Composition of Hog Carcasses as Influenced by Heritable Differences in Rate and Economy of Gain

By G. E. Dickerson

AGRICULTURAL EXPERIMENT STATION
IOWA STATE COLLEGE OF AGRICULTURE
AND MECHANIC ARTS

ANIMAL BREEDING SUBSECTION
ANIMAL Husbandry SECTION

BUREAU OF ANIMAL INDUSTRY
UNITED STATES DEPARTMENT OF AGRICULTURE

Cooperating

AMES, IOWA
### CONTENTS

<table>
<thead>
<tr>
<th>Section</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>Summary and conclusions</td>
<td>492</td>
</tr>
<tr>
<td>Introduction</td>
<td>495</td>
</tr>
<tr>
<td>Description of data</td>
<td>497</td>
</tr>
<tr>
<td>Analysis of data</td>
<td>500</td>
</tr>
<tr>
<td>Methods</td>
<td>500</td>
</tr>
<tr>
<td>Definitions of symbols</td>
<td>502</td>
</tr>
<tr>
<td>Variation</td>
<td>503</td>
</tr>
<tr>
<td>Mean squares</td>
<td>503</td>
</tr>
<tr>
<td>Variance components</td>
<td>504</td>
</tr>
<tr>
<td>Heritability estimates</td>
<td>507</td>
</tr>
<tr>
<td>Covariation</td>
<td>510</td>
</tr>
<tr>
<td>Growth rate and carcass composition</td>
<td>510</td>
</tr>
<tr>
<td>Feed requirements and carcass composition</td>
<td>513</td>
</tr>
<tr>
<td>Interpretation</td>
<td>514</td>
</tr>
<tr>
<td>Applications to swine improvement</td>
<td>519</td>
</tr>
<tr>
<td>Literature cited</td>
<td>523</td>
</tr>
</tbody>
</table>
SUMMARY AND CONCLUSIONS

The genetic association of carcass character with rate and economy of gain was studied (a) to obtain information on the composition of heritable differences in growth rate, and (b) to learn whether any change in procedures for selecting towards more rapid and economical gains is desirable to offset indirect effects on the carcasses. Data included feed and gain records from weaning to 225 pounds, as well as carcass yields and measurements, from 578 Poland China, 114 Danish Landrace and 54 Landrace-Poland China crossbreds, which were self-fed at the Iowa Station from 1930 to 1942. The excess of sire and line differences over those between litters by the same sire was used to measure heritable variation and covariation. Conclusions are as follows:

1. Differences in rate of gain to 225 pounds due to the pig's own genes were more largely in fat deposition than in bone and muscle growth. Variance due to the sire's transmitted influence was relatively larger and the coefficient of variation was several times larger for yield of fat cuts, ratio of fat to lean cuts and thickness of backfat than for yield of lean cuts and for length of body and leg. Also, for sire and line deviations, rate of gain to 225 pounds was strongly correlated (.6 or more) positively with fatness and negatively with yield of lean cuts and leg length.

2. Rapid fat deposition and low feed requirements tended to be caused by the same genes, as evidenced by strong correlations of the sire's transmitted influence on feed requirement with his effect on the items indicating fatness (—.6 to —.7) and on yield of lean cuts (.6). A combination of less activity and larger appetite tentatively is considered responsible for the hereditary association of lower feed requirements with more rapid fat deposition.

3. A tendency for poor suckling ability to be caused by the same genes responsible for rapid fat deposition and low feed requirements is strongly suggested. Line and dam variances in fatness and feed requirements were smaller relative to the sire variance than would have been expected if direct maternal and transmitted influences had been independent. Also, there was a positive correlation between the dam's more largely direct influence on feed requirement and her largely transmitted influence on fatness. Pigs of the inbred lines with lower net feed requirements were no fatter at slaughter, ap-
parently because their dams were enough poorer milkers to offset the increased fatness otherwise associated with economical gaining ability.

4. The heritable portion of the variation among pigs from the same breed and season of farrowing was estimated from the correlation between paternal half-sibs as about one-third for weight at 180 days of age and for daily gain after weaning, and as over one-half for feed consumed per pound of gain. For carcass traits the estimates varied from less than one-third for yield of lean cuts to one-half for the measure of fatness and to nearly three-fourths for length of carcass. Environment affecting litter mates alike appeared responsible for one-fourth, one-sixth and one-ninth of the variance in 180-day weight, daily gain and feed requirement, respectively, but for little of the variance in any of the carcass characters except dressing percentage. This method gives overestimates of heritability for feed requirements and carcass fatness and underestimates for yield of lean cuts in the carcass, because of the antagonism noted between good milking ability and rapid, economical fattening ability.

5. Differences between inbred lines in yield of the lean cuts were several times larger than expected from heritable variation within the lines, presumably because good suckling ability and slower fat deposition tended to be caused by the same genes.

6. In breeding for more rapid and economical gains, indirect selection for fatter carcasses would be lessened by:
   (a) Basing selection for growth rate on weight at about 4 months of age, before heritable differences in fatness are fully expressed and while a larger part of the variation is due to differences in the suckling ability of the dams.
   (b) Supplementary selection for good milking ability, as indicated by litter size and average weight per pig at some stage of the suckling period.
   (c) Giving more attention to litter and line averages in selecting for rate and economy of post-weaning gain. These steps would shift the emphasis toward economical gains achieved through good milking ability and rapid early growth rather than through rapid deposition of fat.

7. The observed genetic antagonism between good suckling ability and economical fattening ability is important because: (a) It would make selection less effective for both
characteristics. It may explain in part why progress in swine improvement has been slow, with wide fluctuations between types good in mothering ability but poor in rate and economy of fattening, and the opposite extreme. (b) It suggests that maximum performance can be secured only through judicious crossing of different strains of swine. For example, sows of a cross that has exceptionally good milking ability and prolificacy mated to boars from a strain that excels in rate and economy of post-weaning gains would give maximum litter performance.

8. The evidence presented for genetic correlations between different functional characteristics of swine indicates an advantage of selecting between families or inbred lines, where the net or total effects of the genetic differences will be more readily apparent when the selections are made.
Much emphasis is placed on rate of gain in attempts to improve meat animals. However, little attention is given to composition of the carcass, except as it is indicated by the conformation of the live animals, largely because carcass data can be obtained only for progeny or relatives of the animals chosen for breeding purposes. Rate of gain and composition of carcasses are both determined by the growth rates of the constituent tissues. Hence, if there is more heritable variation in fat deposition, for example, than in growth of bone and muscle, selection for faster total gains would increase the rate of fat deposition more than it would the rate of bone and muscle growth, and fatter carcasses would result.

Selection for lower feed requirements per unit of gain could also cause changes in carcass composition, if heritable differences in feed requirements and in composition of gains are caused, to any important extent, by the same genetic factors. Because of the much higher energy content of fat tissue, it might be supposed that the animals whose gains are more largely fat would require larger amounts of feed per unit of weight gain. However, the following considerations suggest the contrary.

(a) Nutrients absorbed in excess of immediate energy requirements can be stored in large amounts only as fat. Therefore, with a constant feed consumption, more efficient absorption or a lower energy requirement for maintenance would increase the rate of fat deposition more than it would growth of nonfatty tissues and at the same time would reduce the amount of feed required per pound of gain. The major portion of the total feed consumption of even rapidly growing animals is used for maintenance rather than growth. Hence, relatively small differences in maintenance requirements would have an important effect on total amount of feed required per unit of gain. Increased feed consumption,
with unchanged efficiency of absorption and maintenance requirement, also would increase both rate of gain and the proportion of fat in the gains. But the greater amounts of energy stored per pound of fat tissue would be at least partly offset by the shorter period of maintenance per pound of gain for the faster gaining animals.

(b) Little energy is required in converting carbohydrate to stored fat in the animal body—only 5 to 6 percent of the energy in carbohydrates, in experiments with young pigs by Wierzuchowski and Ling (38) and with geese by Benedict and Lee (5), and still less in transferring food fat to storage fat according to Forbes and coworkers (17) — whereas energy required for synthesis of protein tissues may be considerably greater.

(c) On the basis of their studies of experimental obesity in dogs and studies of obesity by other investigators, Heinbecker and associates (23) suggest that variations in pituitary, especially hypothalamic, function may be a primary factor causing food intake to exceed food requirements, with resultant obesity. Secondary depression of thyroid or gonad activity, or both, may reduce metabolic needs without affecting appetite. Hunger may be increased in response to lowered blood glucose caused by excessive tissue consumption of carbohydrate, as in pituitary hypofunction, or in response to the greater influence of adrenal cortical hormone following certain hypothalamic deficiencies. Results reported by Benedict and Lee (5) for mice and by Palmer and coworkers (32) for rats both indicate an association of lower food requirements with increased fat deposition. Ritzman and Colovos (34) have shown how fatness and efficient gains are exemplified in the pig as contrasted with sheep and cattle. Conceivably, then, the genetic changes which would reduce feed requirements per unit of live-weight gain in swine might result in fatter carcasses.

