

A COVARIANCE ANALYSIS BETWEEN PUREBRED
AND CROSSBRED POPULATIONS
OF SWINE

By

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in partial fulfillment of the requirements
for the degree of
DOCTOR OF PHILOSOPHY
May, 1966

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ACKNOWLEDGMENTS

The author wishes to express his sincere appreciation to the following persons for their contributions to this investigation: Dr. James A. Whatley, Jr., Associate Director of the Oklahoma Agricultural Experiment Station, for suggesting this problem and for his guidance and counsel during the initial stages of the analysis; Dr. Irvin T. Omtvedt, Associate Professor of Animal Science, for his encouragement and assistance in the analysis of the data and in the preparation of this thesis; Dr. Richard L. Willham, Associate Professor of Animal Science, for his advice and assistance in the development of much of the statistical procedures; members of the Mathematics and Statistics Department, especially Dr. David L. Weeks, Associate Professor, and Edgar A. Butler and William Accola, Graduate Assistants, for their assistance in the analysis of the data; fellow graduate students, who, collectively, gave much encouragement and counsel; and his wife, Edythe, for her understanding, encouragement, and assistance.

TABLE OF CONTENTS

	Page
INTRODUCTION	1
REVIEW OF LITERATURE	3
MATERIALS AND METHODS	9
Data	9
Overall Analysis	10
RESULTS AND DISCUSSION	22
Least Squares Estimates	22
Heritabilities	31
Genetic Correlations	33
Correlated Response to Selection	37
Sire Components of Covariance	41
SUMMARY	50
LITERATURE CITED	53
APPENDIX	58

LIST OF TABLES

Table	Page
I. The Coefficient Matrix ($X'X$) and the Right Hand Side ($X'Y$)	13
II. The Analysis of Variance	15
III. Analysis of Variance for Obtaining Within Line Sire Component of Variance	17
IV. Analysis of Variance for Obtaining Sire Component of Covariance	18
V. Least Squares Estimates of the Effects of Station, Year, Season, Sex, Line, Age of Dam, Inbreeding of Litter, Management, and Litter Size at Weaning on 56 Day Weight, Postweaning Average Daily Gain, and Probed Backfat	23
VI. Analysis of Variance for Adjusted 56 Day Weaning Weight	26
VII. Analysis of Variance for Postweaning Average Daily Gain	28
VIII. Analysis of Variance for Probed Backfat	30
IX. A Comparison of Heritability Estimates in the Purebred and Crossbred Populations	32
X. A Comparison of Genetic Correlations Between Three Traits Within Purebred and Crossbred Populations	34
XI. Ratios of Correlated Response to Direct Response for the Three Traits	39
XII. Analysis of Variance of 56 Day Weight	42
XIII. Analysis of Variance of Average Daily Gain	42
XIV. Analysis of Variance of Probed Backfat	43

LIST OF TABLES (Continued)

Table	Page
XV. Values Necessary to Evaluate the Genetic Covariance Between Purebred Paternal Half-sibs and Between Purebred and Crossbred Paternal Half-sibs	44
XVI. Values Necessary for Comparing Crossbred Response From Intra-population Selection and From Reciprocal Recurrent Selection	46
XVII. Ratio of the Crossbred Population Mean Change From Reciprocal Recurrent Selection to the Crossbred Population Mean Change From Purebred Mass Selection in Both Sexes	48
XVIII. Comparison Among 56 Day Weight, Average Daily Gain, and Probed Backfat of the Variable Quantities Used to Evaluate R in the Comparison of RRS Against Intra-population Mass Selection	48
XIX. Comparison Among 56 Day Weight, Average Daily Gain, and Probed Backfat of the Variable Quantities and the Computed R in the Comparison of RRS Against Intra-population Half-sib Family Selection	48
XX. Analysis of Variance of 56 Day Weight in the Purebred Population	59
XXI. Analysis of Variance of Average Daily Gain in the Purebred Population	59
XXII. Analysis of Variance of Probed Backfat in the Purebred Population	60
XXIII. Analysis of Variance of 56 Day Weight in the Crossbred Population	60
XXIV. Analysis of Variance of Average Daily Gain in the Crossbred Population	61
XXV. Analysis of Variance of Probed Backfat in the Crossbred Population	61
XXVI. Analysis of Variance of 56 Day Weight in the Purebred Pigs Having both 56 Day Weight and Average Daily Gain Observations	62
XXVII. Analysis of Variance of 56 Day Weight in the Crossbred Pigs Having Both 56 Day Weight and Average Daily Gain Observations	62

LIST OF TABLES (Continued)

Table	Page
XXVIII. Analysis of Variance of 56 Day Weight in the Purebred Pigs Having Both 56 Day Weight and Probed Backfat Observations	62
XXIX. Analysis of Variance of Average Daily Gain in the Purebred Pigs Having Both Average Daily Gain and Probed Backfat Observations	63
XXX. Analysis of Variance of 56 Day Weight in the Crossbred Pigs Having Both 56 Day Weight and Probed Backfat Observations	63
XXXI. Analysis of Variance of Average Daily Gain in the Crossbred Pigs Having Both Average Daily Gain and Probed Backfat Observations	63
XXXII. Analysis of Covariance Between 56 Day Weight and Average Daily Gain Within the Purebred Population . . .	64
XXXIII. Analysis of Covariance Between 56 Day Weight and Average Daily Gain Within the Crossbred Population . .	64
XXXIV. Analysis of Covariance Between 56 Day Weight and Probed Backfat Within the Purebred Population	64
XXXV. Analysis of Covariance Between 56 Day Weight and Probed Backfat Within the Crossbred Population	65
XXXVI. Analysis of Covariance Between Average Daily Gain and Probed Backfat Within the Purebred Population	65
XXXVII. Analysis of Covariance Between Average Daily Gain and Probed Backfat Within the Crossbred Population	65

INTRODUCTION

It has been estimated that approximately 85 percent of all pigs slaughtered in the United States are crossbreds. Perhaps a large portion of these crossbred pigs are not produced by well planned and executed crossbreeding programs, but it still reflects the great importance of this mating system to the swine industry. One reason for crossbreeding is that of combining desirable traits from several breeds into one population. Another reason for crossbreeding is the heterosis, or hybrid vigor, that results in certain performance traits. Breeding systems, specifically reciprocal recurrent selection, had been designed by plant breeders to maximize the expression of heterosis in corn. This selection scheme was later modified for use in hogs and several research institutions initiated breeding experiments to evaluate its effectiveness.

Reciprocal recurrent selection for improving crossbred performance involves selection among purebreds based on the performance of crossbred half-sibs by the same sire. In order to evaluate the effectiveness of this method of selection certain specific population parameters must be estimated. These parameters are: 1) S_{cc} , or the paternal half-sib covariance among individuals within a two population cross resulting from crossing males of one breed on females of another; 2) S_{cp} , or the paternal half-sib covariance between purebred and crossbred half-sibs having the same sire, and 3) the phenotypic variance of the selection

criterion within both the purebred and the crossbred populations. With these parameter estimates, the predicted response in the crossbred population from a given amount of selection pressure applied both by reciprocal recurrent selection and by various methods of intra-population selection can be obtained. Ratios of the predicted response from reciprocal recurrent selection to the predicted response from intra-population selection can then be used as a measure of the relative effectiveness of reciprocal recurrent selection.

The objectives of this study were: 1) to estimate specific population parameters within both purebred and crossbred populations of swine for 56 day weight, average daily gain, and probed backfat, 2) use the estimates to evaluate the relative effectiveness of reciprocal recurrent selection versus various methods of intra-population selection for improving crossbred performance, and 3) use these same estimates to predict trait response to indirect selection within each of the two populations.

REVIEW OF LITERATURE

Of the breeding techniques developed for increasing hybrid vigor in corn, that of reciprocal recurrent selection for specific combining ability proposed by Comstock et al. (1949) has been modified for adaptation to animals on an experimental basis. This modification, as outlined by Comstock and Robinson (1956), consists of mating males of a third breed on two-breed cross females. This permits heterosis for maternal traits to be obtained by the use of crossbred dams. Selection of replacements for the pure breeds is made on the basis of their crossbred progeny performance. Experimental evidence on the amount of progress that can be obtained by this type of selection is limited. Also, only limited experimental evidence is available on the rate of improvement in cross performance when intra-population selection procedures are applied to the pure breeds.

The most extensive breeding experiments to evaluate the utility of reciprocal recurrent selection procedures in animal populations have been those with Drosophila (Bell et al., 1955; Rasmuson, 1956; Kojima and Kelleher, 1963). Using two experiments, Bell et al. (1955) compared reciprocal selection, recurrent cross selection, and inbreeding and hybridization with conventional closed population selection based on individual and family merit. In their first experiment covering 16 generations the closed population method was inferior to all other selection methods for increasing egg production. In their second

experiment, which lasted for 39 generations, response of egg production to the closed population method of selection was rapid, reaching a peak early in the trial and then remaining essentially plateaued. The two populations under recurrent cross and reciprocal selection showed continuous improvement and surpassed the plateaued population at about the fifteenth generation. The performance of the progeny produced from crosses between the populations under continuous inbreeding was essentially equal to those under reciprocal selection.

Further analysis of this experiment (Bell, 1957; Brown and Bell, 1961) suggested that the cause of the plateau in the closed population was a loss of additive genetic variance.

Rasmuson (1956) likewise compared reciprocal recurrent selection against closed flock selection for egg production in Drosophila. After 20 generations of selection the reciprocal recurrent selection population had a six percent advantage over the closed population.

Kojima and Kelleher (1963) also conducted a comparative study of full-sib family selection and reciprocal recurrent selection schemes for egg production in Drosophila. Full-sib family selection was conducted through 13 cycles of selection and reciprocal recurrent selection was conducted through 16 cycles of selection. The pattern of response to full-sib family selection showed very little improvement in egg production. However, egg production in the reciprocal recurrent program increased approximately linearly through the tenth cycle. It then ceased to increase and remained essentially plateaued for the remaining cycles.

Breeding experiments with Tribolium have shown reciprocal recurrent selection to be an inefficient method of improving highly heritable traits. Bell and Moore (1958) reported that in a 16 generation selection

experiment for body size ($h^2 = 0.60 - 0.80$), the superiority of individual and family selection over reciprocal recurrent selection was evident by the third cycle.

Methods of applying reciprocal recurrent selection programs to poultry have been outlined by Bell et al. (1952) and Comstock and Robinson (1956) but results of actual breeding experiments are very limited. Bell et al. (1952) emphasized that one of the important points was to hold inbreeding at a minimum in the segregating populations. This would be necessary since response to selection would depend on maintaining genetic variability within the populations. The ultimate objective of the reciprocal recurrent selection program would be to fix eventually those alleles in the segregating populations that combined for maximum heterosis in crosses.

Griesbach (1962) applied reciprocal recurrent selection to broilers with ten-week weight of the crossbred progeny as the selection criterion. Selection was applied over five generations. As the experiment progressed the purebred broilers from the selected strains increased in weight at approximately the same rate as the crossbreds from the same strains, but combining ability had not been improved.

Comstock and Robinson (1956) reported that reciprocal selection for eight-week weight of chickens would yield improvement of practical significance. However, they posed the question of whether conventional intra-population selection in the parent populations would improve the cross more rapidly. The population parameters required to estimate the expected genetic progress in crossbreds from various intra- and inter-population selection schemes have been outlined by Enfield (1960) and Comstock (1961).

