td>
<td>20</td>
<td>.126</td>
<td>.250</td>
</tr>
<tr>
<td>5011</td>
<td>7</td>
<td>36</td>
<td>.181</td>
<td>.231</td>
</tr>
<tr>
<td>5030</td>
<td>9</td>
<td>39</td>
<td>.436</td>
<td>1.706</td>
</tr>
<tr>
<td>5040</td>
<td>14</td>
<td>64</td>
<td>.063</td>
<td>.162</td>
</tr>
<tr>
<td>6044</td>
<td>21</td>
<td>119</td>
<td>.165</td>
<td>.512</td>
</tr>
<tr>
<td>6056</td>
<td>6</td>
<td>28</td>
<td>.270</td>
<td>.699</td>
</tr>
<tr>
<td>6300</td>
<td>13</td>
<td>78</td>
<td>.244</td>
<td>.529</td>
</tr>
<tr>
<td>6321</td>
<td>21</td>
<td>106</td>
<td>.188</td>
<td>.372</td>
</tr>
<tr>
<td>7030</td>
<td>10</td>
<td>45</td>
<td>.197</td>
<td>.329</td>
</tr>
<tr>
<td>7150</td>
<td>11</td>
<td>49</td>
<td>.045</td>
<td>.072</td>
</tr>
<tr>
<td>7251</td>
<td>6</td>
<td>37</td>
<td>-.132</td>
<td>-.210</td>
</tr>
<tr>
<td>7364</td>
<td>8</td>
<td>38</td>
<td>.266</td>
<td>.484</td>
</tr>
<tr>
<td>7376</td>
<td>9</td>
<td>55</td>
<td>-.040</td>
<td>-.108</td>
</tr>
<tr>
<td>7394</td>
<td>4</td>
<td>12</td>
<td>.416</td>
<td>1.233</td>
</tr>
</tbody>
</table>

Intra-sire | 150 | 756 | .152 | .307 |
Figure 10. Intra-Sire Regression of 180-Day Weight of Offspring on 180-Day Weight of Dam. Points Plotted as Deviations from the Average of Offspring and Mates of Each Sire.
dam was 52 pounds below average weight (Figure 10). Such an extreme litter would naturally have a large influence on the regression line when each pig was given equal weight, but this influence would not be so great when the dams were weighted equally.

The effect of the sire on the offspring weight was eliminated by computing the regression on an intra-sire basis. The only hereditary variance in the offspring then came from the dams. Since the dams only transmit half of their inheritance, the regression coefficient is doubled to give .614 as the fraction of the variance in 180-day weight that was hereditary. This fraction includes all of the additively genetic fraction of the variance and perhaps about one-fourth of the epistatic variance.

Correlations between Relatives

It was pointed out in the previous section that the dam-offspring correlation for 180-day weight in these data was an underestimate because the dams were selected. To the extent that 180-day weight is hereditary the selection of the parents would tend to skew the distribution of the offspring somewhat toward the heavy weights. Thus the correlations between sibs of various kinds would also be biased in the direction of smallness, although the error
introduced by the selection would not be nearly as large for sib correlations as for the dam-offspring correlation. The distribution of the pigs is given in Figure 2. As was to be expected there was some skewness in the direction of the heavy weight classes. However, this skewness might have arisen from other causes than the selection of the parents.

If the sires were selected more intensely than the dams the correlation between paternal half-sibs would be underestimated more than the correlation between maternal half-sibs. Weights at 180 days were available only on the sires of 929 of the total 1394 pigs. The average weight of these sires was 194.0 pounds. The weights of the dams of 841 pigs averaged 187.4 pounds. The average weight of all the pigs in the generation of the parents on which weights were available was 181.1 pounds. Both parents were selected but the sires averaged twice as far above their generation average as the dams did. However, if allowance is made for a sex difference in weight, the sires were no more intensely selected than the dams were. The average sex difference in these data was seven pounds and the difference in the weight of the sires and the weight of the dams was only 6.6 pounds in favor of the sires. The selection differential for the sires was no higher than that for the dams, and therefore the paternal half-sib correlation should not be underestimated any more than the maternal half-sib
correlation.