The association of heritable variations in rate and economy of gain with those in carcass composition, to which the present study is limited, is only a part of the larger picture of genetic relationships between important functional characteristics of swine. This picture must be completed before the most effective selection procedures for swine improvement can be devised. The present study (9) was intended to provide information on the nature of heritable differences in rate and economy of gain and, more specifically, to determine whether any change in selection procedures may be desirable because of changes in carcass composition that may result indirectly from selection for rapid and economical gains.
DESCRIPTION OF DATA

The feed and gain records and the carcass yields and measurements of 578 Poland China, 114 Danish Landrace, and 54 Landrace-Poland China crossbred pigs were studied. These pigs were fed at the Iowa Agricultural Experiment Station from 1930 to 1942. The number of pigs represented from each season and type of mating is shown in table 1. Until 1938 the pigs were from a single herd of Poland China or of Danish Landrace, each closed to outside blood, or were first crosses between these two herds. Beginning in 1938 the Poland China hogs were from 12 different lines, each bred within itself. The original Poland China line was subdivided to form six separate lines; and of the remaining six lines, two were started from crosses between four of the other lines. The pigs were fed in groups of litter mates, usually four, chosen at weaning as representative of the entire litter.

The primary data pertaining to rate and economy of gain were: (a) weight at 180 days of age, (b) average daily gain and (c) total feed consumed for 100 pounds of gain, from weaning or shortly thereafter (56, 60 or 70 days) to a live weight of about 225 pounds. Both measures of growth rate—weight at 180 days and daily gain—were used, because the former has been commonly used in selecting for growth rate and the latter measures rate of gain for exactly the same period during which feed records were kept. Weight and daily gain were observed for each pig individually, but feed consumption was obtained only for each pen of litter mates as a unit. The pigs were self-fed a mixed ration and a mineral supplement in concrete pens used for Record of Performance testing. Carcass observations were taken, as a rule, only on the first three pigs to reach 225 pounds among the four in the test litter. Because some of the better gilts among the test litters were occasionally retained for breeding and because of death losses, fewer than three pigs were slaughtered from a few litters. Each pig was kept without feed for 24 hours before slaughter. Carcasses were chilled 48 hours before cutting the right side to measure yields of the wholesale cuts. The following carcass data were studied:

A. Yields, as a percentage of the slaughter weight:
   1. Total chilled carcass (head on, leaf fat and kidney in).
   2. Lean cuts: sum of trimmed ham, trimmed loin and picnic shoulder (Boston butt not taken).
   3. Fat cuts: sum of trimmed belly, fat back and leaf fat.
<table>
<thead>
<tr>
<th>Season of farrowing F—Fall S—Spring</th>
<th>Type of matings</th>
<th>Poland China lines (P.C.)</th>
<th>Landrace (L)</th>
<th>Lines of P.C.</th>
<th>Sires within line or cross</th>
<th>Litters within sire</th>
<th>Within litters</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total 20 39 9 5 22 18 9 16 346 69 25 114 54 40</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**Table 1.** Numbers of pigs slaughtered from each season and type of mating, and source of degrees of freedom within season and breed or cross.
TABLE 1—Continued:

<table>
<thead>
<tr>
<th>Source of Variation</th>
<th>Degrees of freedom</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sires within line or cross</td>
<td>1 0 0 0 0 1 0 0 37 7 0 9 7 62</td>
</tr>
<tr>
<td>Litters within sire</td>
<td>2 6 0 0 2 1 0 3 62 5 4 20 6 111</td>
</tr>
<tr>
<td>Within litters</td>
<td>13 26 6 3 14 11 6 9 227 45 17 72 36 485</td>
</tr>
</tbody>
</table>

* Line B was founded on a cross of C and F and line A from a cross of K and G. Hence, litters from these lines were considered as either A or B line, during the seasons in which the same sire produced litters from sows of two different lines. Six degrees of freedom between lines of sows mated to same boar were omitted from the final analysis.

† These include 3 pigs each from crosses of lines CXD and EXK.
B. Index of fatness:
   4. Ratio of fat cuts to lean cuts, x 100.
C. Dimensions of chilled carcass:
   5. Sum of backfat thicknesses at first and last ribs and at last lumbar vertebra (inches).
   6. Length of body, from aitchbone to anterior edge of first rib (inches).
   7. Length of hind leg, from aitchbone to upper border of hoof (inches).

It is recognized that backfat, clear plate and leaf fat would have been more strictly fat cuts. Also, trimmed loin, Boston butt, and the skinned ham and picnic would have been more satisfactory as lean cuts. However, weights of clear plate and Boston butt were not always taken, and the hams and picnics were not skinned. Variation in yield of trimmed belly is mostly in fat, as shown by Warner et al. (36), whereas variation in yield of trimmed ham and picnic is more largely in muscle and bone. Hence, the classification of cuts indicated above seems justifiable for the present purpose of characterizing the fatness of the hogs from the available carcass data. Similarly, thickness of backfat has been shown to be closely correlated with ether extract in the edible portion of the carcass by Hankins and Ellis (21).

The fact that all pigs were slaughtered at nearly the same live weight means that the pigs having the high yields of fat will automatically have the lower yields of lean, except as their total carcass yields are higher. However, slaughtering all hogs at nearly the same live weight should not of itself introduce any automatic association of carcass composition with rate of gain or feed consumption. Any errors in final weights and differences in amount of “fill” at weighing would tend to cause carcass yields to be negatively correlated with observed rate of gain and positively with feed eaten per unit of gain in live weight, whether or not slaughter weight was standardized. Hale and Godbey (19) have shown that weighing errors are very small, but differences in fill may be more important.

ANALYSIS OF DATA

METHODS

The magnitude of any genetic change in carcass composition that would result from selection for rapid gains and low feed requirements per unit of gain depends on (a) the extent to which differences among individual pigs in rate and economy of gain are heritable or transmissible, (b) the de-
### TABLE 2.—ANALYSIS OF VARIANCE AND COVARIANCE.

<table>
<thead>
<tr>
<th>Source of mean square</th>
<th>D/F</th>
<th>Intralitter, $V(A)$</th>
<th>Dam, $\bar{V}(B)$</th>
<th>Sire, $\bar{V}(C)$</th>
<th>Line, $\bar{V}(D)$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lines of Poland China within seasons</td>
<td>40</td>
<td>.42$V(G)$ + $V(E)$</td>
<td>2.81[$.17V(G)$ + $0.68V(G_m)$ + $V(E_m)$]</td>
<td>4.33[$.17V(G)$]</td>
<td>4.77[$(0.35V(G)+V(G_m))$]</td>
</tr>
<tr>
<td>Sire progenies within line and season</td>
<td>82</td>
<td>.46$V(G)$ + $V(E)$</td>
<td>2.88[$.20V(G)$ + $0.80V(G_m)$ + $V(E_m)$]</td>
<td></td>
<td>5.08[$.20V(G)$]</td>
</tr>
<tr>
<td>Litters, within sire, line and season</td>
<td>111</td>
<td>.46$V(G)$ + $V(E)$</td>
<td>2.83[$.20V(G)$ + $0.80V(G_m)$ + $V(E_m)$]</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pigs within litters</td>
<td>485</td>
<td>.46$V(G)$ + $V(E)$</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

* When each source of variation is independent of all others. For the composition of the mean products between two variables 1 and 2, the corresponding covariance is substituted for each of the variances, for example, $\text{Cov} (G_1G_2)$ for $V(G)$. See page 502 of the text for definitions of symbols.
gree to which heritable deviations in carcass composition and
in rate and economy of gain are correlated, that is, are
merely different expressions of the same genes, and (c) the
size of heritable differences in composition of carcasses. In-
formation on these points was obtained from an analysis of
variance and covariance (table 2), in which the excess of
differences between sire progenies and lines of breeding over
differences between litters by the same sire was used as a
measure of the heritable variation and covariation. The usual
parent-offspring relationships could not be used because none
of the observations except weight at 180 days could be ob-
tained for the parents.