Of these parameters, the genetic correlation between the intra-population effects of genes and their effects in the population cross is of primary interest, since this correlation must be relatively high for intra-population selection to be effective in improving cross performance (Comstock and Robinson, 1956). Estimates of these correlations between purebred and crossbred progeny having the same sire have been reported for various traits in poultry by Comstock (1956), Comstock and Robinson (1956), and Enfield (1960). For eight-week weight these estimates have ranged from 0.24 to 0.87. This suggests that conventional intra-population, or purebred, selection procedures would effectively improve cross performances. However, Enfield (1960) states that whether selection on the basis of purebred performance will be as effective as family selection based on the performance of the crossbred offspring is contingent upon the genetic variances and covariances in the crossbred population itself. In his study the estimates of the sire component of genetic variance for egg production in the crossbreds (1.27) was considerably larger than in the purebreds (0.50), the total phenotypic variances for these two populations being 22.88 and 18.51, respectively. These sire components indicated that even though a large genetic correlation existed between purebred and crossbred half-sib families (0.92), selection on the basis of crossbred performance should be more effective in improving the cross.

Unfortunately, available results with swine are based on limited observations. Genetic investigations of this nature require large amounts of data to obtain small standard errors on parameter estimates. To obtain such amounts of data requires long term breeding experiments, and results of such extensive breeding experiments are only now becoming available.

Estimates of the covariance of sire effects in limited purebred and crossbred populations of swine for weaning weight, average daily gain, and backfat probe have been reported by Enfield and Rempel (1962). These estimates based upon data from 56 sires with both purebred and crossbred progeny were: weaning weight, -2.42 ± 3.67 ; average daily gain, 0.0040 ± 0.0018 ; and backfat probe, 0.0005 ± 0.0007 . They state that the product of the ratio of four times the sire component of covariance divided by the phenotypic variance in the purebreds and the average selection differential in the two purebreds gives the expected improvement in the crossbreds. Estimates of these ratios computed from data in their study were: weaning weight, $-.17$; average daily gain, 0.42 , and backfat probe, 0.07 . These ratios can be viewed as being similar to heritability in the purebreds.

A similar study has been reported by Robison et al. (1964) in which they used five Duroc and eight Yorkshire boars with both purebred and crossbred progeny. The traits investigated were weight and backfat measured at 140 days of age. Genetic correlations for probed backfat between the purebred and crossbred progeny were 0.21 for the Durocs and >1.00 for the Yorkshires. The Duroc boars also had a mean of six purebred daughters and 28 crossbred daughters that produced litters. Their estimates of genetic correlations between purebred and crossbred performance for number farrowed and number raised were $-.74$ and <-1.00 , respectively.

Taylor et al. (1965), from a comparison of litter records from purebred and crossbred daughters of 35 boars, estimated the genetic correlation for litter weight at 21 days to be 0.185 . From this same comparison they estimated the genetic correlation for litter weight

at 56 days to be 0.612. Negative variance components prevented estimates of other genetic correlations from being obtained.

Although not uniquely a part of any program to evaluate the effectiveness of selection for improving crossbred performance, the study of correlated response lends itself to such investigations because of the scale of data involved. Observations of responses in one character when selection was applied to another has suggested that it might be possible to achieve significant improvement in one trait more efficiently by indirect selection for a correlated trait. The theoretical aspects of and the computational formula for predicting response by indirect selection have been presented by Falconer (1960).

Actual experiments with swine in which the ratio of correlated response from indirect selection to direct response from selection has been estimated are very limited. Ward et al. (1964) reported that the ratio of correlated response to direct response for daily gain, when direct selection was for weaning weight, was 0.53. When direct selection was applied to average daily gain the ratio of correlated response to direct response in weaning weight was 0.91. This is analogous to stating that about 90 percent of the possible progress in weaning weight is obtained by selection for average daily gain, whereas only about 50 percent of the potential progress in average daily gain is obtained by direct selection for weaning weight.

MATERIALS AND METHODS

Data

The data for this investigation were obtained from the experimental swine breeding herds maintained at Stillwater and Ft. Reno in the Oklahoma project of the Regional Swine Breeding Laboratory. The data included the progeny records of all purebred boars that sired both purebred and crossbred litters during a period of 18 seasons (fall 1955 through spring 1964). The performance traits studied were weaning weight, average daily gain, and probed backfat. All weaning weights were adjusted to a 56 day equivalent by procedures developed by Whatley and Quaife (1937). Probed backfat measurements were the average of four readings taken at approximately two inches on each side of the mid-dorsal line over the first rib and mid-loin regions. These probes were made at the conclusion of the postweaning feeding period and were then converted to a 200 pound equivalent by methods described by Durham and Zeller (1955) and Durham (1958). All gilt probes were converted to a barrow equivalent by methods developed by Enfield (1957) and all boar probes were converted to a barrow equivalent by adding 0.20 inches to their adjusted 200 pound probe. Postweaning average daily gain for barrows and gilts represents the average daily gain from weaning to market weight of approximately 200 pounds. The postweaning feeding period of boars was concluded as they reached approximately 175 pounds. All pigs were full-fed during this postweaning period.

Overall Analysis

The method of fitting constants was used to estimate the independent effect of each of the independent variables on the three performance traits. This was performed by least squares procedures (Harvey, 1960) based on the following model for 56 day weight and average daily gain:

$$Y_{ijklmnopqr} = \mu + s_i + y_j + t_k + c_l + a_m + i_n + r_o + b_p + \beta_{1wq} + \beta_{2wq}^2 + e_{ijklmnopqr}$$

where:

$Y_{ijklmnopqr}$ is adjusted 56 day weight and postweaning average daily gain, respectively, for the two models.

μ is a random effect common to all individuals.

s_i is the effect of the i th station and $i = 1, 2$. $s_1 =$ Stillwater and $s_2 =$ Ft. Reno.

y_j is the effect of the j th year and $j = 1, 2, 3, \dots, 10$.

$y_1 = 1955, y_2 = 1956, y_3 = 1957, \dots, y_{10} = 1964$.

t_k is the effect of the k th season and $k = 1, 2$. $t_1 =$ spring and $t_2 =$ fall.

c_l is the effect of the l th line and $l = 1, 2, 3, \dots, 6$. $c_1 =$ line 8 (Duroc), $c_2 =$ line 9 (Beltsville #1), $c_3 =$ line 14 (Hampshire), $c_4 =$ line 8 x 9 (Duroc male x Beltsville #1 female), $c_5 =$ line 9 x 8 (Beltsville #1 male x Duroc female), and $c_6 =$ line 14 x (8.9) and 14 x (9.8).

a_m is the effect of the m th age of dam and $m = 1, 2, 3, \dots, 7$.

$a_1 = 1.0$ years, $a_2 = 1.5$ years, $a_3 = 2.0$ years, $\dots, a_7 = 4.0$ years.

i_n is the effect of the nth level of inbreeding of the individual pig and $n = 1, 2, 3, \dots, 6$. $i_1 = 0-4\%$, $i_2 = 5-9\%$, $i_3 = 10-14\%$, $i_4 = 15-19\%$, $i_5 = 20-24\%$, and $i_6 = 25\%$ and greater.

r_o is the effect of the oth management system and $o = 1, 2$ for 56 day weight. $r_1 =$ pasture to weaning and $r_2 =$ confinement to weaning. For average daily gain $o = 1, 2, 3, 4$ and $r_1 =$ pasture before and after weaning, $r_2 =$ pasture before weaning-confinement after weaning, $r_3 =$ confinement before weaning-pasture after weaning, and $r_4 =$ confinement before and after weaning.

b_p is the effect of the pth sex and $p = 1, 2, 3$. $b_1 =$ gilt, $b_2 =$ boar, and $b_3 =$ barrow.

$B_{1w_q} + B_{2w_q^2}$ are linear and quadratic effects due to the qth litter size at weaning and $q = 1, 2, 3, \dots, 13$. $w_1 =$ one pig, $w_2 =$ two pigs, $w_3 =$ three pigs, \dots , $w_{13} = 13$ pigs.

$e_{ijklmnopqr}$ is a random error unique for each pig.

The model for probed backfat was

$$Y_{ijklmnop} = \mu + s_i + y_j + t_k + c_l + a_m + i_n + r_o + e_{ijklmnop}$$

where:

$Y_{ijklmnop}$ is probed backfat adjusted to a 200 pound barrow equivalent.

$e_{ijklmnop}$ is a random error unique for each pig.

and all remaining terms are defined identically to the corresponding terms in the model for average daily gain.

All models were constructed under the assumption that no interactions existed among the effects and that all errors were normally

and independently distributed about a mean of zero and had a common variance σ^2 .

The normal equations for the three traits, with probed backfat as an illustration, were

$$[X'X][\beta] = [X'Y]$$

with $[X'X]$ and $[X'Y]$ being the coefficient matrix and the right hand side (RHS), respectively, in Table I, and $[\beta]$ being the vector of variables included in the model. The restriction imposed because of dependency among the normal equations was that the sum of the constant estimates within each given class sum to zero. This was accomplished by setting the last equation in each class equal to zero, thus maintaining a full rank matrix. No restrictions were imposed on the normal equations for the linear and quadratic effects of litter size since these equations were not dependent. Estimates of the least squares constants were then computed by

$$[\hat{\beta}] = [X'X]^{-1} [X'Y]$$

The standard errors of the estimated constants were obtained by

$$s\hat{c}_i = \sqrt{c_{ii}\hat{\sigma}_e^2}$$

where c_{ii} is the corresponding diagonal inverse element for that constant and $\hat{\sigma}_e^2$ is the error mean square. The formula for calculating the error mean square was

$$\hat{\sigma}_e^2 = 1/(\text{error d.f.}) \left[\sum_{\text{all}} y^2_{ijklmnop} - R(\mu, s_i, y_j, t_k, c_l, a_m, i_n, r_o) \right]$$

TABLE I

THE COEFFICIENT MATRIX ($X'X$) AND THE RIGHT HAND SIDE ($X'Y$)^{1,2}

	Coefficient Matrix								RHS
	μ	s_i	y_j	t_k	c_l	a_m	i_n	r_o	
u	$n \dots \dots$	$n_i \dots \dots$	$n \cdot j \dots \dots$	$n \cdot k \dots \dots$	$n \dots l \dots$	$n \dots m \dots$	$n \dots n \dots$	$n \dots o \dots$	$Y \dots \dots$
s_i	$n_i \dots \dots$	$n_i \dots \dots$	$n_{ij} \dots \dots$	$n_i \cdot k \dots \dots$	$n_i \dots l \dots$	$n_i \dots m \dots$	$n_i \dots n \dots$	$n_i \dots o \dots$	$Y_i \dots \dots$
y_j	$n \cdot j \dots \dots$	$n_{ij} \dots \dots$	$n \cdot j \dots \dots$	$n \cdot jk \dots \dots$	$n \cdot j \cdot l \dots \dots$	$n \cdot j \cdot m \dots \dots$	$n \cdot j \cdot n \dots \dots$	$n \cdot j \cdot o \dots \dots$	$Y \cdot j \dots \dots$
t_k	$n \cdot k \dots \dots$	$n_i \cdot k \dots \dots$	$n \cdot jk \dots \dots$	$n \cdot k \dots \dots$	$n \cdot kl \dots \dots$	$n \cdot k \cdot m \dots \dots$	$n \cdot k \cdot n \dots \dots$	$n \cdot k \cdot o \dots \dots$	$Y \cdot k \dots \dots$
c_l	$n \dots l \dots$	$n_i \dots l \dots$	$n \cdot j \cdot l \dots \dots$	$n \cdot kl \dots \dots$	$n \dots l \dots$	$n \dots lm \dots$	$n \dots l \cdot n \dots$	$n \dots l \cdot o \dots$	$Y \dots l \dots$
a_m	$n \dots m \dots$	$n_i \dots m \dots$	$n \cdot j \cdot m \dots \dots$	$n \cdot k \cdot m \dots \dots$	$n \dots lm \dots$	$n \dots m \dots$	$n \dots mn \dots$	$n \dots m \cdot o \dots$	$Y \dots m \dots$
i_n	$n \dots n \dots$	$n_i \dots n \dots$	$n \cdot j \cdot n \dots \dots$	$n \cdot k \cdot n \dots \dots$	$n \dots l \cdot n \dots$	$n \dots mn \dots$	$n \dots n \dots$	$n \dots n \cdot o \dots$	$Y \dots n \dots$
r_o	$n \dots o \dots$	$n_i \dots o \dots$	$n \cdot j \cdot o \dots \dots$	$n \cdot k \cdot o \dots \dots$	$n \dots l \cdot o \dots$	$n \dots m \cdot o \dots$	$n \dots n \cdot o \dots$	$n \dots o \dots$	$Y \dots o \dots$

¹ $n \dots \dots$ = total number of observations.