In the following sections correlations will be given for litter mates and paternal and maternal half-sibs, although it should be remembered that the observed correlations are probably at least a little lower than they would have been in an unselected population.

**Litter mate and paternal half-sib correlations**

Correlations between 180-day weights of litter mates and paternal half-sibs can be deduced from the analysis of variance between litters and between sires. To be strictly accurate intraclass correlations should be deduced from the variance between groups of similar size (that is, \( k \) in Fisher's (1936) notation should be constant). In these data the number of pigs per litter and the number of pigs per sire were not constant, but corrections for this variance in group size were made by using the average group size minus the variance in group size divided by the total number of pigs. When the variance in group size is small and the number of individual pigs is large, the use of the average group size without this correction introduces only a very little error.

A summary of the analyses of variance for each season of each year (farrow) is given in Table 13. The
Table 13.

Analysis of Variance due to Litter and Sire.

<table>
<thead>
<tr>
<th>Farrow</th>
<th>Source of variance</th>
<th>Intraclass r's</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Total D/f M.S.</td>
<td>Between litters D/f M.S.</td>
</tr>
<tr>
<td>1934 spring</td>
<td>205 926.2</td>
<td>34 2157.0</td>
</tr>
<tr>
<td>1934 fall</td>
<td>86 702.9</td>
<td>12 1699.6</td>
</tr>
<tr>
<td>1935 spring</td>
<td>206 677.5</td>
<td>35 1586.7</td>
</tr>
<tr>
<td>1935 fall</td>
<td>54 918.7</td>
<td>10 2626.4</td>
</tr>
<tr>
<td>1936 spring</td>
<td>186 915.1</td>
<td>38 2373.7</td>
</tr>
<tr>
<td>1937 spring</td>
<td>188 859.5</td>
<td>41 1711.7</td>
</tr>
<tr>
<td>1937 fall</td>
<td>61 901.9</td>
<td>11 2057.0</td>
</tr>
<tr>
<td>1938 spring</td>
<td>400 1315.8</td>
<td>78 3253.1</td>
</tr>
<tr>
<td>Intra-farrow</td>
<td>1386 975.9</td>
<td>259 2364.0</td>
</tr>
</tbody>
</table>
intraclass correlations between litter mates and paternal half-sibs are also given in the last two columns. In the bottom line of Table 13 all of the data are combined, thus obtaining an average picture of the situation which exists among contemporary pigs; that is, after eliminating the effects of differences between one farrowing season and another. The intra-farrow mean square between litters was much larger than the mean square within litters and this difference was highly significant statistically. The mean square between sires* was also significantly larger than the mean square between litters from the same sire.

It was not thought necessary to make any corrections for sex differences in this analysis because the number of pigs of each sex would be nearly balanced within litters and within paternal half-sib groups. Effects of inbreeding and age of dam were probably balanced between the paternal half-sib groups by the manner in which the sows were mated to the boars. That is, the breeding schedules were so arranged that within each farrow the mates of each boar averaged almost the same in age and in their relationship to the boar to which they were bred. However, these two factors

*Only 23 different sires were used, but because some sires were used in more than one breeding season and each farrow was analyzed separately, the data were treated as if there were 37 sires.
would not have been balanced as between litters. They would tend to make the litter mate correlation slightly higher than it would have been if all dams had been the same age and all litters had been equally inbred.

The variance in Table 13 was broken down into the following three constituents:

\[ A = \text{intra-litter variance} = 656.9. \]

\[ B = \text{increase in variance if paternal half-sibs.} \]

\[ C = \text{increase in variance if not paternal half-sibs.} \]

Thus \( A = \) variance found within random pairs of litter mates. \( A + B = \) variance found within random pairs of paternal half-sibs. \( A + B + C = \) variance found within random pairs of non-sibs. Maternal half-sibs were not involved since the analysis was on an intra-farrow basis and a sow of course could have only one litter in one season.