DEFINITIONS OF SYMBOLS

In the analysis of variance or of covariance indicated in
table 2, and elsewhere in this paper, definitions of symbols
are as follows:

\[ V(A), V(B), V(C), \text{ and } V(D) \text{ are the variances (average }
\text{squared deviations from mean per individual) from intra-}
litter, dam, sire and line differences, respectively, with
\text{expected values (8) of}
\]

\[ V(A) = \frac{(1 - f')}{2} . V(G) + V(E), \]

\[ V(B) = \frac{(1 + f' - 2f)}{4} [V(G) + 4 V(G_m)] + V(E_m), \]

\[ V(C) = \frac{(1 + f' - 2f)}{2} . V(G) \text{ and } V(D) = \]

\[ 2(f - f_o) [V(G) + V(G_m)] \]

\[ k, k' \text{ and } k'' \text{ are the exact numbers of times that dam,}
sire and line deviations, respectively, are represented in
each mean square, as calculated from the actual unequal fre-
quences from formulas developed earlier (25).}

\[ V(G) \text{ is the variance from additive effects of gene differ-
ences among pigs in a noninbred population.}
\]

\[ V(M) \text{ is the variance from environment and from gene}
interaction that is alike for litter mates, and is further divis-
able into variance from heritable differences, } V(G_m), \text{ and }
\text{from nonheritable differences, } V(E_m), \text{ among the dams.}
\]

\[ V(E) \text{ is the variance from nonheritable differences among}
litter mates.}

\[ f', f \text{ and } f_o \text{ are Wright's (39) average inbreeding coef-
fi cients for parents, for offspring and for all possible crosses} \]
between the lines, respectively. Within lines, \( f^r = 0.08 \) and \( f = 0.14 \), but for the 40 degrees of freedom between lines of Poland Chinas, \( f^r = 0.15, f = 0.24 \), and \( f_o = 0.06 \).

**VARIATION MEAN SQUARES**

An analysis of the variation among pigs of the same breed or cross and farrowed in the same season is given in table 3. Variation in slaughter weight was significantly greater between than within the lines of Poland Chinas. Hence, the mean squares for the carcass items were adjusted for linear intralitter regression on slaughter weight. Differences between sire progenies were larger than those between litters of the same sire for every characteristic in table 3 except weight at slaughter, and particularly so for carcass fatness and length of leg and carcass. Only in yield of lean cuts and in leg length were differences between lines of Poland

**TABLE 3.—ANALYSIS OF VARIANCE IN RATE AND ECONOMY OF GAIN AND IN CARCASS ITEMS FOR POPULATION SHOWN IN TABLES 1 AND 2.**

<table>
<thead>
<tr>
<th>Variable</th>
<th>( (1) )</th>
<th>( (2) )</th>
<th>( (3) )</th>
<th>( (4) )</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Within litters</td>
<td>Litters within sires</td>
<td>Sires within line or cross</td>
<td>P.C. lines within season</td>
</tr>
<tr>
<td><strong>GAIN AND FEED ITEMS:</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>180-day wt.—lbs.</td>
<td>485</td>
<td>1219**</td>
<td>1530</td>
<td>1682</td>
</tr>
<tr>
<td>Daily gain—lbs.</td>
<td>0.0163</td>
<td>0.0306**</td>
<td>0.0333</td>
<td>0.0420</td>
</tr>
<tr>
<td>Feed Gain ( \times 100 )—lbs.</td>
<td>(820)†</td>
<td>1652**</td>
<td>2473*</td>
<td>2449</td>
</tr>
<tr>
<td>Slaughter wt.—lbs.</td>
<td>33</td>
<td>36</td>
<td>34</td>
<td>64**</td>
</tr>
<tr>
<td><strong>CARCASS ITEMS:</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Yields, as % of live weight</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total carcass</td>
<td>2.19</td>
<td>3.58**</td>
<td>4.79</td>
<td>4.40</td>
</tr>
<tr>
<td>Lean cuts</td>
<td>1.36</td>
<td>1.66</td>
<td>2.14</td>
<td>4.18**</td>
</tr>
<tr>
<td>Fat cuts</td>
<td>1.79</td>
<td>2.31*</td>
<td>3.71*</td>
<td>3.49</td>
</tr>
<tr>
<td>Ratio: Fat cuts/Lean cuts ( \times 100 )</td>
<td>22.9</td>
<td>26.4</td>
<td>49.3**</td>
<td>56.4</td>
</tr>
<tr>
<td>Depth of backfat—in.</td>
<td>.186</td>
<td>.264**</td>
<td>.409*</td>
<td>.350</td>
</tr>
<tr>
<td>Length of carcass—in.</td>
<td>.409</td>
<td>.746**</td>
<td>1.276**</td>
<td>1.417</td>
</tr>
<tr>
<td>Length of hind leg—in.</td>
<td>.294</td>
<td>.376*</td>
<td>.649**</td>
<td>.884</td>
</tr>
</tbody>
</table>

† The mean squares for the carcass items were adjusted for the linear intralitter regression on slaughter weight, so that degrees of freedom within litters are 484 (Snedecor (35) Section 12.7).

‡ The intra-litter variance of 820 for feed/100 pounds of gain is based on 419 degrees of freedom and was obtained from an analysis (11) of data on Duroc hogs fed individually from 72 days of age to a live weight of 225 pounds at the Alabama Agricultural Experiment Station.

** Indicates statistical significance at the .01 level and * at the .05 level.
China's appreciably larger than those between boar progenies within lines. However, inbreeding was higher and the numbers per sire and per dam were smaller in the seasons from which the degrees of freedom between lines came than in the seasons from which the degrees of freedom within lines came (tables 1 and 2). Thus the error appropriate for the line mean square would be smaller than the sire mean square in table 3. Also, the expected line variance, \( V(D) \), is reduced about one-fourth because of the average relationship between the lines (see table 2). If sire differences between lines of Poland China are included with those within lines, intraseason differences among all sires (102 d. f.) are significant at the .10 level or below for all items. Variation is considerably greater between litters of the same sire than among litter mates for all items except the ratio of fat to lean cuts.

VARIANCE COMPONENTS

To show the relative importance of genetic and environmental sources of variation, the variances (mean squared deviations per individual) due to intralitter, dam, sire and line variation are calculated in table 4. The sire variance provides an estimate of the total variance due to the pigs' own genes in a herd of one breed and inbred no more than the foundation stock of the lines studied here (i.e. \( V(G) = 5 V(C) \)). The sire and intralitter variances together provide an estimate of the nonheritable variance among litter mates (i.e. \( V(E) = V(A) - .46 V(G) = V(A) - 2.3 V(C) \)). Under the usual assumption of independence of the deviations from different sources, variance from direct environmental influence of the dam (e.g. intra-uterine nourishment and suckling ability) may be estimated from the dam and sire variances (i.e. \( .8V(G_m) + V(E_m) = V(B) - V(C) \)). In the foundation stock, variance from the sow's direct environmental influence would be somewhat greater than in these data (e.g. \( V(M) = V(G_m) + V(E_m) = 1.11 [V(B) - V(C)] \) if \( V(G_m) = V(E_m) \)). However, some of the same genes of the dam may affect both her transmitted influence and her direct maternal influence on the performance of her pigs. The dam variance would be increased by a positive correlation between the dam's transmitted and her direct influence and would be reduced by a negative one, since \( V(B) = .2V(G) + .8 V(G_m) + .8 \text{Cov}(GG_m) + V(E_m) \). Correlation between transmitted and direct sow influences on performance would affect the line variance, \( V(D) = .35 [V(G) + V(G_m) + 2 \text{Cov}(GG_m)] + V(E_m) \), relatively more than the dam variance, since \( V(G) \) and \( V(G_m) \)
**TABLE 4.—ESTIMATES OF GENETIC AND ENVIRONMENTAL VARIANCES.**

<table>
<thead>
<tr>
<th>Variable</th>
<th>Intra-litter V(A)</th>
<th>Dams V(B)</th>
<th>Sires V(C)</th>
<th>Lines V(D)</th>
<th>In non-inbred population V(G)</th>
<th>V(M)</th>
<th>V(E)</th>
</tr>
</thead>
<tbody>
<tr>
<td>180-day wt.—lbs.</td>
<td>485.1</td>
<td>259.1</td>
<td>58.6</td>
<td>68.6</td>
<td>292.8</td>
<td>222.8</td>
<td>350.4</td>
</tr>
<tr>
<td>Daily gain—lbs.</td>
<td>.01631</td>
<td>.00503</td>
<td>.00147</td>
<td>.00161</td>
<td>.00736</td>
<td>.00398</td>
<td>.01292</td>
</tr>
<tr>
<td>Feed Gain × 100—lbs.</td>
<td>820†</td>
<td>293.6</td>
<td>158.8</td>
<td>72.1</td>
<td>794.1</td>
<td>149.7</td>
<td>454.7</td>
</tr>
<tr>
<td>Slaughter wt.—lbs.</td>
<td>33.5</td>
<td>.8</td>
<td>.0</td>
<td>5.9</td>
<td>0</td>
<td>.8</td>
<td>33.5</td>
</tr>
</tbody>
</table>

Yields, as % live wt.:

<table>
<thead>
<tr>
<th></th>
<th>Total carcass</th>
<th>Lean cuts</th>
<th>Fat cuts</th>
<th>Ratio: Fat cuts to Lean cuts x 100</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>2.186</td>
<td>.490</td>
<td>.234</td>
<td>4.33</td>
</tr>
<tr>
<td></td>
<td>1.362</td>
<td>.104</td>
<td>.094</td>
<td>.178</td>
</tr>
<tr>
<td></td>
<td>1.789</td>
<td>.182</td>
<td>.274</td>
<td>1.75</td>
</tr>
</tbody>
</table>

Ratio:

<table>
<thead>
<tr>
<th></th>
<th>Fat cuts</th>
<th>Lean cuts</th>
<th>Depth of backfat—ins.</th>
<th>Length of carcass—ins.</th>
<th>Length of hind leg—ins.</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>22.92</td>
<td>1.22</td>
<td>.186</td>
<td>.409</td>
<td>.294</td>
</tr>
</tbody>
</table>

* Calculated from the formulas and mean squares in tables 2 and 3, respectively, as follows:

\[
V(A) = (1); \quad V(B) = \frac{2.83}{(4) - V(E) + 0.42 + (2.81 + 4.33) \cdot 17}; \quad V(C) = 5V(M) - 2.81 \cdot 0.85V(B); \quad V(D) = \frac{4.77}{(4) - V(E) + 0.42 + 4.33 \cdot 17}; \quad V(G) = 5V(C); \quad V(M) = 1.11V(B) - V(C); \quad V(E) = V(G_m) + Cov(GG_m) + V(E_m), \quad V(E) = V(E_m).
\]

† See footnote, table 3.

are equally represented, and V(Em) is absent, in the line variance.

The dam and line variances in table 4 furnish considerable evidence for negative correlation between transmitted and direct sow influences on pig performance. If G and Gm are independent, V(B) must always be larger than the sire variance, V(C), except for sampling errors. Actually V(B) was only about two-thirds V(C) for yield of fat cuts, one-half V(C) for leg length, and one-fourth V(C) for ratio of fat to lean cuts. These are larger discrepancies than seem reasonably ascribable to chance. Furthermore, if other factors have not reduced line differences, V(D) should be at least 1.75 V(C) in this analysis, especially for variables much influenced by direct maternal environment. However, V(D) was found to be negligible for depth of back fat. for
total yield of carcass and for yield of fat cuts, and much smaller than expected for all other observations except yield of lean cuts, for which $V(D)$ was nearly five times $V(C)$. These results strongly suggest that the correlation between transmitted and direct maternal influences is negative for fatness and positive for muscle development in the carcass. Nonrandom variation among litter mates could arise from competition for food. Such variation would tend to be the same in different litters, and would contribute less to the mean square between litters than to the within-litter mean square. It could have caused an underestimate of $V(B)$. However, it would not have biased the estimates of $V(C)$ or $V(D)$. Hence, the explanation that antagonism exists between direct and transmitted maternal influences is favored. $V(D)$ was only slightly larger than $V(C)$ for 180-day weight and for average daily gain after weaning and was only one-half $V(C)$ for feed per unit of gain. This suggests that the genes which cause pigs of a line to gain more economically (and perhaps to a lesser degree those causing more rapid gain) also cause the sows of that line to be poorer mothers,

**TABLE 5.—MEANS, VARIABILITY IN A NON-INBRED POPULATION, AND FRACTIONS OF TOTAL VARIANCE ASCRIBED TO GENETIC AND ENVIRONMENTAL SOURCES.**

<table>
<thead>
<tr>
<th>Observation</th>
<th>Mean ±46 pigs</th>
<th>Standard deviation*</th>
<th>Coef. var.</th>
<th>Fraction of variance ascribed to:</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Pig's own genes V(G)</td>
</tr>
<tr>
<td>180-day wt.—lbs.</td>
<td>196.9</td>
<td>29.4</td>
<td>14.9</td>
<td>.34</td>
</tr>
<tr>
<td>Daily gain—lbs.</td>
<td>1.392</td>
<td>.156</td>
<td>11.2</td>
<td>.31</td>
</tr>
<tr>
<td>Feed × 100—lbs.</td>
<td>394.2</td>
<td>37.4</td>
<td>9.5</td>
<td>.57</td>
</tr>
<tr>
<td>Slaughter wt.—lbs.</td>
<td>218.5</td>
<td>5.9</td>
<td>2.7</td>
<td>.00</td>
</tr>
<tr>
<td>Yields, as % live wt.:</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total carcass</td>
<td>79.9</td>
<td>1.78</td>
<td>2.2</td>
<td>.38</td>
</tr>
<tr>
<td>Lean cuts</td>
<td>34.9</td>
<td>1.28</td>
<td>3.7</td>
<td>.29</td>
</tr>
<tr>
<td>Fat cuts</td>
<td>19.2</td>
<td>1.55</td>
<td>8.1</td>
<td>.52</td>
</tr>
<tr>
<td>Ratio:</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fat cuts × 100</td>
<td>55.0</td>
<td>5.57</td>
<td>10.1</td>
<td>.59</td>
</tr>
<tr>
<td>Lean cuts</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Depth of backfat—in. (Sum of three places)</td>
<td>4.44</td>
<td>.51</td>
<td>11.5</td>
<td>.54</td>
</tr>
<tr>
<td>Length of carcass—in.</td>
<td>30.49</td>
<td>.84</td>
<td>2.8</td>
<td>.73</td>
</tr>
<tr>
<td>Length of hind leg—in.</td>
<td>23.17</td>
<td>.64</td>
<td>2.8</td>
<td>.58</td>
</tr>
</tbody>
</table>

* Standard deviation = $\sqrt{V(G) + V(M) + V(E)}$

† $V(M)$ approximates $V(G_m) + Cov(GG_m) + V(E_m)$. See footnote *, table 4.

‡ See footnote †, table 3.
thus cancelling much of the line variation in performance of the pigs.

**HERITABILITY ESTIMATES**

In table 5 the portion of the total individual variance ascribed to heritable differences in the pigs themselves (G) was about one-third for 180-day weight and for daily gain after weaning, and over one-half for feed required per pound of gain. For the carcass traits, it varied from less than one-third for yield of lean cuts to nearly three-fourths for length of carcass. Environment which is alike for litter mates (M) appeared to account for one-fourth, one-sixth and one-ninth of the variance in 180-day weight, daily gain and feed requirement, respectively, but seemed to have little influence on any of the carcass characters except dressing percentage.

The actual results to be expected from individual selection for a given trait are affected not only by the fraction of the variance due to the pig’s own genes (G) but also by that due to heritable differences in the dam’s direct environmental influence (G_m) and by any tendency for the transmitted and maternal influences to supplement or cancel one another because of being merely different expressions of the same genes, r(GG_m). It can be shown from fig. 1 that heritability should correspond to

\[
H_1 = \frac{V(G) + 0.5V(G_m) + 1.5\text{Cov}(GG_m)}{V(G) + 0.5V(G_m) + \text{Cov}(GG_m) + V(E_m) + V(E)},
\]

in terms of the variances of table 4. This definition of heritability includes only the permanent effects of selection on individual performance. It corresponds to the regression of offspring performance on average performance of the parents, provided (a) environmental influences on the dam’s performance do not affect the environment she provides for her pigs, and (b) only a negligible part of the regression is due to favorable gene combination effects which will be broken up and lost in later generations.

The present data provide no method of estimating V(G_m), V(E_m) and Cov(GG_m), separately. Hence, heritability is calculated in table 5 as the portion of the variance due to the pig’s own genes. This is

\[
H_2 = \frac{V(G)}{V(G) + V(G_m) + \text{Cov}(GG_m) + V(E_m) + V(E)},
\]

for the variables in which dam variance equalled or exceeded sire variance (B > C). It is evident that if Cov(GG_m)

\[
\text{In terms of the path coefficients of fig. 1, the heritability or regression of transmitting ability (G + G_m) on individual performance (X) is}
\]

\[
b_{G_m} + b_{G_m^a} = g_t^2 + g_m^2 + 1.5g_tg_mr_{G_m},
\]
is zero, actual heritability, $H_1$, is greater than $H_2$ to the extent that $G_m$ is a source of variation. When $V(G_m)$ is at all important, the actual heritability $H_1$ will be still larger if $\text{Cov}(GG_m)$ is positive but smaller if $\text{Cov}(GG_m)$ is negative. However, the size of $V(G_m)$ and the size and direction of $\text{Cov}(GG_m)$ will have just the opposite effect on the estimates of $H_2$ in table 5. That is, $H_2$ will be smaller the larger $V(G_m)$ and the more positive $\text{Cov}(GG_m)$ but larger the more negative $\text{Cov}(GG_m)$. Since the data suggest that $r(GG_m)$ is strongly negative for carcass fatness and for feed per unit of gain, $H_2$ may overestimate actual heritability ($H_1$) for these variables. For example, it was estimated in table 4 that $V(G) = 794$, $V(M) = 150$ and $V(E) = 455$ for feed requirement. If $V(G_m) = V(E_m) = 250$, then $V(M) = 500 + \text{Cov}(GG_m) = 150$; $\text{Cov}(GG_m) = 150 - 500 = -350$; and $r(GG_m) = -\frac{350}{446} = -.79$.