$n_i \dots \dots$ = total number of observations in the i th station.

$n_{ij} \dots \dots$ = total number of observations in the i th station and j th year.

$Y \dots \dots$ = total of all probed backfat measurements.

$Y_i \dots \dots$ = total of all probed backfat measurements in the i th station.

² $i = 1, 2; j = 1, 2, \dots, 10; k = 1, 2; l = 1, 2, \dots, 6; m = 1, 2, \dots, 7; n = 1, 2, \dots, 6; o = 1, 2, 3, 4.$

where $\sum_{\text{all}} Y^2_{ijklmnop}$ is the total sum of squares, and $R(\mu, s_i, y_j, t_k, c_l, a_m, i_n, r_o)$ is the total reduction in the sum of squares due to fitting the mean and all constants. This reduction was calculated by multiplying the vector of constants, $[\beta]$, times the right hand side, $[X'Y]$.

The analysis of variance for probed backfat, which shows the partitioning of the total reduction in sum of squares, is given in Table II. The total sum of squares, reduction sum of squares, and error sum of squares were computed identically to the method used for obtaining the standard errors. The procedure for obtaining the sum of squares for each of the direct effects was

$$S. Sqs. = [X'] [Z_x^{-1}] [X]$$

where $[X']$ is the row vector of the constant estimates of a given set, $[Z_x^{-1}]$ is the inverse of the segment of the inverse corresponding by row and column to this given set, and $[X]$ is the column vector of this set of constants.

Before obtaining phenotypic variances, sire components of variance and covariance, or genetic correlations among the three traits, each observation in the original body of data was adjusted by adding or subtracting the appropriate least squares constants in each of the classes characterizing that observation. For example, an arbitrary backfat probe of 1.50 inches measured on a pig represented by the following classes: station, Stillwater; year, 1955; season, spring; line, 8; age of dam, 1.0; inbreeding of litter, 0; and pre- and postweaning management, pasture-pasture, would have an adjusted probe obtained in the following manner (Table V)

TABLE II
THE ANALYSIS OF VARIANCE

Source of Variation	Degrees of Freedom ¹	Sum of Squares ²	Mean Square	Expected Mean Squares ³
Direct effects				
Station	I-1	SS _s	MS _s	$\sigma_e^2 + k_s \sigma_s^2$
Year	J-1	SS _y	MS _y	$\sigma_e^2 + k_y \sigma_y^2$
Season	K-1	SS _t	MS _t	$\sigma_e^2 + k_t \sigma_t^2$
Line	L-1	SS _c	MS _c	$\sigma_e^2 + k_c \sigma_c^2$
Age of dam	M-1	SS _a	MS _a	$\sigma_e^2 + k_a \sigma_a^2$
Inbreeding of pig	N-1	SS _i	MS _i	$\sigma_e^2 + k_i \sigma_i^2$
Management	O-1	SS _r	MS _r	$\sigma_e^2 + k_r \sigma_r^2$
Error (residual)	$N - [(1+I+\dots+O) - 7]$	SS - SS _{tr}	MS	σ_e^2

¹N = total number of observations, I = number of stations, J = number of seasons, L = number of lines, M = number of age of dam groups, N = number of inbreeding groups, O = number of management groups.

²SS - SS_{tr} = total sum of squares minus total reduction in sum of squares due to fitting constants.

³k_s, k_y, . . . , k_r approximate the average number of observations in each subgroup, computed by

$$k_i = 1/\text{d.f.}(n_{..} - \sum_i n_{i.}^2/n_{..})$$

$$\begin{aligned} \text{adjusted backfat probe} &= 1.50 + 0.032 - 0.117 - 0.036 - 0.131 + 0.033 \\ &\quad - 0.028 + 0.000 \end{aligned}$$

Following adjustment, each observation was now represented as

$$T_{ijkl} = \mu + s_i + l_{ij} + d_{ijk} + e_{ijkl}$$

where

T_{ijkl} = the adjusted phenotypic observation of each of the three traits on the l th individual in the k th litter in the j th line sired by the i th sire.

μ = an effect common to all individuals.

s_i = an effect common to all individuals by the i th sire.

l_{ij} = an effect common to all individuals in the j th line by the i th sire.

d_{ijk} = an effect common to all individuals in the k th litter in the j th line by the i th sire.

e_{ijkl} = a random error unique for each pig.

T_{ijkl} was the observational unit employed in all subsequent analyses.

The form of the analysis of variance for obtaining the within line sire component of variance for each of the three traits is given in Table III.

The form of the analysis of variance (Method I of Henderson, 1953) for obtaining the sire component of covariance between purebred and crossbred observations for each of the three traits is given in Table IV. The sire component of variance taken from this analysis was considered a valid estimate of the sire component of covariance between purebred and crossbred offspring, since it can be shown that the

TABLE III

ANALYSIS OF VARIANCE FOR OBTAINING WITHIN LINE SIRE COMPONENT OF VARIANCE

Source	d.f. ¹	Mean Square ^{1,2}	Expected Mean Square ³
Among sires	$(n_{..}-1) - \sum_i (n_{i.}-1)$	$\frac{1}{\text{sire d.f.}} \left(\sum_i \frac{Y_{i..}^2}{n_{i.}} - \frac{Y_{..}^2}{n_{..}} \right)$	$\sigma_w^2 + k_2 \sigma_d^2 + k_3 \sigma_s^2$
Among litters/sires	$\sum_i (n_{i.}-1) - \sum_{ij} (n_{ij}-1)$	$\frac{1}{\text{litter d.f.}} \left(\sum_{ij} \frac{Y_{ij.}^2}{n_{ij}} - \sum_i \frac{Y_{i..}^2}{n_{i.}} \right)$	$\sigma_w^2 + k_1 \sigma_d^2$
Individuals	$\sum_{ij} (n_{ij}-1)$	$\frac{1}{\text{individual d.f.}} \left(\sum_{ijk} Y_{ijk}^2 - \sum_{ij} \frac{Y_{ij.}^2}{n_{ij}} \right)$	σ_w^2

¹ $n_{..}$ = total number of individuals.

$n_{i.}$ = total number of individuals by the i th sire.

n_{ij} = total number of individuals in the j th litter by the i th sire.

² Y_{ijk} = the k th individual in the j th litter by the i th sire.

$${}^3k_1 = \frac{1}{D-S} \left(n_{..} - \sum_i \frac{\sum_j n_{ij}^2}{n_{i.}} \right) \quad k_2 = \frac{1}{S-1} \left(\sum_i \frac{\sum_j n_{ij}^2}{n_{i.}} - \frac{\sum_{ij} n_{ij}^2}{n_{..}} \right) \quad k_3 = \frac{1}{S-1} \left(n_{..} - \frac{\sum_i n_{i.}^2}{n_{..}} \right)$$

where S = number of sires and D = number of litters.

TABLE IV
ANALYSIS OF VARIANCE FOR OBTAINING SIRE COMPONENT OF COVARIANCE

Source ¹	d.f. ²	Mean Square ^{1,2,3}	Expected Mean Square ⁴
S	$(n_{...}-1) - \sum_i (n_{i...}-1)$	$\frac{1}{S \text{ d.f.}} \left(\sum_i \frac{Y_{i...}^2}{n_{i...}} - \frac{Y_{...}^2}{n_{...}} \right)$	$\sigma_w^2 + k_{10}\sigma_d^2 + k_{11}\sigma_{s1}^2 + k_{12}\sigma_1^2 + k_{13}\sigma_s^2$
L	1	$\frac{1}{L \text{ d.f.}} \left(\sum_j \frac{Y_{.j..}^2}{n_{.j.}} - \frac{Y_{...}^2}{n_{...}} \right)$	$\sigma_w^2 + k_6\sigma_d^2 + k_7\sigma_{s1}^2 + k_8\sigma_1^2 + k_9\sigma_s^2$
SxL	$(n_{...}-1) - \sum_i (n_{i...}-1)$	$\frac{1}{SxL \text{ d.f.}} \left(\sum_{ij} \frac{Y_{ij..}^2}{n_{ij.}} - \sum_i \frac{Y_{i...}^2}{n_{i...}} - \sum_j \frac{Y_{.j..}^2}{n_{.j.}} + \frac{Y_{...}^2}{n_{...}} \right)$	$\sigma_w^2 + k_2\sigma_d^2 + k_3\sigma_{s1}^2 + k_4\sigma_1^2 + k_5\sigma_s^2$
D/L/S	$\sum_{ij} (n_{ij.}-1) - \sum_{ijk} (n_{ijk}-1)$	$\frac{1}{D \text{ d.f.}} \left(\sum_{ijk} \frac{Y_{ijk.}^2}{n_{ijk}} - \sum_{ij} \frac{Y_{ij.}^2}{n_{ij.}} \right)$	$\sigma_w^2 + k_1\sigma_d^2$
I	$\sum_{ijk} (n_{ijk}-1)$	$\frac{1}{I \text{ d.f.}} \left(\sum_{ijkl} \frac{Y_{ijkl}^2}{n_{ijkl}} - \sum_{ijk} \frac{Y_{ijk.}^2}{n_{ijk}} \right)$	σ_w^2

¹S = sires, L = lines, D = litters, I = individuals.

² $n_{...}$ = total number of individuals, $n_{i...}$ = total number of individuals by the ith sire, $n_{.j.}$ = total number of individuals in the jth line, $n_{ij.}$ = total number of individuals in the jth line by the ith sire, n_{ijk} = total number of individuals in the kth litter in the jth line by the ith sire.

³ Y_{ijkl} = the lth individual in the kth litter in the jth line by the ith sire.