The mean square between litters by the same sire contains \( A + \left( \frac{1394}{267} - 4.73 \right) B. \) The variance in size of litter was 4.73, which is so small that the use of an average group size would have made very little difference in calculating \( B. \)

\[ 5.22 \times B + 656.9 = 2,153.4 \]

\[ B = 286.6 \]

The mean square between sires contains the mean square between litters by the same sire plus \( \left( \frac{1394}{37} - \frac{303.2}{1394} \right) C. \)
Correcting the average group size of paternal half-sibs for
the variance in the group sizes only changed the average
group size from 37.68 to 37.46.

\[
37.46 - 2.153.4 = 4.034.2
\]

\[C = 50.2\]

The variance, broken up into portions ascribable
to the three factors, is shown below.

\[A = 656.9 = 66.1 \text{ per cent}\]
\[B = 286.6 = 29.8 \text{ per cent}\]
\[C = 50.2 = 5.1 \text{ per cent}\]

Total = 993.7 = 100.0 \text{ per cent}

Within litters the variance is 28.3 plus 5.1 or
33.9 per cent less than the total variance which would have
existed in a population of pigs all from different litters
and each by a different sire. This corresponds to an intra-
farrow correlation between litter mates of .359 for 180-day
weight.

Paternal half-sibs are alike only in that they
have the same sire. Therefore the correlation between
paternal half-sibs corresponds to the fraction which the C
term above constitutes of \(A + B + C\), which is .051. If all
of the pigs had been by the same sire but out of different
dams, the total variance would have been reduced 5.1 per
cent.

Since these correlations were deduced from mean
squares that were highly significant statistically, the correlations were highly significant also.

The biometric relation between the 180-day weights of paternal half-sibs (0 and 0') is shown in Figure 11 in terms of Wright's (1934) path coefficients. H and H' are the heredities of the pigs; that is, their genotypes (G₀ and G₀') as modified phenotypically by dominance (D) and epistasis (I). G₆ and G₆' are the genotypes of the dams and Gₛ is the genotype of the sire of the half-sibs. E and E' are the environmental factors affecting the weight of 0 and 0'. m is the correlation between genotypes of parents (the correlation between dams would be about the same as that between sire and dam because of the mating policy), and the other small letters are path coefficients.

If there were no correlations between dominance deviations and epistatic deviations of paternal half-sibs (true for dominance deviations in a random breeding population, but not entirely true for epistatic deviations), then

\[ r_{00'} = h^2 g^2 a^2 s^2 (1+3m) + s^2 r_{EE}' = .051. \]

Since the paternal half-sib correlation was computed on an intra-farrow basis and there was no attempt to treat the progeny of one sire differently from the progeny of another sire, \( s^2 r_{EE}' \) should be close to zero. This correlation was obtained on the offspring produced by all
Figure 11. Biometric basis of the Phenotypic Correlation between Paternal Half-Sibs (0 and 0').
sires in each farrow. (Sires that were used in more than
one farrow have a paternal half-sib group for each farrow in
which they were used and are counted as different sires.)

\[ ab = \frac{1}{2} \sqrt{\frac{1+F'}{1+F}} \]  

where \( F' \) is the inbreeding of the parental
generation and \( F \) is the inbreeding of the offspring genera-
tion. This ab term does not deviate very far from 1/2
except with extreme inbreeding systems. In these data the
average inbreeding of the offspring \( (F) \) was 14.7 per cent
and the average inbreeding of their parents \( (F') \) weighted
according to the number of offspring each produced was 9.3
per cent. Then

\[ ab = \frac{1}{2} \sqrt{\frac{1.093}{1.147}} = .488, \text{ and} \]

\[ m = \frac{2F}{1+F'} = \frac{.294}{1.095} = .269 \]