With these assumptions,

$$H_1 = \frac{794 + 125 - 525}{794 + 250 - 350 + 250 + 455} = \frac{394}{1399} = .28,$$

as compared to $H_2 = \frac{794}{794 + 250 - 350 + 250 + 455} = \frac{1399}{1399} = .57$.  

This tendency to overestimate heritability was reduced in the case of yield of fat cuts, ratio of fat to lean and length.
of leg, for which $B < C$, by calculating heritability in table 5 as

$$H_3 = \frac{1.25 V(B) + 3.75 V(C)}{1.25 V(B) + 3.75 V(C) + E} = \frac{V(G) + V(G_m) + Cov(GG_m) + 1.25 V(E_m)}{V(G) + V(G_m) + Cov(GG_m) + 1.25 V(E_m) + V(E)}. $$

However, these values of $H_3$ are still too large as compared to $H_1$ unless $V(G_m)$ and $V(E_m)$ are both zero, because $V(E_m)$ is included as heritable and $V(G_m)$ is given too much and $r(GG_m)$ too little weight.

The present estimates of $H_2$ for 180-day weight and daily gain (.34 and .31) are thought to be as much as .06 too high, because the variance among litter mates was reduced by selecting from each litter the four pigs whose weaning weights were most nearly average for that litter. For example, Whatley (37) found the intra-litter variance of 180-day weight to be 657 in the Iowa Poland China herd when all pigs of each litter were included, as compared to 485 in the present analysis of litter samples. The selection on size at weaning probably did not bias the estimates of heritability for the carcass observations appreciably because it would reduce the intra-litter variance in the carcass items only to the extent of their squared correlation with weaning weight. The intra-litter variance of feed requirements was taken from the Alabama data (11), which included all pigs raised in each litter, for the period from 72 days of age to a final weight of 225 pounds. Hence, the estimates of $H_2$ for feed requirement in table 5 would be unaffected by the reduced intra-litter variation in rate of gain in the Iowa data.

The actual heritability of traits that are much influenced by heritable differences in the dam's direct influence would be estimated with least bias from the regression of offspring performance on the average performance of the parents. This was done in another study of data from the Alabama selection experiment (11), and the regressions found were .26 for feed requirement and .43 for daily gain. These results support the view that the variance method of the present study has given overestimates of heritability for feed requirements as compared to daily gain (.57 and .31, respectively, in table 5) because of a larger negative correlation between transmitted and direct maternal influences for feed requirements than for rate of gain.

Earlier estimates of heritability for some of the items studied here are in reasonable agreement with the present findings. Among pigs fed in Danish performance tests, Lush (28) concluded that heritability was about one-half for length of body and thickness of backfat, one-fourth for aver-
age daily gain, as compared with present estimates of .73, .54
and .31, respectively (table 5). Other estimates for herita-
bility of growth rate are .3 to .4 for 180-day weight by What-
ley (37); .25 for 168-day weight by Baker et al. (3); .3 for
180-day weight by Hazel et al. (22); .14 for 180-day weight
and .31 for daily gain by Comstock et al. (6); and .2 to .4
for daily gain and .27 for 168-day weight by Nordskog et al.
(31). Krider et al. (27) have estimated heritability of 180-
day weight from cumulative effects of selection as about .18.

Of particular significance in table 5 are the higher pro-
portions of variance due to the pig's own genes and the
larger coefficients of variation for the three measures of
fatness as compared with yield of the lean cuts (H₃ = .52,
.59, and .54 vs. 29; c.v. = 8.1, 10.1 and 11.5 vs. 3.7). Al-
though heritability was high for length of carcass (.74)
and for length of hind leg (.58), and hence also for rate
of bone growth, the coefficients of variation were small
(2.8) for both. These facts indicate clearly that heritable
differences in rate of gain to slaughter weight were more
largely differences in rate of fat deposition than in rate of
muscle and bone growth. It is, therefore, apparent that
effective selection solely for a more rapid rate of gain would
tend to increase fatness at slaughter. The analysis of co-
variance which follows, provides more direct quantitative
evidence concerning the association of heritable differences
in carcass characters with those in rate of gain, as well as
with those in feed requirement.

COVARIATION
GROWTH RATE AND CARCASS COMPOSITION

The differences between sire progenies and between lines
are more largely genetic than difference between litters by
the same sire (see table 2). Likewise, the simple correla-
tions between carcass items and the measures of rate and
economy of gain in table 6 are more largely genetic when
based on means of lines or of sire progenies within lines (the
rows with 39 and 61 degrees of freedom) than when based
on means of litters within sire progenies (the row with 110
degrees of freedom). Hence, the direction and statistical
significance of the genetic correlations may be deduced
from these simple correlations. For example, the correla-
tion between depth of backfat and average daily gain was
.43 among lines and .31 among sire progenies within lines,
both of which differ significantly in the positive direction
from the correlation of —.07 among litters of the same sire.
This indicates a significant tendency for the genes which
cause more rapid gain also to cause thicker backfat at 225
TABLE 6.—CORRELATIONS OF CARCASS OBSERVATIONS WITH LIVE WEIGHT AT 180 DAYS (W), AVERAGE DAILY GAIN (R) AND FEED REQUIRED FOR 100 POUNDS OF GAIN (F).

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>Degrees of freedom</th>
<th>Variable</th>
<th>Yields, as % livewt.</th>
<th>Ratio: Fat cuts</th>
<th>Depth of backfat</th>
<th>Length of carcass</th>
<th>Length of hind leg</th>
<th>r for P=.05, P=.01</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Total carcass</td>
<td>Lean cuts</td>
<td>Fat cuts</td>
<td>Lean cuts</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Poland China lines within seasons</td>
<td>39</td>
<td>W</td>
<td>.00</td>
<td>-.31</td>
<td>.44†</td>
<td>.35†</td>
<td>-.08</td>
<td>-.28</td>
</tr>
<tr>
<td></td>
<td></td>
<td>R</td>
<td>-.12</td>
<td>-.41†</td>
<td>.46†</td>
<td>.50†</td>
<td>-.12</td>
<td>-.46</td>
</tr>
<tr>
<td></td>
<td></td>
<td>F</td>
<td>-.02</td>
<td>.02</td>
<td>.12</td>
<td>.08</td>
<td>-.02</td>
<td>.21</td>
</tr>
<tr>
<td>Sire progenies within line or cross and season</td>
<td>61</td>
<td>W</td>
<td>-.18</td>
<td>-.07</td>
<td>.07</td>
<td>.08</td>
<td>.16</td>
<td>-.02</td>
</tr>
<tr>
<td></td>
<td></td>
<td>R</td>
<td>-.10</td>
<td>-.18</td>
<td>.24</td>
<td>.24</td>
<td>.31†</td>
<td>-.06</td>
</tr>
<tr>
<td></td>
<td></td>
<td>F</td>
<td>.15</td>
<td>.20</td>
<td>-.14†</td>
<td>-.17†</td>
<td>-.04</td>
<td>.10</td>
</tr>
<tr>
<td>Litters within sire, line or cross and season</td>
<td>110</td>
<td>W</td>
<td>-.19</td>
<td>-.01</td>
<td>-.01</td>
<td>-.02</td>
<td>-.11</td>
<td>.02</td>
</tr>
<tr>
<td></td>
<td></td>
<td>R</td>
<td>-.19</td>
<td>-.06</td>
<td>.02</td>
<td>.04</td>
<td>-.07</td>
<td>-.10</td>
</tr>
<tr>
<td></td>
<td></td>
<td>F</td>
<td>.27</td>
<td>.03</td>
<td>.22</td>
<td>.17</td>
<td>.26</td>
<td>.01</td>
</tr>
<tr>
<td>Among litter mates</td>
<td>484</td>
<td>W</td>
<td>-.19</td>
<td>-.18</td>
<td>.02</td>
<td>.08</td>
<td>-.01</td>
<td>.05</td>
</tr>
<tr>
<td></td>
<td></td>
<td>R</td>
<td>-.21</td>
<td>-.24</td>
<td>.07</td>
<td>.14</td>
<td>-.09</td>
<td>.01</td>
</tr>
<tr>
<td></td>
<td></td>
<td>F</td>
<td>.21</td>
<td>.10</td>
<td>.05</td>
<td>.00</td>
<td>.12</td>
<td>.05</td>
</tr>
<tr>
<td>Within line or cross and season</td>
<td>657</td>
<td>W</td>
<td>-.18</td>
<td>-.12</td>
<td>.02</td>
<td>.06</td>
<td>-.00</td>
<td>.03</td>
</tr>
<tr>
<td></td>
<td></td>
<td>R</td>
<td>-.19</td>
<td>-.19</td>
<td>.09</td>
<td>.14</td>
<td>.10</td>
<td>-.03</td>
</tr>
<tr>
<td></td>
<td></td>
<td>F*</td>
<td>.21</td>
<td>.10</td>
<td>.05</td>
<td>.00</td>
<td>.12</td>
<td>.05</td>
</tr>
</tbody>
</table>