TABLE IV (CONTINUED)

$$k_1 = \frac{1}{L \text{ d.f.}} \left[N - \sum_{ij} \left(\sum_k \frac{n_{ijk}^2}{n_{ij}} \right) \right]$$

$$k_2 = \frac{1}{SxL \text{ d.f.}} \left[\sum_{ij} \left(\sum_k \frac{n_{ijk}^2}{n_{ij\cdot}} \right) - \sum_i \left(\sum_{jk} \frac{n_{ijk}^2}{n_{i\cdot\cdot}} \right) - \sum_j \left(\sum_{ik} \frac{n_{ijk}^2}{n_{\cdot j\cdot}} \right) + \right.$$

$$k_3 = \frac{1}{SxL \text{ d.f.}} \left[N - \sum_i \left(\sum_j \frac{n_{ij\cdot}^2}{n_{i\cdot\cdot}} \right) - \sum_j \left(\sum_i \frac{n_{ij\cdot}^2}{n_{\cdot j\cdot}} \right) + \left(\sum_{ij} \frac{n_{ij\cdot}^2}{N} \right) \right]$$

$$\left. \left(\sum_{ijk} \frac{n_{ijk}^2}{N} \right) \right]$$

$$k_4 = \frac{1}{SxL \text{ d.f.}} \left[\left(\sum_j \frac{n_{\cdot j\cdot}^2}{N} \right) - \sum_i \left(\sum_j \frac{n_{ij\cdot}^2}{n_{i\cdot\cdot}} \right) \right]$$

$$k_5 = \frac{1}{SxL \text{ d.f.}} \left[\left(\sum_i \frac{n_{i\cdot\cdot}^2}{N} \right) - \sum_j \left(\sum_i \frac{n_{ij\cdot}^2}{n_{\cdot j\cdot}} \right) \right]$$

$$k_6 = \frac{1}{L \text{ d.f.}} \left[\sum_j \left(\sum_{ik} \frac{n_{ijk}^2}{n_{\cdot j\cdot}} \right) - \left(\sum_{ijk} \frac{n_{ijk}^2}{N} \right) \right]$$

$$k_7 = \frac{1}{L \text{ d.f.}} \left[\sum_j \left(\sum_i \frac{n_{ij\cdot}^2}{n_{\cdot j\cdot}} \right) - \left(\sum_{ij} \frac{n_{ij\cdot}^2}{N} \right) \right]$$

$$k_8 = \frac{1}{L \text{ d.f.}} \left[N - \left(\sum_j \frac{n_{\cdot j\cdot}^2}{N} \right) \right]$$

$$k_9 = \frac{1}{L \text{ d.f.}} \left[\sum_j \left(\sum_i \frac{n_{ij\cdot}^2}{n_{\cdot j\cdot}} \right) - \left(\sum_i \frac{n_{i\cdot\cdot}^2}{N} \right) \right]$$

$$k_{10} = \frac{1}{S \text{ d.f.}} \left[\sum_i \left(\sum_{jk} \frac{n_{ijk}^2}{n_{i\cdot\cdot}} \right) - \left(\sum_{ijk} \frac{n_{ijk}^2}{N} \right) \right]$$

$$k_{11} = \frac{1}{S \text{ d.f.}} \left[\sum_i \left(\sum_j \frac{n_{ij\cdot}^2}{n_{i\cdot\cdot}} \right) - \left(\sum_{ij} \frac{n_{ij\cdot}^2}{N} \right) \right]$$

$$k_{12} = \frac{1}{S \text{ d.f.}} \left[\sum_i \left(\sum_j \frac{n_{ij\cdot}^2}{n_{i\cdot\cdot}} \right) - \left(\sum_j \frac{n_{\cdot j\cdot}^2}{N} \right) \right]$$

$$k_{13} = \frac{1}{S \text{ d.f.}} \left[N - \left(\sum_i \frac{n_{i\cdot\cdot}^2}{N} \right) \right]$$

covariance between a randomly selected individual in the purebred line by a given sire and a randomly selected individual in the crossbred line by the same sire equals σ_s^2 . Given that $E(s_i, l_{ij}) = E(s_i, d_{ijk}) = E(s_i, e_{ijkl}) = E(s_i, l_{ij}') = E(l_{ij}, l_{ij}') = E(l_{ij}', d_{ijk}') = E(l_{ij}', e_{ijkl}') = E(s_i, d_{ij'k}') = E(l_{ij}, d_{ij'k}') = E(d_{ijk}, d_{ij'k}') = E(d_{ij'k}', e_{ijkl}') = E(s_i, e_{ij'k'l}') = E(l_{ij}, e_{ij'k'l}') = E(d_{ijk}, e_{ij'k'l}') = E(e_{ijkl}, e_{ij'k'l}') = 0$, we have that

$$\text{Cov}(T_{ijkl}, T_{ij'k'l}') = E[(T_{ijkl} - E(T_{ijkl}))(T_{ij'k'l}' - E(T_{ij'k'l}'))]$$

Expressing the T_{ijkl} values in forms of the model,

$$E[(\mu + s_i + l_{ij} + d_{ijk} + e_{ijkl} - E(\mu + s_i + l_{ij} + d_{ijk} + e_{ijkl}))(\mu + s_i + l_{ij}' + d_{ij'k}' + e_{ij'k'l}' - E(\mu + s_i + l_{ij}' + d_{ij'k}' + e_{ij'k'l}'))] = E(\mu + s_i + l_{ij} + d_{ijk} + e_{ijkl} - \mu)(\mu + s_i + l_{ij}' + d_{ij'k}' + e_{ij'k'l}' - \mu) = E(s_i + l_{ij} + d_{ijk} + e_{ijkl})(s_i + l_{ij}' + d_{ij'k}' + e_{ij'k'l}') = \sigma_s^2$$

Data from only those sires having both purebred and crossbred observations for the trait considered were used in obtaining sire components of variance and covariance. To obtain the sire component of covariance between 56 day weight and average daily gain, 56 day weight and probed backfat, and average daily gain and probed backfat, the mean cross products were estimated from analyses of variance of the sums of the traits. Thus, since $\sigma^2(x+y) = \sigma_x^2 + \sigma_y^2 + 2\sigma_{xy}$, σ_{xy} was obtained in the following manner:

$$\sigma_{xy} = (\sigma^2(x+y) - \sigma_x^2 - \sigma_y^2)/2.$$

The sire component of σ_{xy} was obtained by utilizing the expectation of the covariance. In obtaining the sums only those individuals having

both observations for the two traits involved were included. Genetic correlations between traits were then computed from the within line sire components by

$$r_g = \widehat{\text{cov}}_s / \sqrt{\widehat{\sigma}_{s_x}^2 \widehat{\sigma}_{s_y}^2}.$$

Standard errors of genetic correlation coefficients were obtained by methods given by Reeve (1955), and the standard errors of heritability estimates were obtained by methods described by A.S.A.P. (1960).

RESULTS AND DISCUSSION

Least Squares Estimates

The least squares estimates of the effects of the factors influencing 56 day weight, average daily gain, and probed backfat are presented in Table V.

For 56 day weight, all variables included in the model contributed significantly to the total variation (Table VI).

A 56 day weight difference existed among lines with the crossbred pigs (lines 8 x 9, 9 x 8, and 14 x 8.9) exceeding the purebreds (lines 8, 9, and 14). The actual heterosis expressed in this trait by the three crossbred lines was 4.5 pounds.

The advantage of spring farrowing over fall farrowing in this investigation is similar to that reported by Godbey and Godley (1961) and Noland et al. (1964).

Fifty-six day weight increased with increasing age of dam. Nordskog et al. (1944) reported that pigs farrowed from sows were approximately four pounds heavier than pigs from gilts. Chambers and Whatley (1951) and Omtvedt and Whatley (1966) also reported weaning weights of pigs from sow litters to exceed those from gilt litters.

With the exception of litters with inbreeding coefficients over 25 percent, 56 day weight decreased with an increase in inbreeding. Dickerson et al. (1954) reported a nonsignificant increase in weaning weights with increased inbreeding in the litter. This lack of reduced

TABLE V

LEAST SQUARES ESTIMATES OF THE EFFECTS OF STATION, YEAR, SEASON, SEX,
 LINE, AGE OF DAM, INBREEDING OF LITTER, MANAGEMENT, AND
 LITTER SIZE AT WEANING ON 56 DAY WEIGHT, POSTWEANING
 AVERAGE DAILY GAIN, AND PROBED BACKFAT

	56 Day Weight (lbs.)	Average Daily Gain (lbs.)	Probed Backfat (inches)
Mean	41.3 ± 0.4	1.485 ± 0.041	1.547 ± 0.018
Station			
Stillwater	1.7 ± 0.1	0.078 ± 0.008	-.032 ± 0.006
Ft. Reno	-1.7 ± 2.6	-.078 ± 0.178	0.032 ± 0.097
Year			
1955	-1.5 ± 0.3	-.076 ± 0.022	0.117 ± 0.022
1956	-.6 ± 0.2	0.008 ± 0.015	0.129 ± 0.012
1957	-3.0 ± 0.2	-.082 ± 0.014	-.045 ± 0.009
1958	-.8 ± 0.2	0.021 ± 0.012	0.028 ± 0.008
1959	-.7 ± 0.2	-.008 ± 0.012	-.007 ± 0.008
1960	1.5 ± 0.2	-.017 ± 0.014	0.013 ± 0.009
1961	1.1 ± 0.1	-.013 ± 0.010	-.053 ± 0.010
1962	-2.0 ± 0.1	-.058 ± 0.009	-.084 ± 0.006
1963	-2.6 ± 0.2	0.075 ± 0.013	-.065 ± 0.011
1964	8.5 ± 1.1	0.152 ± 0.079	-.032 ± 0.043
Season			
Spring	1.2 ± 0.1	0.000 ± 0.005	0.036 ± 0.004
Fall	-1.2 ± 2.6	0.000 ± 0.178	-.036 ± 0.097

TABLE V (CONTINUED)

	56 Day Weight (lbs.)	Average Daily Gain (lbs.)	Probed Backfat (inches)
Sex			
Gilt	-1.2 ± 0.1	-.083 ± 0.005	
Boar	3.6 ± 0.1	0.047 ± 0.010	
Barrow	-2.4 ± 2.1	0.035 ± 0.145	
Line			
8	-2.2 ± 0.1	0.050 ± 0.010	0.131 ± 0.007
9	-3.0 ± 0.2	-.079 ± 0.014	-.022 ± 0.010
14	-2.9 ± 0.1	-.112 ± 0.010	-.023 ± 0.007
8x9	4.3 ± 0.1	0.065 ± 0.009	-.019 ± 0.007
9x8	1.2 ± 0.1	0.057 ± 0.010	-.013 ± 0.008
14x(8-9)	2.6 ± 1.5	0.020 ± 0.103	-.055 ± 0.056
Age of dam (years)			
1.0	-4.7 ± 0.3	-.022 ± 0.025	-.033 ± 0.016
1.5	-.9 ± 0.4	-.012 ± 0.025	-.029 ± 0.016
2.0	0.8 ± 0.4	-.036 ± 0.026	-.017 ± 0.016
2.5	0.4 ± 0.4	0.014 ± 0.027	-.011 ± 0.017
3.0	0.2 ± 0.4	-.044 ± 0.030	0.001 ± 0.019
3.5	0.7 ± 0.4	-.012 ± 0.033	0.018 ± 0.021
4.0	3.6 ± 1.4	0.112 ± 0.095	0.071 ± 0.052
Inbreeding of litter (%)			
0-4	0.2 ± 0.2	-.004 ± 0.012	0.028 ± 0.008
5-9	0.4 ± 0.2	0.014 ± 0.015	0.059 ± 0.010

TABLE V (CONTINUED)

	56 Day Weight (lbs.)	Average Daily Gain (lbs.)	Probed Backfat (inches)
10-14	1.7 ± 0.2	0.015 ± 0.014	-0.001 ± 0.009
15-19	-0.6 ± 0.2	-0.009 ± 0.015	-0.008 ± 0.010
20-24	-3.0 ± 0.3	-0.029 ± 0.022	-0.042 ± 0.014
25+	1.3 ± 1.5	0.013 ± 0.103	-0.036 ± 0.056
Prewaning management			
Pasture	1.0 ± 0.1		
Confinement	-1.0 ± 2.6		
Pre- and postweaning management			
Pasture-pasture		-0.156 ± 0.013	0.000 ± 0.013
Pasture-confinement		0.096 ± 0.010	0.011 ± 0.008
Confinement-pasture		-0.027 ± 0.030	-0.048 ± 0.018
Confinement-confinement		0.087 ± 0.126	0.037 ± 0.069
Litter size at weaning			
Litter size (linear)	0.93 ± 0.08	0.0164 ± 0.0093	
Litter size (quadratic)	-0.09 ± 0.01	-0.0012 ± 0.0006	

TABLE VI
ANALYSIS OF VARIANCE FOR ADJUSTED 56 DAY WEANING WEIGHT

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Squares
Direct effects			
Station	1	23,645.5	23,645.5*
Year	9	58,890.1	6,543.3*
Season	1	4,927.4	4,927.4*
Line	5	7,312.5	1,462.5*
Age of dam	6	22,506.5	3,751.1*
Inbreeding	5	3,166.5	633.3*
Management	1	1,676.0	1,676.0*
Sex	2	17,761.7	8,880.8*
Litter size	2	10,238.1	5,119.0*
Error	6717	475,820.7	70.8

*P < .005.

performance was credited to the effectiveness of selection against any depression that may have existed in the more highly inbred litters. Godbey and Godley (1961) found the mean 56 day weight to decrease about three percent as inbreeding increased from an average of three to 60 percent. Noland et al. (1964) reported inbreeding of the litter to have a significant influence on weaning weight, although no linear trend was evident in their data.