Assuming \( e^2 r_{EE} \) as equal to zero and substituting
the above values for \( ab \) and \( m \) into the formula,

\[ r_{00} = .24 \left( 1+3(.269) \right) h^2 g^2 = .051 \]

\[ h^2 g^2 = .117 \]

This estimate of the genetic portion of the variance
in 180-day weight is very much less than the other estimates
obtained in this study. As was stated earlier the correla-
tion on which this estimate is based is probably an under-
estimate because of the selection of the parents. Also the
The correlation between genotypes of parents (m) and the ab term are relative to a foundation group of animals born about 1925, whereas the .051 is relative to the genetically more homogenous group born in a single season in this experiment. The correlation between paternal half-sibs would have been larger if it had been computed on a population composed of many lines all descended from the original foundation group of 1925; that is, none of the original genetic heterogeneity had been lost by inbreeding and discarding all but one line as was done in this experiment. Since the phenotypic correlation was relative to the present herd m should also be relative to this herd in order to make the two comparable for computing \( h^2g^2 \). Relative to the present herd m is zero and ab is 1/2, because the average relationship of each boar to his mates was about the same for all boars used in the same season. \( h^2g^2 \) then is 20.4 per cent, which more accurately describes the situation in the present herd than the figure of 11.7 per cent.

Whatever error there was in the paternal half-sib correlation was multiplied in obtaining the additive genetic fraction of the variance (\( h^2g^2 \)). Sampling errors that entered into the correlation were also multiplied by the method of calculating \( h^2g^2 \). The estimate of 20.4 per cent thus obtained from the paternal half-sib correlation probably is below the true value of \( h^2g^2 \), but its sampling error is large.
The biometric relation between litter mates is shown in Figure 12. In this diagram the same symbols are used as those in Figure 11, except that the primes are omitted from the symbols for the litter mate to distinguish it from the paternal half-sib. In terms of path coefficients,

\[ r_{oo} = 2h^2g^2a^2b^2(1+m) + h^2d^2r_{DD} + h^2r^2_{II} + e^2r_{EE} = .339 \]

Substituting the value of 1/2 for ab and zero for m,

\[ r_{oo} = \frac{h^2g^2}{2} + h^2d^2r_{DD} + h^2r^2_{II} + e^2r_{EE} = .339 \]

Obviously it is impossible to determine \( h^2g^2 \) from this correlation without knowing something about the magnitudes of the dominance, epistatic, and environmental correlations between litter mates. There would be some environmental correlation between litter mates because of their close association previous to birth and during the suckling period. Therefore it is logical to suppose that there were many environmental factors that affected litter mates alike but that these were distributed almost at random as between non-litter mates.

Correlations due to dominance \( (r_{DD}) \), which are zero for parent and offspring and half-sib correlations in random breeding populations, tend to make full-sibs more alike than individuals that are not full-sibs. \( (r_{DD} = .25 \) between full-sibs in a random breeding population, but only
Figure 12. Biometric basis of the Phenotypic Correlation between Litter Mates.
\( h^2d^2 \) of this is in the observed correlation and this may be a small fraction.) Epistatic effects of gene combinations are also correlated between litter mates, to a degree not yet thoroughly explored. A consideration of all these factors makes an estimate of the additive genetic portion of the variance impossible from the correlation between litter mates. However, the fact that the observed \( r (.339) \) is so much larger than twice that between paternal half-sibs is strong indication that the environmental effect or the epistatic deviations or both, perhaps with some dominance deviations also, are large enough to be practically important. Dominance deviations alone cannot account for much of this excess unless dominance is complete and all of the recessive alleles are much scarcer than the dominant alleles (in a random breeding population \( d^2 = \frac{q}{2(1-q)} \) times \( g^2 \)).

**Maternal half-sib correlation**

The 267 litters included in this study were from 151 sows. The existence of a number of cases of two or more litters from the same sow made possible a study of the correlation between maternal half-sibs. It was not possible to eliminate the effect of year and season in computing this correlation because a sow could only produce one litter at
one farrowing season. Maternal half-sibs then of necessity must have been born in different years or at least in different seasons of the same year.