† Indicates statistical significance at the .01 level for the deviation from the corresponding correlation among litters within sire, line and season (110 d. f.), based on Fisher’s z-test.
†† Indicates the .05 level of significance for such deviations.
* The correlation among litter averages within the same line or cross and season, with 172 degrees of freedom.

pounds live weight. The correlations of daily gain with yield of fat cuts and with the ratio of fat to lean were similar to those with backfat thickness. However, the correlations of daily gain with yield of the lean cuts and with length of hind leg were almost exactly the reverse. This is in agreement with the small negative correlation between daily gain and total carcass yield. There was no noticeable difference between the line, the sire and the litter correlations of daily gain with length of carcass. These results indicate, as did the variance analysis, that more of the genes which increase the individual’s own rate of gain act by accelerating fat deposition than by stimulating bone and muscle growth. Such genes therefore tend to produce fatter carcasses at a given live weight. The correlations of the carcass items with weight at 180 days were similar to those with average daily gain, but were smaller, particularly among sire progenies within lines.

In table 7, the correlations are shown separately for the
TABLE 7.—INDIRECT ESTIMATES OF CORRELATION* OF CARCASS OBSERVA-
TIONS WITH W, R AND F, FOR HERITABLE AND ENVIRONMENTAL
DEVIATIONS.

<table>
<thead>
<tr>
<th>Source of deviations</th>
<th>Variable</th>
<th>Yields as % liveweight</th>
<th>Correlations with</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Total carcass</td>
<td>Lean cuts</td>
</tr>
<tr>
<td>Sire's influence</td>
<td>W</td>
<td>-.23</td>
<td>-.36</td>
</tr>
<tr>
<td>within lines, V(C)</td>
<td>R</td>
<td>.21</td>
<td>-.61</td>
</tr>
<tr>
<td></td>
<td>F†</td>
<td>-.13</td>
<td>.64</td>
</tr>
<tr>
<td>Dam's influence</td>
<td>W</td>
<td>-.14</td>
<td>.36</td>
</tr>
<tr>
<td>within lines, V(B)</td>
<td>R</td>
<td>-.15</td>
<td>.36</td>
</tr>
</tbody>
</table>
| Non-heritable influ-
| ences among litter-
| mates, V(E)          | W        | -.18         | -.13      | -.10     | -.04                     | -.44          | .15            | .08            |
|                      | R        | -.35         | -.15      | -.23     | -.13                     | -.41          | -.01           | -.05           |

*These estimates are based on covariances and variances obtained by difference between two or more independent sets of mean squares and products. Hence, their sampling errors are not limited to the range +1 to −1.
† Having no estimate of the intra-litter covariance between feed requirement and the carcass items, these correlations could not be calculated for the intra-litter environmental (E) and the dam (B) deviations, and the sire variances and covariances were calculated as follows:

\[ V(C') = \frac{V(E)}{5.08} = 0.1V(B) + V(C). \]  

(V(C) = variance of carcass deviations, V(B) = variance of dam deviations, V(E) = variance of non-heritable deviations among littermates.)

These provide a clearer quantitative picture of the same relationships indicated indirectly by the simple correlations of table 6. The correlations for the sire deviations (upper row in table 7) indicate the extent to which a pig's own inherited carcass composition and rate and economy of gain are merely different physiological expressions of the same genes. There is excellent agreement between the genetic correlations of carcass composition with rate of gain in table 7 and the corresponding independently derived correlations among means of Poland China lines in table 6. The latter were somewhat smaller, apparently because the correlation between dam deviations in rate of gain and fatness at final weight (table 7) was slightly negative. The negative correlation of rate of gain with backfat thickness and with yields of carcass, especially of fat cuts, for non-heritable deviations among litter mates is presumed to be largely a consequence of differences in fill having opposite effects on gain in live weight and carcass yields.

In earlier studies of some of these relationships there was no attempt to separate the gross correlations into their genetic and environmental components. Those gross correlations (table 8) are in substantial agreement with the corresponding total correlations in the present study (bottom
line of table 6). For example, the total correlation for back-fat thickness was .10 with rate of gain and .12 with feed requirement in the present data, values similar to those summarized in table 8. This agreement for the total correlation does not necessarily mean that the correlations among means of sire progenies and litters and among litter-mates, had these been calculated in earlier studies, would also harmonize with present results. However, the similarity in the gross correlations does suggest that the present data were comparable to those studied by others.

FEED REQUIREMENTS AND CARCASS COMPOSITION

Feed requirement per unit of gain and rate of gain would be expected to show opposite associations with carcass composition because of the negative total correlation of about .7 between the two (Evvard et al., (15); Lush, (28); and present data, including the pigs for which carcass records were not taken). In general this was found to be the case. In table 6 the correlations of feed requirement with the three items indicating fatness were negative among sire progenies and differed significantly in the negative direction from the same correlations among litters of the same sire. Evidently the sires which transmitted ability to make the more economical gains also transmitted a tendency to store the larger amounts of body fat before reaching market weight.

TABLE 8.—SUMMARY OF TOTAL CORRELATIONS WITHIN BREEDS OF RATE AND ECONOMY OF GAIN WITH THICKNESS OF BACKFAT AND CARCASS LENGTH, AS REPORTED IN THE LITERATURE.

<table>
<thead>
<tr>
<th>Carcass trait</th>
<th>Correlation with</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Rate of gain</td>
</tr>
<tr>
<td>thickness of backfat</td>
<td>.05†</td>
</tr>
<tr>
<td></td>
<td>.14‡</td>
</tr>
<tr>
<td></td>
<td>.13§</td>
</tr>
<tr>
<td></td>
<td>Positive†</td>
</tr>
<tr>
<td>length of body</td>
<td>None*</td>
</tr>
<tr>
<td></td>
<td>-.12†</td>
</tr>
<tr>
<td></td>
<td>-.09†</td>
</tr>
<tr>
<td></td>
<td>Negative</td>
</tr>
</tbody>
</table>

* Correlations among litter averages quoted by Lush (28) from studies of Danish data by Jesperson and Madsen in 1931 and by Lauridsen in 1934.
† Correlations among 236 litter averages for 1 year by Lush (28).
‡ Correlations with age at live weight of 88 kg. for individual pigs, obtained by Folke Jarl (26), with sign reversed.
§ Same as †, reported by Axelsson (1).
|| Correlation with growth during later stages of fattening in data from Netherlands stations reported by Rijssenbeek in 1936, as quoted by McMeekan (30).
† Donald (14).
The deviations of the correlations between feed and the carcass items among lines of Poland Chinas in table 6 from the corresponding correlations among sire progenies indicate that, for line deviations, higher feed requirement was associated with longer legs and possibly with longer bodies and lower dressing percentage. However, the line deviations do not show the clear cut association of lower feed requirement with increased yields of fat which the sire deviations showed (table 7). In fact the same positive correlation between fatness and feed requirements which is evident among litters of the same sire in table 6 also shows up to some extent among the means of lines within seasons. Since the line, and especially the dam, deviations are partly due to differences in the direct maternal influence of the dams, it appears that maternal environment favorable to low feed requirements is also associated with less fat storage at 225 pounds. However, it is not clear from these correlations alone whether the reduced fatness is the direct result of an increased milk supply from the sow or is the indirect result of slower fattening ability transmitted by better milking sows to their pigs. Environmental differences in fill also would tend to cause low feed requirements to be correlated with smaller carcass yields and shorter legs. This tendency would affect the correlation among litters of the same sire more than among line means, and may partly explain the larger positive values for the former.