Boars were the heaviest at 56 days, gilts the lightest, and barrows intermediate. Craig et al. (1956) and Noland et al. (1964) reported boars to be significantly heavier than gilts at 56 days of age but Godbey and Godley (1961) reported no sex difference.

Individual 56 day weights increased as litter size at weaning increased from one to five, but as litter size at weaning increased beyond this, individual 56 day weights decreased. This response is similar to that reported by others (Menziess-Kitchin, 1937; Godbey and Godley, 1961; and Ontvedt and Whatley, 1966).

Of the factors thought to influence average daily gain, the inbreeding of the litter and litter size at weaning were statistically non-significant sources of variation (Table VII). Comstock and Winters (1944) reported a regression of average daily gain on percent inbreeding of $-.0017$ pounds. Winters et al. (1943) obtained a correlation of $-.17$ between inbreeding and average daily gain. Whatley (1942) obtained a correlation of $-.17$ between inbreeding and the 180 day weight of pigs born in the same farrowing season. Smith and Donald (1939) observed no significant influence of litter size at weaning on post weaning growth. Likewise, Fredeen and Plank (1963) reported no effect of litter size at weaning on postweaning average daily gain.

TABLE VII
ANALYSIS OF VARIANCE FOR POSTWEANING AVERAGE DAILY GAIN

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Squares
Direct effects			
Station	1	0.545	0.545**
Year	9	22.200	2.467**
Season	1	0.388	0.388**
Line	5	37.729	7.546**
Age of dam	6	1.357	0.226*
Inbreeding	5	0.199	0.040
Management	3	57.309	19.103**
Sex	2	19.689	9.844**
Litter size	2	0.150	0.075
Error	5628	266.872	0.047

*P < .05.
**P < .005.

The seasonal difference in growth rate noted in this study which favored spring farrowed pigs, though statistically significant, was quite small. Whatley (1942) found a highly significant difference in 180 day weights in favor of fall farrowed pigs, but Crampton and Ashton (1946) reported that in Canada pigs finished in cold pens during the winter grew more slowly than summer-fed pigs.

Age of dam effects were significant in this study with pigs out of four year old dams gaining considerably more rapidly than those out of younger dams. However, other investigators (Whatley, 1942; Nordskog et al., 1944) have not found age of dam to influence postweaning growth rate.

Boars were the most rapid gaining sex, followed by barrows, and then gilts. Comstock et al. (1944), Bennett and Coles (1946), and Omtvedt et al. (1965) have also reported differential growth rates in favor of the males.

The constants obtained for type of management show a favorable effect of confinement rearing after weaning on postweaning average daily gain. The beneficial effect of confinement rearing on postweaning growth rate at this station has been reported earlier (Whatley et al., 1959).

Probed backfat was significantly influenced by station, season, line, inbreeding, and management (Table VIII). A paucity of published studies on factors influencing probed backfat prevents many comparisons of the results of this investigation with others.

Crampton and Ashton (1946) found carcass backfat to be less during the colder seasons of the year. A similar effect of season was observed in this investigation. Also, probed backfat decreased with increased

TABLE VIII
ANALYSIS OF VARIANCE FOR PROBED BACKFAT

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Squares
Direct effects			
Station	1	0.454	0.454**
Year	9	7.509	0.834**
Season	1	3.249	3.249**
Line	5	18.931	3.786**
Age of dam	6	0.289	0.048
Inbreeding	5	0.974	0.195**
Management	3	0.326	0.109*
Error	3357	86.739	0.026

*P < .01.

**P < .005.

inbreeding which is in agreement with the effect of inbreeding on carcass fatness noted by Gregory and Dickerson (1952).

Figs reared in confinement after weaning had greater backfat probes than those raised on pasture. This difference in response to the two types of postweaning management at this station was reported earlier by Whatley et al. (1959).

Heritabilities

Estimates of the heritability of each of the traits studied were obtained by the formula

$$h^2 = (4\hat{\sigma}_g^2)/(\hat{\sigma}_p^2)$$

with the quantity $4\hat{\sigma}_g^2$ equal to the sire component of variance for each of the traits divided by the genetic relationship of the individuals used in the analysis and $\hat{\sigma}_p^2$ equal to the total phenotypic variance. Estimates of the sire components of variance for 56 day weight, average daily gain, and probed backfat in each of the two populations are given in Appendix Tables XX, XXI, XXII, XXIII, XXIV, and XV. The corresponding heritability estimates are presented in Table IX.

The estimates of heritability of 56 day weight obtained in this study were $0.03 \pm .06$ in the purebred line and $0.19 \pm .09$ in the crossbred line. The larger heritability in the crossbreds indicates that a greater portion of the total variation in this population arose from genetic causes. These estimates plus those reported by others indicate the variation in this trait to arise largely from nongenetic causes. Bywaters (1937) reported a heritability estimate of 0.04, Comstock et al. (1942) obtained an estimate of zero, and Baker et al. (1943) reported

TABLE IX
A COMPARISON OF HERITABILITY ESTIMATES IN THE
PUREBRED AND CROSSED POPULATIONS

Population	Trait		
	56 Day Weight	Avg. Daily Gain	Probed Backfat
Purebred	0.03 ± .06	0.28 ± .06	0.55 ± .12
Crossbred	0.19 ± .09	0.39 ± .10	0.47 ± .13

it to be 0.15. Estimates reported by Craig et al. (1956) ranged from 0.03 to 0.24. More recently, Ward et al. (1964) obtained an estimate of 0.18.

The heritable portion of the total variation in average daily gain in this study was estimated to be 0.28 ± .06 in the purebreds and 0.39 ± .10 in the crossbreds. Reviews of published estimates of the heritability of average daily gain have been presented by Craft (1953, 1958) and Fredeen (1953). Craft (1958) reported the average estimate to be 0.29, and Fredeen (1953) reported it to be 0.30. More recent estimates reported by EL-Issawi and Rempel (1961) are based on relatively more degrees of freedom than many of the previous studies. Their heritability estimate based on intra-sire regression of offspring on dam, with 451 degrees of freedom, was 0.14 ± .10. Gross regression of offspring on dam, with 1,419 degrees of freedom, gave an estimate of 0.28 ± .06. This latter estimate is identical with the estimate of 0.28 ± .06 obtained in the purebred population in this investigation.

The heritability estimates for live probes within the two populations in the present study were similar: 0.55 ± .12 in the purebreds and 0.47 ± .13 in the crossbreds. Direct comparisons of these estimates

with others are limited since more estimates of heritability of backfat thickness are available that have been made on carcasses than on live hogs. In the review by Craft (1958), the average estimate for carcass backfat thickness was 0.49. Of seven studies cited by Fredeen (1953) the mean estimate was 0.48. The average realized heritability of probed backfat in the two-way selection experiment reported by Hetzer and Zeller (1956) was 0.41. An analysis of the genetic variation in live probes made at a constant age by Cox (1964) gave a heritability estimate of 0.25. The reason suggested for this relatively low estimate was that measuring at a constant age probably increased the environmental component among pigs within a litter over what would be obtained by measuring at a nearly constant weight. Grey et al. (1965) reported the realized heritability of backfat probe in two lines which they studied to be 0.54 and 0.43, respectively. Estimates for backfat probe obtained by Louca and Robison (1965) indicated moderate heritability (0.20 - 0.30).

Genetic Correlations

The ability to predict indirect response to selection requires estimates of the genetic correlation between the traits involved in addition to estimates of the heritability of the traits. The genetic correlations between 56 day weight and average daily gain, 56 day weight and probed backfat, and average daily gain and probed backfat obtained in this study are given in Table X. Unfortunately, few published estimates of genetic correlations are available for comparison.

The genetic correlation between weaning weight and average daily gain in the purebreds was $0.29 \pm .50$, and the corresponding correlation

TABLE X

A COMPARISON OF GENETIC CORRELATIONS BETWEEN THREE TRAITS
WITHIN PUREBRED AND CROSSED POPULATIONS

Population	Traits		
	56 Day Weight - Avg. Daily Gain	56 Day Weight - Probed Backfat	Avg. Daily Gain - Probed Backfat
Purebred	0.29 ± .50	-.05 ± .53	-.07 ± .18
Crossbred	0.20 ± .21	0.61 ± .16	-.39 ± .18

in the crossbreds was $0.20 \pm .21$. These estimates are smaller than others reported in the literature. Dickerson and Grimes (1947) obtained a genetic correlation of 0.65 between 72 day weight and average daily gain, and Vogt *et al.* (1963) and Ward *et al.* (1964) obtained genetic correlations of 0.47 and 0.69, respectively, between 56 day weight and average daily gain.

A potential cause of part of the differences in genetic correlations between weaning weights and postweaning growth rate would be differences in the age of the pigs at weaning. Weaning weights taken at more advanced ages would be expected to be more highly correlated with postweaning average daily gain. This would result from the fact that differences in weights at older ages would reflect more nearly actual differences in daily gain than would be true of weights at younger ages. Craig *et al.* (1956), for example, reported the genetic correlation between birth weight and 154 day weight to be zero, but this increased to 0.78 between 56 day weight and 154 day weight. While approximately 78 percent of the pigs used in the present investigation were weaned at 56 days, the remaining 22 percent were weaned at 42 days and their

weights then adjusted to 56 days. However, pigs in these two groups were not studied separately and their respective contributions to the calculated correlation cannot be evaluated.

Differences in the milk production of the sows between investigations could be another cause of differences in the weaning weight-average daily gain correlations. Heavier weaning weights resulting from heavy milking sows could result in a lower genetic correlation with postweaning growth rate than weights from pigs that were not provided with an optimum preweaning environment. Data taken from Allen et al. (1959), for example, showed a significant difference among different breeds and crosses in the amount of milk produced per pig during lactation. The importance of preweaning environment is further indicated by studies reported by Hazel et al. (1943) who showed that 50 percent of the variation in growth rate to 56 days of age was caused by an environment common to all individuals within a litter.