In Table 14 the 266 degrees of freedom between litters were broken down into 150 between dams and 116 between litters from the same dam. The mean square between dams was larger than the mean square between litters from the same dam and the difference was statistically significant. The mean square between litters from the same dam included some full-sib litters as well as litters that were only half-sibs.

In Table 15 a separate analysis of variance is shown for the 42 full-sib litters. In this table there were 22 degrees of freedom between full-sib litters from the same dam and the mean square was 1,426.6. The degrees of freedom, sum of squares, and mean square for full-sib litters from Table 15 are included in Table 14. By their use the mean square between litters from the same dam was broken down into that between half-sib litters from the same dam and between full-sib litters from the same dam.

The variance in Table 14 comes from four different sources.

\[ A = \text{variance within litters} = 656.9. \]

\[ J = \text{increase in variance for full-sibs born in different litters}. \]
Table 14.

Analysis of Variance Showing the Effect of Dam.

<table>
<thead>
<tr>
<th>Source of variance</th>
<th>D/f</th>
<th>Sum of squares</th>
<th>Mean square</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total</td>
<td>1393</td>
<td>1,543,958</td>
<td>1,108.4</td>
</tr>
<tr>
<td>Between litters</td>
<td>266</td>
<td>803,614</td>
<td>3,021.1</td>
</tr>
<tr>
<td>Between dams</td>
<td>150</td>
<td>543,739</td>
<td>3,624.9</td>
</tr>
<tr>
<td>Between litters from the same dam</td>
<td>116</td>
<td>239,375</td>
<td>2,040.3</td>
</tr>
<tr>
<td>Between half-sib litters from the same dam</td>
<td>94</td>
<td>222,490</td>
<td>2,430.8</td>
</tr>
<tr>
<td>Between full-sib litters from the same dam</td>
<td>22</td>
<td>31,385</td>
<td>1,426.6</td>
</tr>
<tr>
<td>Within litters</td>
<td>1127</td>
<td>740,344</td>
<td>656.9</td>
</tr>
</tbody>
</table>
Table 15.

Analysis of Variance in Full-Sib Litters.

<table>
<thead>
<tr>
<th>Source of variance</th>
<th>D.f</th>
<th>Sum of squares</th>
<th>Mean square</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total</td>
<td>253</td>
<td>275,076</td>
<td>1,087.3</td>
</tr>
<tr>
<td>Between litters</td>
<td>41</td>
<td>106,631</td>
<td>2,600.6</td>
</tr>
<tr>
<td>Between dams</td>
<td>19</td>
<td>75,246</td>
<td>3,960.3</td>
</tr>
<tr>
<td>Between litters from the same dam</td>
<td>22</td>
<td>31,385</td>
<td>1,426.6</td>
</tr>
<tr>
<td>Within litters</td>
<td>212</td>
<td>168,445</td>
<td>765.7</td>
</tr>
</tbody>
</table>

\( M = \) increase in variance for maternal half-sibs.

\( Y = \) increase in variance if not maternal half-sibs.

The mean square between full-sib litters from the same dam contains \( A + \frac{254}{423} - \frac{3.41}{254} \) \( J \). A correction for the variance in size of full-sib litters only reduced the average size to be used in this formula from 6.05 to 6.04.

\[
6.04 J + 656.9 = 1,426.6
\]

\[
J = 127.4
\]

The mean square between half-sib litters from the same dam is composed of the mean square between full-sib litters from the same dam plus \( \frac{996}{63} - \frac{46.68}{996} \) \( M \).
14.60 M + 1,426.6 = 2,430.8

\[ M = 63.8 \]

The mean square between dams is composed of the mean square between half-sib litters from the same dam plus \( \frac{1394}{151} - \frac{47.21}{1394} \) p.