INTERPRETATION

Changes in the character of hog carcasses will inevitably result if rate of growth is changed more for some tissues or parts than for others. Two related lines of evidence from the present study show that increasing inherent growth rate by selecting directly for more rapid gains to market weight within a breed or line will also result in fatter and shorter legged hogs with little change in dressing percentage. First, heritable variation, relative to the mean, was several times larger for amount of fat than for amount of muscle and bone among carcasses of hogs similar in breeding and slaughtered at a live weight of 225 pounds. Second, heritable increases in rate of gain (i.e., reduced ages at slaughter) were associated with more fat, less muscle and bone and shorter legs in the carcass. Both kinds of evidence indicate that selecting the faster gaining individuals for breeding will increase inherent growth rate more for fatty tissue than for muscle and bone. The association between rate of gain and amount of fat in the carcass would have been much more pronounced had the carcasses been studied at a constant age instead of a fixed live weight.
The present results indicate that the negative correlation between heritable deviations in feed requirements \((F)\) and carcass fatness \((Y)\) is about as large as the corresponding positive correlation between rate of gain \((R)\) and carcass fatness (table 7). This indicates that there is a negative association between \(F\) and \(Y\) independent of \(R\). That is, \(r_{FU} = -0.6\) to \(-0.7\), so that \(r_{FY}\) could not exceed \(-0.6\) to \(-0.7\) if all of \(r_{UY}\) were due to \(r_{FU}\). It would appear that among individuals of the same inherent rate of gain, those which have inherently lower nutritional requirements for maintenance and activity deposit more fat but grow less muscle and bone.

Some results of Axelsson (2) indicate that the correlation between rapid gain and low feed requirements is due to lower daily maintenance requirements, as well as to shorter periods of maintenance, for the rapidly gaining pigs. He found rather large negative correlations (\(-0.56\) for Large White and \(-0.68\) for Improved Landrace) between litter averages for rate of gain and feed consumed per unit of gain in excess of calculated maintenance requirements for the number of days actually on feed. This would indicate that only a part of the negative correlation found between rate of gain and total feed per unit gain can be due to the shorter period of body maintenance for the more rapidly growing pigs. These correlations seem entirely too large to be completely explained as the automatic result of differences in fill at final weight affecting calculated rate of gain and feed consumption oppositely. Therefore, Axelsson’s results suggest either that the faster growing pigs have lower daily energy requirements for maintenance and activity or that they absorb a larger proportion of the nutrients in the feed, or both. In either case they would have larger amounts of nutrients above immediate energy requirements available for storage as depot fat. This would help explain the observed genetic association of increased fat deposition with faster gains and with lower feed requirements per unit of gain.

The conclusion that lower feed requirements and more rapid fat deposition are caused by the same genes in swine is supported by an experiment with genetic obesity in mice by Dickerson and Gowen (10) which was suggested by the results of the swine study. It was found that the extreme fat deposition of the “Yellow” mouse was the result of its inherited lower food requirements for maintenance and activity and higher food consumption. Food requirements per unit of gain in weight were little more than half as large for Yellow mice as for their Non-yellow litter mates. Furthermore, Palmer and Kennedy (32) and their students at the
Minnesota station have shown that rats of their high-efficiency strain gain more rapidly and require much less food per unit of gain, and that their gains are more largely fat, than rats of the low-efficiency strain. Heat losses for maintenance, activity and heat increment were enough smaller for the efficient strain to account for most or all of their storage of a larger proportion of the food energy than the inefficient strain. All of these results emphasize the distinction between the increase in feed requirements during the fattening period of a given animal, which is widely quoted, and the reduced feed requirements associated with the ability of some animals to fatten more rapidly than others, which seems to have been ignored.

The indirect effect which selection for more rapid and economical gains has on carcass composition may also be affected by heritable differences in the sow's direct influence on her pigs' performance and by any tendency for transmitted and direct maternal influences to be caused by the same genes. Antagonism between good suckling ability and ability to fatten rapidly with low feed requirements is strongly suggested by the apparent cancelling of the direct by the transmitted influences on carcass fatness (V(B) and V(D) both smaller than V(C) in table 4) and on feed requirements and rate of gain (V(D) much smaller than expected, especially for feed requirement). In this connection it should be mentioned that Lush (28) found the correlation between maternal half-sib litters to be smaller than that between paternal half-sib litters for feed per unit gain (.12 vs. .29) and for thickness of backfat (.34 vs. .44) and belly (.28 vs. .42), whereas these two kinds of correlations were similar for rate of gain (.23 and .24) and for length of body (.41 and .39). Further evidence from the present study is that the correlation of feed requirement with carcass fatness was positive among litters of the same sire and to a lesser degree among line averages, but was negative among the transmitted sire deviations (tables 6 and 7). Also, the correlation between rate of gain and carcass fatness was negative for dam deviations but was positive for sire deviations (table 7).

As a working hypothesis, it is assumed that the direct environmental influence of the inherently better milking dam is to increase fat deposition more than bone and muscle growth before weaning. This would reduce feed requirements and increase rate of gain after weaning. Hazel and coworkers (22) have shown that there is a positive correlation between gain before and after 56 days for the variation due to litter environment. A tendency for the sows with better milking ability to transmit genes for slower
fat deposition, faster bone and muscle growth, higher feed requirements, but only slightly slower total gain could then explain the positive correlation between the dam’s predominantly direct influence on feed requirement and her more largely transmitted effect on the fatness of her pigs at 225 pounds. It could also explain why the tendency for the dam and line variances to be small relative to the sire variance was most pronounced for carcass fatness, less for feed requirements and least for daily gain and 180-day weight, and why the line variance in yield of lean cuts was much larger than expected. Under these assumptions, direct and transmitted influences on yield of lean cuts would tend to be positively correlated, at least among line means, where differences in fatness were very small.

Superficially the nutritional experiments of McMeekan (30) suggest that favorable maternal environment would reduce rather than increase the fatness of pigs at 225 pounds. If this were true in the present data, one would need to assume that the better milking sows transmitted genes more largely for fat gains, tending to cancel their direct influence, in order to explain the small dam and line variances in carcass fatness. This assumption seems unreasonable because good milking ability is generally associated with poor fattening ability and a more active and nervous temperament, as in different breeds of cattle, particularly. Also, it would require a positive correlation between direct and transmitted influences on feed requirement, since fatter carcasses and lower feed requirements tend to be caused by the same genes. Actually a negative correlation was indicated by the line variance being much smaller than expected if direct and transmitted influences were uncorrelated. An explanation which seems to fit all the facts reasonably well is that McMeekan’s “low plane” of nutrition from birth to 16 weeks seriously retarded bone and muscle growth, whereas the variation in inherent suckling ability of sows in the present study was not sufficiently extreme or prolonged to affect materially growth of any but the fat tissue. Crampton (7) and Donald (14) have also concluded that the relationship between McMeekan’s nutritionally induced growth variations and carcass fatness is not representative of the association existing among pigs fed similarly.

The studies of large, intermediate and small-type Poland China swine reported by Zeller (40), Hankins (20), Hetzer and Brier (24) and Phillips and Zeller (33) provide additional evidence that inherently greater fat deposition is associated with poorer sucking ability, as well as with poorer inherited fertility and prenatal nutrition and mortality. The fat, small-type pigs gained more slowly and re-
quired a little more feed than those of the less fat, large
and intermediate types. This appears to have been due to
poorer maternal environment provided by the small-type
sows, as evidenced by the smaller litters and lighter weights
at birth and weaning for small-type pigs, rather than to
any contradiction of the genetic association of fatness with
rapid post-weaning gain and low feed requirement which
is demonstrated by the present study. The large and small-
type strains were presumably developed largely by selecting
for differences in conformation, which were found by Dick-
erson and McClurg (13) to be largely differences in fat-
ness. Hence it may not be surprising that the association
of hereditary fatness with poor reproductive and suckling
ability (directly causing higher feed requirement and slower
gain) should be much more pronounced among the three
distinct types of Poland Chinas than among the inbred
lines in the present study (table 6), in which selection for
conformation was secondary and toward the intermediate
type. The fact that rate of gain was highest and feed re-
quirement was lowest for the intermediate type of Poland
suggests a curvilinear relationship between inherent fatness
and the nutritional influence of the sow. That is, as fatness
declines below an optimum, the improved suckling ability
of the dam may not compensate for the pig's own inher-
ently slower and more expensive gains. This is possibly
because maternal nutrition was already adequate. However,
as fatness increases beyond the optimum, the reduced suck-
ling ability of the sows may reduce gains and increase feed
costs after weaning, in spite of the pig's own inherently
more rapid gain and lower feed requirements.

The decline in litter size when selection is directed solely
toward more rapid gain in the Illinois Hampshire swine ex-
periment (16), and in Goodale's mice, may be the result
of the association between rapid fattening ability and poorer
fertility and suckling ability. The fact that litter size also
declined in the Hampshire line selected for slow growth may
well be the result of the indirect selection for reduced via-
bility and of the progressively greater underdevelopment of
gilts. The latter may have been especially important be-
cause of selecting the slowest growing gilts in each gener-
ation and attempting to breed them at nearly the same age
as the fastest gainers in the rapid line. This interpreta-
tion is supported by the good performance of the one gen-
eration of slow line sows which were retained to farrow at
2 years of age.