The genetic correlations between 56 day weight and probed backfat in this study were $-.05 \pm .53$ in the purebred line and $0.61 \pm .16$ in the crossbred line. No directly comparable estimates are available in the literature. Cummings and Winters (1951), using a composite population of three breeds and crosses of these breeds, reported a simple correlation of essentially zero between 56 day weight and an index of fat cuts. This index was the total weight of the fatbacks, plates, leaf fat, and jowls divided by the cold carcass weight with the leaf fat removed.

The high correlation in the crossbred population indicates that the genes responsible for heavier 56 day weights also contribute to more backfat at slaughter. Unfortunately, there is a large standard

error associated with the estimate in the purebreds. However, under the assumption that the true correlation is approximately zero in the purebreds, the difference between the two populations might be partially explained by differences in preweaning environment between the two populations. The crossbreds could have had more nearly optimum conditions for expressing their genetic capacity to grow to 56 days than did the purebreds. This difference may be the better mothering ability of the crossbred dam. It also may be that the crossbred pigs stimulated greater milk production by their dams. Knowledge of the extent to which 56 day weight differences are caused by actual differences in body fat at this age would be helpful in understanding the true cause of this correlation difference between the two populations.

The lack of genetic variation in 56 day weight in the purebreds in comparison to the greater amount of genetic variation in the crossbreds could also cause the large difference in the correlations between the two populations. That is, the sire component of variance in the purebreds was 0.38 (heritability = 0.03) but in the crossbreds the sire component was 4.49 (heritability = 0.31). Additional estimates of the genetic correlation between 56 day weight and probed backfat are needed since the possibility of a chance correlation this large in the crossbreds cannot be excluded.

The genetic correlation between postweaning average daily gain and probed backfat for the purebreds in this investigation was $-.07 \pm .18$, the corresponding correlation in the crossbreds was $-.39 \pm .18$. Other estimates of the genetic correlation between postweaning growth rate and probed backfat are not available, but Blunn and Baker (1947) reported a genetic correlation of $-.04$ between average daily gain and carcass

backfat depth at the seventh rib. In contrast to this, however, Dickerson (1947) reported a genetic correlation of 1.34 between growth rate and carcass backfat.

The fact that average daily gain was more highly correlated with probed backfat in the crossbreds than in the purebreds in this study could arise in part from the greater genetic variation in average daily gain in the crossbreds. This is suggested by the fact that the sire component of variance in the crossbreds was 0.0036 (heritability = 0.42), but in the purebreds the sire component of variance was 0.0026 (heritability = 0.27).

Correlated Response to Selection

The greatest value of the parameter estimates obtained in this study is their usefulness in predicting trait response to various types of selection. Expected response of a given trait has characteristically been the product of the heritability of that trait and the selection differential. Methods of computing genetic correlations between traits, however, has permitted the extension of response prediction. The existence of a genetic correlation between two traits, for example, results in a correlated response in one when all selection is on the other. Ratios of correlated response to direct response can then be used as measures of the effectiveness of indirect selection. These ratios are obtained by the following equation (Falconer, 1960):

$$\frac{\text{Correlated response in } x \text{ (CR}_x\text{)}}{\text{Direct response in } x \text{ (DR}_x\text{)}} = r_g \cdot \frac{i_y}{i_x} \cdot \frac{h_y}{h_x}$$

where

x = the trait receiving indirect selection.

y = the trait receiving direct selection.

r_g = the estimate of the genetic correlation between x and y .

h = the square root of the heritability.

i = the intensity of selection (which is considered the same for both traits in this discussion).

These ratios, as calculated for 56 day weight, average daily gain, and probed backfat in this investigation, are presented in Table XI.

Within the purebred population, selection for average daily gain will give 86 percent of the improvement in 56 day weight that would be obtained by direct selection for 56 day weight. Conversely, direct selection for 56 day weight will produce only nine percent of the effect in average daily gain that could be accomplished by selecting directly for growth rate. This 56 day weight response is quite similar to the 91 percent reported by Ward et al. (1964). However, the nine percent response in average daily gain when selection is applied to 56 day weight is lower than the 53 percent estimated by Ward et al. (1964).

Applying indirect selection within the crossbreds through average daily gain to improve 56 day weight would not be as effective as within the purebreds. The lower efficiency of indirect selection for weaning weight within the crossbred population ($CR_x/DR_x = 0.28$) is caused primarily by the greater increase in heritability of 56 day weight relative to that for average daily gain.

Improving postweaning growth rate indirectly through selection pressure applied to probed backfat would be approximately half as effective within the purebreds ($CR_x/DR_x = -.19$) as it would be within

TABLE XI

RATIOS OF CORRELATED RESPONSE TO DIRECT RESPONSE FOR THE THREE TRAITS¹

Population	56 Day Weight When Selection Is for		Average Daily Gain When Selection Is for		Probed Backfat When Selection Is for	
	Average Daily Gain	Probed Backfat	56 Day Weight	Probed Backfat	56 Day Weight	Average Daily Gain
Purebred	0.86	-.20	0.09	-.19	-.01	-.03
Crossbred	0.28	0.97	0.14	-.43	0.39	-.36

¹Ratios computed by methods described by Falconer (1960) where

$$\frac{\text{Correlated response in } x}{\text{Direct response in } x} = r_g \cdot \frac{i_y}{i_x} \cdot \frac{h_y}{h_x}$$

and

- x = trait receiving indirect selection
- y = trait receiving direct selection
- r_g = estimate of the genetic correlation between x and y
- h = square root of the heritability
- i = intensity of selection.

the crossbreds ($CR_x/DR_x = -.43$). The cause of this difference between the two populations, as well as that for the 56 day weight-average daily gain association, is much the same. That is, the trait receiving indirect selection has a higher heritability relative to the one receiving direct selection in the crossbreds than it has in the purebreds. In addition to this, the genetic correlation between average daily gain and probed backfat was larger in the crossbreds than in the purebreds ($-.39$ vs. $-.07$).

Increasing weaning weight in the purebreds by selecting against probed backfat would be 20 percent as effective as direct selection for weaning weight. In sharp contrast to this, however, was the fact that selection against probed backfat within the crossbreds would decrease 56 day weight 97 percent as effectively as direct selection for decreased weaning weight. This indicates, as suggested in the discussion of genetic correlations, that differences in 56 day weight within the crossbred population could be due largely to differences in body fat at that age.

There would be essentially no response within the purebreds in probed backfat from selection pressure applied to weaning weight ($CR_x/DR_x = -.01$) or to average daily gain ($CR_x/DR_x = -.03$). Moderate responses could be expected in the crossbred line, however, since the corresponding ratios of correlated response to direct response in the crossbreds were 0.39 and $-.36$, respectively. The greater expected response of probed backfat to indirect selection within that line is a consequence of the larger genetic correlation between that trait and the ones receiving direct selection.

Perhaps the most significant point to be extracted from these comparisons of correlated responses to selection is that within the purebred

population improvement in postweaning growth rate and probed backfat must come almost entirely from selection pressure applied directly to these traits. Any improvement in either of these traits obtained as an indirect response from selection applied to another trait will be quite small. However, considerable progress can be made in improving 56 day weight indirectly by selecting for average daily gain. Thus, in any selection program 56 day weight should receive very little attention. Improvement in this trait should come primarily as indirect improvement through selection for greater average daily gain. This is further justified by the fact that growth rate after weaning is often considered to be of greater economic importance than weaning weight itself.

Sire Components of Covariance

The analyses of variance used to estimate the sire components of covariance (S_{cp}) for each of the three traits are given in Tables XII, XIII, and XIV. These covariance estimates were 1.61, 0.0013, and 0.0023 for 56 day weight (98 sire d.f.), average daily gain (98 sire d.f.), and probed backfat (88 sire d.f.), respectively. Corresponding sire component estimates reported by Enfield and Rempel (1962) were -2.42, 0.0040, and 0.0005.

Using the one locus-two allele case in theoretical purebred and crossbred populations, Willham (1965) has shown that each of the S_{cp} terms was an expression of $\frac{1}{2}pq\alpha(\alpha + 2md)$, where p = frequency of one allele, q = frequency of the other allele, α = average effect of a gene substitution in the purebred population, m = difference in gene frequency of either allele between the two populations crossed, and

TABLE XII
ANALYSIS OF VARIANCE OF 56 DAY WEIGHT

Source	Degrees of Freedom	Mean Square	Variance Component
Sires	98	332.71*	1.61
Lines	1	8.63	-.08
Sires x lines	98	205.99**	1.24
Litters/lines/sires	801	187.97	17.63
Individuals	5687	43.11	43.11

*P < .01.

**P < .005.

Table XIII
ANALYSIS OF VARIANCE OF AVERAGE DAILY GAIN

Source	Degrees of Freedom	Mean Square	Variance Component
Sires	98	0.2185*	0.0013
Lines	1	0.0003	0.0000
Sires x lines	98	0.1260**	0.0018
Litters/lines/sires	778	0.0792	0.0076
Individuals	4681	0.0362	0.0362

*P < .01.

**P < .005.

TABLE XIV
ANALYSIS OF VARIANCE OF PROBED BACKFAT

Source	Degrees of Freedom	Mean Square	Variance Component
Sires	88	0.1367*	0.0023
Lines	1	0.0087	0.0000
Sires x lines	88	0.0482*	0.0009
Litters/lines/sires	577	0.0358	0.0043
Individuals	2330	0.0187	0.0187

*P < .005.

d = genotypic value of the heterozygote. By using matings of males from a purebred population with a gene frequency of $pA_1 + qA_2$ on both females from the same population and on females from another purebred population with a gene frequency of $(p-m)A_1 + (q+m)A_2$, the values in Table XV were obtained. From these values the covariance between paternal half-sibs within the purebred population (S_{pp}) was then evaluated as follows:

$$S_{pp} = p^2(q\alpha)^2 + 2pq\left[\frac{1}{2}(q-p)\alpha\right]^2 + q^2(-p\alpha)^2$$

$$= \frac{1}{2}pq\alpha^2$$

Similarly, the covariance between paternal half-sibs within the crossbred population (S_{cc}) was:

$$S_{cc} = p^2[q(\alpha+2md)]^2 + 2pq\left[\frac{1}{2}(q-p)(\alpha+2md)\right]^2 + q^2[-p(\alpha+2md)]^2$$

$$= \frac{1}{2}pq(\alpha+2md)^2$$

TABLE XV

VALUES NECESSARY TO EVALUATE THE GENETIC COVARIANCES
BETWEEN PUREBRED PATERNAL HALF-SIBS AND BETWEEN
PUREBRED AND CROSSED PATERNAL HALF-SIBS

Sires	Frequency	Mean Genotypic Values of Offspring Expressed as Deviations from the Population Mean	
		Purebred	Crossbred
A_1A_1	p^2	$q\alpha$	$q(\alpha+2md)$
A_1A_2	$2pq$	$\frac{1}{2}(q-p)\alpha$	$\frac{1}{2}(q-p)(\alpha+2md)$
A_2A_2	q^2	$-p\alpha$	$-p(\alpha+2md)$

Also, the covariance between purebred and crossbred paternal half-sib
(S_{cp}) was:

$$S_{cp} = p^2(q\alpha)q(\alpha+2md) + 2pq\left(\frac{1}{2}\right)(q-p)\alpha\left(\frac{1}{2}\right)(q-p)(\alpha+2md) + q^2(-p\alpha)-p(\alpha+2md)$$

$$= \frac{1}{2}pq\alpha(\alpha+2md)$$

From these quantities it can be shown that the ratio of S_{cc} to S_{cp} is equal to $(\alpha+2md)/\alpha$. Actual ratios of S_{cc} to S_{cp} obtained in this study for 56 day weight, average daily gain, and probed backfat were 2.1, 3.5, and 1.3, respectively. Since $(\alpha+2md)/\alpha = \alpha/\alpha + (2md)/\alpha = 1 + (2md)/\alpha$ is greater than one, it follows that α and $2md$ are either both positive or both negative. In either case $(\alpha+2md)^2 > \alpha^2$ and since p and q are positive, $\frac{1}{2}pq\alpha^2 < \frac{1}{2}pq(\alpha+2md)^2$.