9.20 F + 2,430.8 = 3,024.9

\[ Y = 129.8 \]

A summary of the variance from the different sources is as follows:

\[ A = 656.9 = 66.8 \text{ per cent} \]
\[ J = 127.4 = 13.0 \text{ per cent} \]
\[ M = 63.8 = 7.0 \text{ per cent} \]
\[ Y = 129.8 = 13.2 \text{ per cent} \]

Total = 962.9 = 100.0 per cent

Although the A terms in both Table 14 and 15 are subject to sampling errors, the A term in Table 14 was used in calculating J because the larger number of observations on which it was based should make it the least subject to sampling errors. It does seem strange that the two A terms should be so different. A test of significance of the mean square within full-sib litters (Table 15) as compared to the mean square within non-full-sib litters proved that the difference between the two was just barely significant.

The probability of such a difference being due to chance was about one in twenty. No logical explanation seems
warranted as to why the mean square between pigs in the same litter should be greater in a sample of data which only included full-sib litters than in the data which did not include full-sib litters. It is true that the dams of the full-sib litters represented a select group. They were above average producers or they would not have been allowed to produce more than one litter. However, this does not seem to offer any explanation for the difference in the intra-litter mean squares between the two groups of data.

When the dams were the same and the sires were different 13.2 per cent (Y) of the variance in 180-day weight disappeared. This corresponds to a correlation of .132 between maternal half-sibs and might be expected to consist of a genetic fraction like that between paternal half-sibs (.051) and an environmental fraction due to permanent differences in the ability of the dams to be good mothers and nurses. Subtracting .051 from .132 yields .081 as an estimate of the importance of those environmental (so far as the pig is concerned) differences between dams. This is probably at least a little too high. M + Y or .070 + .132 gives .202 as the correlation between full-sibs not litter mates. The .070 would include the dominance effects and much of the epistatic effects, along with the genetic effect of having a common sire. Using .051 for the latter yields only .019 for the increase which dominance and
epistasis make in the full-sib correlation over the half-
sib correlation. This indicates that they are not very
important in these data, but this conclusion has a high
sampling error because of the limited numbers involved, the
selection practiced among the parents, and because the esti-
mate is based on differences between mean squares, each
subject to a sampling error.

The correlation between litter mates is \( J + M + Y \)
or \( .130 + .070 + .132 \). The sum of these is \( .332 \) which is
almost the same as the \( .339 \) observed directly. Thirteen
per cent \( (J) \) of the variance was attributed to common
environment as it affected litter mates but not full-sibs
that were born in different litters. In other words 13.0
per cent of the total variance in 180-day weight was caused
by temporary influences which affected litter mates alike
but full-sib litters from the same dam differently. Much of
this was probably caused by differences in age of dam, yearly
and seasonal changes, incidence of infections, temporary
state of health of the dam, and other external factors that
affected litter mates alike. This 13 per cent is clearly
in the environmental part \( (\sigma^2_{RE}) \) of the correlation between
litter mates but some of \( Y \) may also be included in that.

In Figure 13 the correlation between maternal
half-sibs is diagrammed. The same symbols apply as are used
in Figure 11. Double primes are used to designate the
maternal half-sib. The correlation between 180-day weights of pigs that are only maternal half-sibs is:

\[ r_{00} = h^2 g^2 a^2 b^2 (1+3m) + e^2 r_{EE} = .13 \]

This correlation should be the same as the paternal half-sib correlation except for the size of \( e^2 r_{EE} \). A comparison of the two correlations is discussed above.
Figure 13. Biometric basis of the Phenotypic Correlation between Maternal Half-Sibs.
DISCUSSION

Because of environmental correlations between relatives, the magnitude of which is frequently impossible to determine accurately, it is impossible to measure the degree of heritability with an accuracy known to be perfectly correct. Approximations which may describe the situation reasonably well in the population studied can be made but may be too high or too low for other populations in which the environmental variability may be larger or smaller. Non-additive effects of genes (that is, the extent to which the effect of the gene in some combinations and under some conditions is different from its average effect) also affect an analysis of the hereditary variance. These effects of genes are difficult to separate from the environmental variance.