---

5 Also correspondence with Prof. B. W. Fairbanks and his successor, Prof.
J. L. Krider.
6 Correspondence with Dr. H. D. Goodale, Mount Hope Farm, Williamstown,
Mass.
The present findings help in understanding why the Illinois rapid and slow-gaining lines of Hampshire swine showed little or no difference in dry feed required per unit of live weight gain after two generations of selection on rate of gain, particularly for the spring litters fed on pasture. The expected lower feed requirement of the rapid-gaining line would tend to be offset by the indirect selection for poorer suckling ability, and also for less utilization of available pasture because of the reduced activity and greater appetite for grain which is an attribute of rapid fattening ability. The opposite indirect effects of selection would operate in the slow-gaining line. Pigs of the slow-gaining line were reported to be more active and excitable, and to keep the pasture grazed more closely than pigs of the rapid-gaining line.

Unfortunately for our purpose, carcass data have not been obtained in published experiments with selection for rate and economy of gain in swine. However, after three generations of selecting solely for slow and for rapid growth to 180 days of age in two lines of Hampshire swine in the Illinois experiment (16), pigs of the rapid-gaining line were shorter in leg and deeper bodied at 200 pounds than pigs of the slow-gaining line. Similarly, Grimes (11) (18) has observed that pigs from the line of Durocs selected for economical gains appear to be fatter at 225 pounds than pigs of the line selected for high feed requirements. In the present data, the correlations based on line averages (table 6) indicate that selection for either faster gains or lower feed requirements would constitute indirect selection for shorter legs at 225 pounds.

MacArthur’s (29) controlled selection experiment with 60-day body weight in mice closely parallels the Illinois experiment with swine. He found that the strain selected for rapid growth became less active and fatter, with shorter appendages relative to body length, than the strain selected for slow growth rate, in agreement with the results in swine. The major difference was that mature skeletal dimensions were larger and size of litters and mature body weight became about twice as great in the “rapid” as in the “slow”-growing strain. Heritable differences in gain were evidently more largely muscular and skeletal in mice than in swine.

APPLICATIONS TO SWINE IMPROVEMENT

There is some evidence that selecting directly for lower feed requirements might not increase carcass fatness, in spite of the large negative correlation between transmitted
deviations in feed requirement and fatness. The most direct
evidence is that the lines with lower feed requirements
showed no tendency to be fatter at slaughter even though
there was a strong and highly significant tendency for pigs
of the more rapidly gaining lines to be fatter at 225 pounds
(table 6). These correlations among line means are of
special significance, because they are based on equal propor­
tions of the heritable differences in the dam’s direct in­
fluence \( G_m \) and in the pig’s own performance \( G \) (table
2). Inherently low feed requirements and good milking
ability of the dams both would tend to lower feed require­
ments and to increase fatness for a line. However, these
two characteristics appear to be genetically antagonistic.
Thus the lines with lower net feed requirements are appar­
ently enough poorer in milking ability to offset the increased
fatness associated with more economical gaining ability.

One advantage of selecting between lines rather than be­
tween individuals would be that any undesirable effects of
genes for economical gains on reproduction or lactation would
be evident when the selections were made. Selections could
be based on the net or total effects of genes influencing
economy. This objective would be partly attained by se­
lecting mainly on the basis of litter averages. The heritable
differences between litter mates would tend to be ignored
and heritable differences in the dam’s influence would re­
ceive relatively more attention. For the dam’s influence,
reduced fatness was evidently more closely associated with
smaller feed requirement than with increased rate of gain
(tables 6 and 7). Thus selection for lower feed requirements
would be less likely to increase carcass fatness if based on
litter averages instead of individual feed records. Also,
more of the reduction in feed requirements would be due
to improved suckling ability. However, it appears that in
selecting for more rapid gain to market weight, use of litter
averages would only partially eliminate the indirect selec­
tion for fatness.

It seems rather clear that selecting for rapid gain up to
about 4 months of age would be less likely to increase
fatness at 225 pounds than selecting for rate of gain to
the slaughter weight. McMeekan (30) has emphasized the
marked increase in rate of fat deposition relative to rate of
muscle growth which occurs between 3 and 4 months
of age in swine. Insofar as muscle growth and fat deposition
are influenced by different groups of genes or oppositely by
some genes, heritable differences in early rate of gain would
be more nearly independent of inherent fatness of gains.
This supposition harmonizes with the fact that in the present
data, transmitted deviations in 180-day weight (gain to an
average live weight of 197 pounds) and fatness of carcass were less closely correlated than those in daily gain (weaning to 225 pounds) and fatness. Also, Donald (14) found that backfat thickness at slaughter had a negative correlation with weaning weight but a slightly positive one with rate of gain from 10-12 weeks to slaughter. Likewise, Crampton (7) found that fatness of carcass was nearly independent of the rate of gain from 60 days to 100 pound live weight. The finding of Hazel and associates (22) that the genetic correlation was no higher than + .7 between gains in consecutive 56-day periods and was only + .45 between gains in the 0-56 and in the 112-168 day periods also indicates that different genes affect muscle growth and fat deposition. Hazel included line differences with sire differences in estimating the heritable variation. Thus any tendency for rapid fattening and poor suckling ability to be caused by the same genes would reduce the net sire plus line deviations in gain more for the 112-168 day period than for earlier periods. This may explain why his estimate of heritability was lower for gain in the 112-168 day than in the 56-112 day period (.17 vs. .28), as compared with the estimates by Nordskog et al (31) of .45 and .28, respectively, which were based on sire deviations within lines. The foregoing suggests that selection for rapid gains to about 4 months of age would probably reduce indirect selection for fatness and yet improve rate of gain to market weight about as rapidly as selection based directly on rate of gain to slaughter weight.

The surprisingly large line differences in yield of the lean cuts (V(D) = 5 V(C), instead of the expected 1.75 V(C), tables 3 and 4) are of special interest, because they indicate opportunity for effective selection between lines for higher yields of the more valuable cuts. These large line differences, together with the fact that dam and sire influences were nearly equal (table 4) suggest that good suckling ability of sows directly increased muscle and bone growth as well as fat deposition of pigs to weaning and, again, that good suckling ability was correlated with inherently slower fat deposition after weaning.

The general effect of genetic antagonism between the different desirable characteristics is to make selection less effective for all of them. Hence, the negative genetic correlation of economy of gain and rapid fattening with suckling ability and with yield of lean cuts in the carcass helps explain why progress in swine improvement has been slow, even though much of the variation in each of the desired characteristics is hereditary. If selection is directed solely toward rapid and economical fattening, progress may be fairly rapid for a time. But this selection soon will need
to be interrupted while attention is given to repairing the
damage that has been done to yield of lean meat and suck­
ling ability. The net result of this "see-saw" process is
exceedingly slow progress over long periods of time with
wide fluctuations between the two extreme types of swine.
Basing selection on a properly balanced combination of all
the desired characteristics would avoid wide fluctuations in
any one of them, but progress would remain slower than if
different genes controlled each characteristic.

If the pleiotrophic association of rapid fat deposition with
poor suckling ability is as strong as suggested by this study,
it will have an important bearing on the usefulness of inbred
lines of swine and the way they should be combined to ob­
tain the largest litters, most rapid gains and lowest feed
requirements. For example sows of a cross giving out­
standing prolificacy and milking ability but mediocre fattening ability could be mated with boars of a line which
transmits exceptionally rapid and economical gains in crosses,
to obtain maximum performance. Although it would prob­
ably be possible to obtain a high level of both inherent suck­
ling and fattening ability in a single line of breeding, as
appears to be the case with certain breeds of swine, it seems
unlikely that the maximum combination of the two char­
acters can be obtained in any one line or one breed.

The present finding that heritable differences in rate of
gain within a breed or inbred line are largely differences
in rate of fat deposition apparently does not apply to the
genetic increase in rate of gain which generally is obtained
from crossing distinct lines or breeds (i. e. from increasing heterozygosity). Dickerson and coworkers (12) found that
line-cross pigs gained much more rapidly than the inbreds
but were not quite as fat at a live weight of 225 pounds
and required just as much feed per pound of gain. Professor
Winters\(^7\) has also found that crosses between two lines
originating from four different breeds gave exceptionally
rapid gains and high yields of the lean cuts at a live weight
of about 200 pounds. Apparently hybrid vigor increases
the early growth of bone and muscle enough so that slaughter
weight is reached at the same or a somewhat earlier stage
of the fattening or finishing period, as compared with the
inbred pigs. The fact that feed requirements were no lower
and viability was better in the crosses also suggests that
hybrid vigor consists of an increased rate of metabolism
and activity, which would tend to reduce or delay fat deposi­
tion. If this is so, hybrid vigor offers promise for improving
rate of gain and yields of the lean cuts but is likely to reduce
feed costs only indirectly as it is used to improve the suckling
ability of sows.

\(^7\)Correspondence with Prof. L. M. Winters of the Minnesota Experiment
Station.
LITERATURE CITED