This provides a tenable explanation of the cause of the difference in the heritability estimates for both 56 day weight and postweaning average daily gain between the purebred and crossbred populations. The heritability estimate for each of these traits in the purebreds

was equal to $S_{pp}/\frac{1}{4}$, or $(\frac{1}{2}pq\alpha^2)/\frac{1}{4}$. Within the crossbreds each heritability estimate was equal to $S_{cc}/\frac{1}{4}$, or $[\frac{1}{2}pq(\alpha+2md)^2]/\frac{1}{4}$. Thus, for each of these two traits, differences in the heritability estimates between the two populations were caused by md , or the product of the gene frequency differences and the degree of dominance.

Comstock (1961) presented equations using the ratio of S_{cc} to S_{cp} for evaluating the effectiveness of reciprocal recurrent selection (RRS) programs relative to each of several types of intra-population selection (IPS) schemes. Each of these equations is expressed in terms of R , k , k_1 , σ_p , σ_{pi} , S_{cc} , and S_{cp} where R = population mean change as the result of a specified type of IPS, k = selection differential in RRS in standard deviations of the selection criterion, k_1 = selection differential in IPS in standard deviations of the selection criterion, σ_p = phenotypic standard deviation of the selection criterion used in RRS, σ_{pi} = phenotypic standard deviation used in IPS, and S_{cc} and S_{cp} are the same as described above. These values necessary for the equations, which have been obtained for each of the three traits in this study, are outlined in Table XVI.

For RRS compared to IPS within the purebred population, using mass selection with data available on both sexes,

$$R = \frac{1}{4} \cdot \frac{k}{k_1} \cdot \frac{\sigma_{pi}}{\sigma_p} \cdot \frac{S_{cc}}{S_{cp}}$$

The value of $\frac{1}{4}$ must be used since, under mass selection, data are obtained directly from the individuals selected, but in RRS data are obtained from individuals that have a genetic correlation of $\frac{1}{4}$ (half-sibs) with those selected. Comstock (1961) suggests that k/k_1 may

TABLE XVI

VALUES NECESSARY FOR COMPARING CROSSBRED RESPONSE FROM
INTRA-POPULATION SELECTION AND FROM
RECIPROCAL RECURRENT SELECTION

Values ¹	Traits		
	56 Day Weight	Average Daily Gain	Probed Backfat ²
S_{pp}	0.49	0.0034	0.0036
S_{cc}	3.33	0.0046	0.0030
S_{cp}	1.61	0.0013	0.0023
σ_{pi}	7.98	0.218	0.163
σ_p	8.43	0.214	0.160

¹ S_{pp} = sire component of variance in the purebred population.

S_{cc} = sire component of variance in the crossbred population.

S_{cp} = sire component of covariance between the purebred and crossbred populations.

σ_{pi} = phenotypic standard deviation in the purebred population.

σ_p = phenotypic standard deviation in the crossbred population.

² S_{pp} for all 99 sires in this study. S_{pp} for the 88 sires having both purebred and crossbred probed backfat observations could not be obtained because of disruption of computer facilities.

range between 0.4 and 0.8 being larger when programs are large. Thus, both $k = 0.8$ and $k = 1.0$ will be compared against $k_1 = 1$.

Table XVII gives the results of evaluating R for 56 day weight, average daily gain, and probed backfat. These results show that improvement in crossbred performance from IPS within the purebred population would be greater than that obtained by RRS. It should be noted that Comstock (1961) states that the condition $S_{cp} < \sqrt{S_{pp} \cdot S_{cc}}$ is inevitable. This condition does exist in this study for average daily gain and probed backfat but not for 56 day weight. Unfortunately, the extent to which this influences the accuracy of the ratio S_{cc}/S_{cp} for 56 day weight (Table XVIII) cannot be evaluated.

Although half-sib family selection would be much less likely to be used on 56 day weight, average daily gain, and probed backfat than mass selection, this type of intra-population selection was also compared against RRS. The ratio of the crossbred population response from RRS to the crossbred population response from half-sib family selection within the purebreds (Comstock, 1961) is

$$R = \frac{k}{k_1} \cdot \frac{\sigma_{pi}}{\sigma_p} \cdot \frac{S_{cc}}{S_{cp}}$$

For this comparison, k/k_1 was set equal to 1.0. The variable quantities and the computed R are given in Table XIX. The values obtained for R indicate RRS to be superior to half-sib family selection for improving crossbred performance in all three traits.

Unfortunately, other estimates of the ratio of the crossbred response from RRS to the crossbred response from either mass selection or half-sib family selection for the three traits used in this study

TABLE XVII

RATIO OF THE CROSSBRED POPULATION MEAN CHANGE FROM
 RECIPROCAL RECURRENT SELECTION TO THE CROSSBRED
 POPULATION MEAN CHANGE FROM PUREBRED MASS
 SELECTION IN BOTH SEXES

k/k_i	Traits		
	56 Day Weight	Average Daily Gain	Probed Backfat
0.8	0.39	0.72	0.27
1.0	0.49	0.90	0.34

TABLE XVIII

COMPARISON AMONG 56 DAY WEIGHT, AVERAGE DAILY GAIN, AND
 PROBED BACKFAT OF THE VARIABLE QUANTITIES USED TO
 EVALUATE R IN THE COMPARISON OF RRS AGAINST
 INTRA-POPULATION MASS SELECTION

Variable Quantity	Traits		
	56 Day Weight	Average Daily Gain	Probed Backfat
σ_{pi}/σ_p	0.95	1.02	1.02
s_{cc}/s_{cp}	2.07	3.54	1.30

TABLE XIX

COMPARISON AMONG 56 DAY WEIGHT, AVERAGE DAILY GAIN, AND
 PROBED BACKFAT OF THE VARIABLE QUANTITIES AND THE
 COMPUTED R IN THE COMPARISON OF RRS AGAINST
 INTRA-POPULATION HALF-SIB FAMILY SELECTION

Quantity	Traits		
	56 Day Weight	Average Daily Gain	Probed Backfat
σ_{pi}/σ_p	0.95	1.02	1.02
s_{cc}/s_{cp}	2.07	3.54	1.30
R	1.97	3.61	1.33

are not available in the literature. Such estimates, if based on adequate numbers of sire groups, would be invaluable for fully evaluating the utility of reciprocal recurrent selection.

The differences in the values of S_{cp} and S_{cc} for each of the traits in this investigation are reflected by the significant sire by line interactions. To examine the nature of this interaction the mean performance of each boar for each of the three performance traits was tabulated for both lines. Within each trait the boars were then ranked according to the performance of their purebred offspring and this was compared to the order obtained on the basis of their crossbred offspring. This comparison revealed no similarity in the rank of the sires between the two lines. Consequently, boars selected within purebred lines on the basis of their performance in reciprocal recurrent selection programs would not necessarily be the same ones selected in intra-population selection programs.

SUMMARY

The data used in this investigation were obtained from the swine breeding herds maintained at Stillwater and Ft. Reno in the Oklahoma Regional Swine Breeding Laboratory Project. The data included the progeny records of all purebred boars that sired both purebred and crossbred litters during the 18 seasons from fall 1955 through spring 1964. The performance traits studied were 56 day pig weight, post-weaning average daily gain, and probed backfat at 200 pounds live weight. Least squares constants were used to adjust each observation on the three performance traits for differences caused by station, year, season, breed, age of dam, inbreeding of litter, management system, sex, and litter size at weaning. Analyses of variance were then performed on the adjusted observations to obtain sire component estimates.

The estimate of the heritability of 56 day weight was $0.03 \pm .06$ in the purebreds and $0.19 \pm .09$ in the crossbreds. For average daily gain the heritability estimates were $0.28 \pm .06$ in the purebreds and $0.39 \pm .10$ in the crossbreds. Estimates of the heritability of probed backfat were similar in both populations, being $0.55 \pm .12$ in the purebreds and $0.47 \pm .13$ in the crossbreds.

The genetic correlations between 56 day weight and average daily gain, 56 day weight and probed backfat, and average daily gain and probed backfat were $0.29 \pm .50$, $-.05 \pm .53$, and $-.07 \pm .18$, respectively, in the purebred populations. The corresponding genetic correlations in the crossbred population were $0.20 \pm .21$, $0.61 \pm .16$, and $-.39 \pm .18$.

Ratios of correlated response to direct response were computed using the heritability estimates and genetic correlations. Comparisons of the correlated responses to selection showed that within the purebred population improvement in postweaning growth rate and probed backfat must come almost entirely from selection pressure applied directly to these traits. Any improvement obtained as an indirect response would be relatively small. In contrast to this, 56 day weight would show considerable indirect response from selection pressure applied to average daily gain. Within the crossbreds, selection against probed backfat would decrease 56 day weight almost as effectively as direct selection against 56 day weight. Also, average daily gain would be increased by selection against probed backfat. In addition, probed backfat would be increased by selection for 56 day weight but decreased by selection for average daily gain.

The sire components of covariance between purebred and crossbred offspring were 1.61, 0.0013, and 0.0023 for 56 day weight, average daily gain, and probed backfat, respectively. Ratios of these sire components of covariance to the sire components of variance within the crossbreds were used to evaluate the effectiveness of reciprocal recurrent selection relative to intra-population selection schemes for improving crossbred performance. The results indicated that improvement in crossbred performance from intra-population mass selection on both sexes within the purebred population would be greater for all three traits than that obtained by reciprocal recurrent selection. However, reciprocal recurrent selection was superior to half-sib family selection within the purebreds for improving crossbred performance for the three traits.

Significant sire by line interactions existed for all three traits. The nature of this interaction suggests that boars selected on the basis of their performance in reciprocal recurrent selection programs would not necessarily be the same ones selected in intra-population selection programs.

LITERATURE CITED

- Allen, A. D., J. F. Lasley, and L. F. Tribble. 1959. Milk production and related performance factors in sows. Mo. Agr. Exp. Sta. Res. Bul. 712.
- A.S.A.P. 1960. Techniques and Procedures in Animal Production Research. American Society of Animal Production.
- Baker, M. L., L. N. Hazel, and C. F. Reinmiller. 1943. The relative importance of heredity and environment in the growth rate of pigs at different ages. J. Animal Sci. 2:1.
- Bell, A. E. 1957. Genetic and phenotypic changes in Drosophila populations under selection. Proc. Sixth Poultry Breeders Roundtable, April 27-28, 1957. Chicago, Illinois.
- Bell, A. E. and C. H. Moore. 1958. Further comparisons of reciprocal recurrent selection with conventional methods of selection for the improvement of quantitative characteristics. Proc. X International Congress of Genetics. p. 20.
- Bell, A. E., C. H. Moore, B. B. Bohren, and D. C. Warren. 1952. Systems of breeding designed to utilize heterosis in the domestic fowl. Poult. Sci. 31:11.
- Bell, A. E., C. M. Moore, and D. C. Warren. 1955. The evaluation of new methods for the improvement of quantitative characteristics. Cold Spring Harbor Symposia on Quantitative Biology 20:197.
- Bennett, J. A. and J. H. Coles. 1946. A comparative study of certain performance and carcass characteristics of Yorkshire barrows and gilts. Sci. Agr. 26:265.
- Blunn, Cecil T. and Marvel L. Baker. 1947. The relation between average daily gain and some carcass measurements. J. Animal Sci. 6:424.
- Brown, W. P. and A. E. Bell. 1961. Genetic analysis of a "plateaued" population of Drosophila melanogaster. Genetics 46:408.
- Bywaters, J. H. 1937. The heredity and environmental portions of the variance in weaning weights of Poland China pigs. Genetics 22:457.
- Chambers, Doyle and J. A. Whatley, Jr. 1951. Heterosis in crosses of inbred lines of Duroc swine. J. Animal Sci. 10:505.