In this study estimates of the genetic fraction of the individual variance in 180-day weight varied from as low as 20 per cent to as high as 61 per cent. This may seem to be a large amount of variability in the results, but when it is considered that all of the answers were dependent on sampling errors that may have been large, it is not surprising that the different answers vary as much as they do. All of the estimates came from the same general set of data (analyzed differently of course), although many pigs could
be included in one analysis but not in another, as for example pigs from unweighed dams could be included in the full-sib and half-sib correlations but not in the regression of offspring on dams. If several different sets of data had been analyzed more confidence could be placed in the results, because the size of the sampling errors would have been reduced and it would be less likely that the condition found in this population was highly unusual and peculiar to it.

The estimates of the genetic fraction of the variance in this study included all of the additively genetic variance but only a part of the variance due to dominance and epistasis. The size of this latter variance could not be judged accurately but the indications are that it is small, and that most of the genetic variance is due to the simple action of genes combining additively. In a study of the weaning weight in the same herd as the one from which the present data came, Bywaters (1937) estimated that the non-additive effects of genes were almost four times as important as the additively genetic effects. This estimate had a high sampling error because it was derived from a comparison of only two correlations (the paternal half-sib and parent-offspring correlations). Obviously, the non-additive effects of genes cannot be this important in the present data. If they were, the variance in 180-day weight would be almost completely genetic and this is highly
improbable. More direct proof of the relatively low importance of dominance and epistasis was found in a comparison of the correlation between full-sibs not litter mates and the correlation between maternal half-sibs. Only about .02 of the increase in the full-sib correlation over the half-sib correlation seemed due to dominance and epistasis. If dominance and epistatic effects were very large, there should be a larger increase than this.

Bywaters (1937) used correlations between relatives in estimating the heritability of weaning weight. In doing so no allowance was made for the fact that the parents might have been a selected group. It is true that in his data selection of the parents on the basis of weaning weight could scarcely have been as important as selection for 180-day weight in the present data. However, if there was any marked selection for weaning weight, the correlation between relatives was underestimated, and consequently the fraction of one-fifth which he obtained for the hereditary portion of the variance in weaning weight was also an underestimate.

The correlations between the 180-day weights of certain relatives are given below along with similar correlations (in parentheses) for weaning weights as given by Bywaters.
Litter mates: \(.339 \pm .453\)
Full-sibs not litter mates: \(.202\)
Offspring-dam: \(.152 \pm .050\)
Maternal half-sibs: \(.132 \pm .114\)
Paternal half-sibs: \(.061 \pm .017\)

With the exception of the correlation between litter mates the correlations were higher for 180-day weight than for weaning weight. This is not surprising because the environment created by the dam should influence weight at weaning more than at 180 days. The longer the pig has been away from the influence of the dam, the more opportunity there has been for its own genes affecting weight to be expressed. Previous to weaning, the influence of these genes is partially covered up by the good or bad nursing and mothering ability of the dam. The higher litter mate correlation at weaning than at 180 days probably results from the large amount of environment common to litter mates previous to weaning. The effect of this environment is lessened from weaning to 180 days. Consequently the correlation at 180 days is less than at weaning in spite of the fact that the hereditary similarity of the litter mates is expressed more fully at 180 days than at weaning.

Other evidence to show that with advancing age the heredity of the individual has a greater influence on its weight is seen in Figure 5. This graph, in which birth
weight, weaning weight, and 180-day weight are plotted against the per cent of inbreeding, shows little if any decrease in birth weight and only a slight decrease in weaning weight with an increase in inbreeding, as compared to the regression line for 180-day weight which has a marked downward slope. Assuming that the inbreeding increased the proportion of less desirable genes for rate of gain (which were in the homozygous condition where their effects could be seen), the effects of these genes were not nearly so noticeable at birth and weaning as at 180 days.
SUMMARY AND CONCLUSIONS

1. A study was made of the influence of heredity on rate of gain in an inbred herd of Poland-China pigs. Weight at 180 days was used as the measure of rate of gain. The data included 1394 pigs in 267 litters which were out of 151 sows and by 23 boars. The average weight of the pigs was 180.3 pounds and the intra-farrow standard deviation was 31.3 pounds. The distribution of the pigs was skewed slightly toward the heavy weights.

2. The average inbreeding of the pigs was 14.7 per cent, and the average inbreeding of their sires and dams was 9.3 per cent. A correlation of \(-.171 \pm .026\) was observed between the inbreeding and the 180-day weight of the pig. The regression coefficient of 180-day weight on the inbreeding was \(-.76\) pounds for each one per cent increase in inbreeding. The correlation between the average weight of the pigs in each litter and the inbreeding of the litter was \(-.190 \pm .059\), and the correlation between the average weight of the pigs in each litter and the inbreeding of the dam was \(-.042 \pm .061\). The inbreeding of the litter accounted for 3.6 per cent of the variance in average litter weight, whereas the effect of the dam's inbreeding was negligible.

3. The intra-litter multiple correlation of 180-
day weight as dependent on weaning weight and birth weight was 0.579. The intra-litter correlation between 180-day weight and weaning weight was 0.550 ± 0.021; 180-day weight and birth weight, 0.426 ± 0.024; and weaning weight and birth weight, 0.485 ± 0.025. From the multiple regression equation it was determined that weaning weight would be twice as important as birth weight in predicting 180-day weight. Including birth weight along with weaning weight added only a little to the usefulness of the latter as a basis for predicting 180-day weight.

4. The variance between pigs born in the spring and pigs born in the fall was 12.8 per cent larger than between pigs born in the same season, but in a descriptive sense limited to these particular data in which there were many more spring pigs than fall pigs only three per cent of the total variance was lost when the seasonal difference was eliminated.

5. The variance between pigs born in different years was 11 per cent larger than that between pigs born in the same year.

6. The age of dam had little influence on the weight of her pigs at 180 days. What little advantage there was in favor of pigs from older dams may have been due to the fact that the older dams were more intensely selected, partly on the basis of litters they had previously produced,
rather than to the fact that they were superior nurses because of the age effect alone.

7. Gilts weighed about four per cent less than barrows and boars at 180 days. The variance between pigs of unlike sex was about two per cent larger than the variance between pigs of the same sex.

8. The intra-lot regression of the variance in 180-day weight on the relationship between 843 pairs of pigs indicated that 30 per cent of the individual intra-lot variance was due to genetic factors and 70 per cent to non-genetic factors.

9. The intra-sire regression of the weight of the offspring from high and low mates on the weight of their dams (.233) indicated that about 46.6 per cent of the variability had a hereditary basis. In computing this regression each set of full-sibs was given equal weight. In data including 101 dams and 756 pigs in which each pig was given equal weight, the intra-sire regression coefficient of offspring on dam was .307 and the estimate of heritability from this figure was 61.4 per cent.

10. Correlations observed between different relatives were: .339 between litter mates, .202 between full-sibs not litter mates, .152 between offspring and dam, .130 between maternal half-sibs, and .051 between paternal half-sibs. Because the parents were selected, these correlations
(particularly the .152 which directly involved the parental phenotype) very likely were underestimates of what would be found in an entirely unselected population.

11. From the correlation between paternal half-sibs it was estimated that the genetic fraction of the variance was about 20 per cent.

12. Eight per cent of the variance in 180-day weight was due to permanent differences in the ability of the dams as nurses and mothers. Thirteen per cent was due to temporary changes in environment as they affected litter mates alike but full-sibs not litter mates differently.

13. The general conclusion that can be drawn from this study is that the genetic portion of the individual variance in 180-day weight in the herd studied was somewhere between 20 and 60 per cent.
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