- Comstock, R. E. 1956. Genetic variance for eight week weight in strains and crosses. *Poult. Sci.* 35:1137. (Abstr.).
- Comstock, R. E. 1961. Reciprocal recurrent selection with reference to swine breeding. Twenty-fourth Annual Rept. Regional Swine Breeding Laboratory. Ames, Iowa.
- Comstock, R. E. and H. F. Robinson. 1956. Findings relative to reciprocal recurrent selection. *Proc. of the International Genetics Symp.*, 1956. p. 461.
- Comstock, R. E., H. F. Robinson, and P. H. Harvey. 1949. A breeding procedure designed to make maximum use of both general and specific combining ability. *Agron. J.* 41:360.
- Comstock, R. E. and L. M. Winters. 1944. A comparison of the effects of inbreeding and selection on performance in swine. *J. Animal Sci.* 3:381.
- Comstock, R. E., L. M. Winters, and J. N. Cummings. 1944. The effect of sex on the development of the pig. III. Differences in growth rate between gilts and barrows by lines of breeding. *J. Animal Sci.* 3:120.
- Comstock, R. E., L. M. Winters, P. S. Jordan, and O. M. Kiser. 1942. Measures of growth rate for use in swine selection. *J. Agr. Res.* 65:379.
- Cox, D. F. 1964. Heritability of backfat thickness measured on the live pig at a constant age. *J. Animal Sci.* 23:447.
- Craft, W. A. 1953. Results of swine breeding research. *U.S.D.A. Circ.* 916.
- Craft, W. A. 1958. Fifty years of progress in swine breeding. *J. Animal Sci.* 17:960.
- Craig, J. V., H. W. Norton, and S. W. Terrill. 1956. A genetic study of weight at five ages in Hampshire swine. *J. Animal Sci.* 15:242.
- Crampton, E. W. and G. C. Ashton. 1946. The effect of a vitamin B mixture, of protein, and of proportion of protein of animal origin in the supplements to barley and to wheat in the bacon hog ration. *Sci. Agr.* 26:43.
- Cummings, J. N. and L. M. Winters. 1951. A study of factors related to carcass yields in swine. *Minn. Agr. Exp. Sta. Tech. Bul.* 195.
- Dickerson, G. E. 1947. Composition of hog carcasses as influenced by heritable differences in rate and economy of gain. *Iowa Agr. Exp. Sta. Res. Bul.* 354.

- Dickerson, G. E., C. T. Blunn, A. B. Chapman, R. M. Kottman, J. L. Krider, E. J. Warwick, and J. A. Whatley, Jr. 1954. Evaluation of selection in developing inbred lines of swine. North Central Regional Publ. No. 38.
- Dickerson, G. E. and J. C. Grimes. 1947. Effectiveness of selection for efficiency of gain in Duroc swine. *J. Animal Sci.* 6:265.
- Durham, R. M. 1958. Personal communication.
- Durham, Ralph M. and John H. Zeller. 1955. Using the probing technique in selecting breeding swine on farms. *J. Animal Sci.* 14:1180. (Abstr.).
- El-Issawi, H. F. and W. E. Rempel. 1961. Heritability of growth rate in inbred swine based on a crossbred foundation. *J. Animal Sci.* 20:593.
- Enfield, F. D. 1957. Heritability of carcass length, carcass backfat thickness, and loin lean area in swine. M.S. Thesis, Oklahoma State University.
- Enfield, F. D. 1960. Quantitative inheritance in poultry with special reference to genetic correlations between purebred and crossbred half-sib families. Ph. D. Thesis, University of Minnesota.
- Enfield, F. D. and W. E. Rempel. 1962. Covariance of sire effects in purebred and crossbred populations of swine. *J. Animal Sci.* 21:971. (Abstr.).
- Falconer, D. S. 1960. *Quantitative Genetics.* The Ronald Press, New York.
- Fredeen, H. T. 1953. Genetic aspects of Canadian bacon production. Canada Dept. of Agr., Ottawa, Publ. 889.
- Fredeen, H. T. and R. N. Plank. 1963. Litter size and pre- and post-weaning performance in swine. *Can. J. Animal Sci.* 43:135.
- Godbey, E. G. and W. C. Godley. 1961. Effects of inbreeding and other factors on weights, measurements, and mortality of pigs. *S. C. Agr. Exp. Sta. Tech. Bul.* 1004.
- Gray, R. C., L. F. Tribble, B. N. Day, and J. F. Lasley. 1965. Five generations of selection for thinner backfat. *J. Animal Sci.* 24:848.
- Gregory, K. E. and G. E. Dickerson. 1952. Influence of heterosis and plane of nutrition on rate and economy of gains, digestion and carcass composition of pigs. *Mo. Agr. Exp. Sta. Res. Bul.* 493.
- Griesbach, L. 1962. A test of the reciprocal recurrent selection technique with chicken broilers. *Can. J. Animal Sci.* 42:145.

- Harvey, Walter R. 1960. Least-squares analysis of data with unequal numbers. Agr. Res. Service. U.S.D.A., ARS-20-8.
- Hazel, L. N., M. L. Baker, and C. F. Reinmiller. 1943. Genetic and environmental correlations between the growth rates of pigs at different ages. J. Animal Sci. 2:118.
- Henderson, C. R. 1953. Estimation of variance and covariance components. Biometrics 9:226.
- Hetzer, H. O. and J. H. Zeller. 1956. Selection for high and low fatness in Duroc and Yorkshire swine. J. Animal Sci. 15:1215. (Abstr.).
- Kojima, K. and Therese M. Kelleher. 1963. A comparison of purebred and crossbred selection schemes with two populations of Drosophila pseudoobscura. Genetics 48:57.
- Louca, A. and O. W. Robison. 1965. Heritability and genetic correlations in swine. J. Animal Sci. 24:850. (Abstr.).
- Menzies-Kitchin, A. W. 1937. Fertility, mortality, and growth rate in pigs. J. Agr. Res. 27:611.
- Noland, P. R., W. Gifford, and C. J. Brown. 1964. Effects of inbreeding in a Poland China line of swine on certain productivity traits. Ark. Agr. Exp. Sta. Bul. 681.
- Nordskog, A. W., R. E. Comstock, and L. M. Winters. 1944. Hereditary and environmental factors affecting growth rate in swine. J. Animal Sci. 3:257.
- Omtvedt, I. R., C. M. Stanislaw, L. E. Walters, D. R. Rule, and P. J. Cunningham. 1965. The effect of sex on feedlot and carcass traits in swine. Okla. Agr. Exp. Sta. Misc. Pub. 76:20.
- Omtvedt, I. R., J. A. Whatley, Jr., and R. L. Willham. 1966. Some production factors associated with weaning records in swine. J. Animal Sci. (In Press).
- Rasmuson, Marriane. 1956. Recurrent reciprocal selection. Results of three model experiments on Drosophila for improvement of quantitative characters. Hereditas 42:397.
- Reeve, E. C. R. 1955. The variance of the genetic correlation coefficient. Biometrics 11:357.
- Robison, O. W., A. Louca, and J. E. Legates. 1964. Purebred and crossbred performance of paternal half-sibs of swine. J. Animal Sci. 23:853. (Abstr.).
- Smith, A. D. B. and H. P. Donald. 1939. Analysis of post-weaning growth in pigs. J. Agr. Sci. 29:274.

- Taylor, J. C., R. H. Miller, and H. O. Hetzer. 1965. Genetic correlations between straightbred and crossbred swine. *J. Animal Sci.* 24:852. (Abstr.).
- Vogt, D. W., R. E. Comstock and W. E. Rempel. 1963. Genetic correlations between some economically important traits in swine. *J. Animal Sci.* 22:214.
- Ward, H. K., W. E. Rempel, and F. D. Enfield. 1964. Genetic relationship of weaning weight with post-weaning growth rate in swine. *J. Animal Sci.* 23:651.
- Whatley, J. A., Jr. 1942. Influence of heredity and other factors on 180-day weight in Poland China swine. *J. Agr. Res.* 65:249.
- Whatley, J. A., Jr., I. T. Omtvedt, J. B. Palmer, and D. F. Stephens. 1959. A comparison of pasture and confinement systems for raising hogs. *Okla. Agr. Exp. Sta. Misc. Pub.* 55:8.
- Whatley, J. A., Jr. and E. L. Quaife. 1937. Adjusting weights of pigs to a standard age of 56 days. *Proc. Am. Soc. Animal Prod.* 30:126.
- Willham, R. L. 1965. *Animal Breeding*. Mimeographed notes.
- Winters, L. M., R. E. Comstock, R. E. Hodgson, O. M. Kiser, P. S. Jordan, and D. L. Dailey. 1943. Experiments with inbreeding swine and sheep. *Minn. Agr. Exp. Sta. Bul.* 364.

A P P E N D I X

TABLE XX
ANALYSIS OF VARIANCE OF 56 DAY WEIGHT IN THE
PUREBRED POPULATION

Source	Degrees of Freedom	Mean Square	Variance Component	% of Variance
Sires	98	214.59*	0.49	0.77
Litters	456	180.02*	21.76	34.13
Individuals	3054	41.51	41.51	65.10

*P < .005.

TABLE XXI
ANALYSIS OF VARIANCE OF AVERAGE DAILY GAIN IN THE
PUREBRED POPULATION

Source	Degrees of Freedom	Mean Square	Variance Component	% of Variance
Sires	98	0.1429*	0.0034	6.90
Litters	443	0.0848*	0.0085	17.86
Individuals	2545	0.0374	0.0374	78.57

*P < .005.

TABLE XXII
ANALYSIS OF VARIANCE OF PROBED BACKFAT IN THE
PUREBRED POPULATION

Source	Degrees of Freedom	Mean Square	Variance Component	% of Variance
Sires	98	0.1123*	0.0036	13.85
Litters	416	0.0346*	0.0040	15.38
Individuals	1642	0.0184	0.0184	70.77

*P < .005.

TABLE XXIII
ANALYSIS OF VARIANCE OF 56 DAY WEIGHT IN THE
CROSSED POPULATION

Source	Degrees of Freedom	Mean Square	Variance Component	% of Variance
Sires	98	324.11*	3.33	4.68
Litters	345	198.49*	22.88	32.14
Individuals	2633	44.97	44.97	63.18

*P < .005.

TABLE XXIV
ANALYSIS OF VARIANCE OF AVERAGE DAILY GAIN IN THE
CROSSBRED POPULATION

Source	Degrees of Freedom	Mean Square	Variance Component	% of Variance
Sires	98	0.2016*	0.0046	9.83
Litters	335	0.0718*	0.0075	16.03
Individuals	2136	0.0347	0.0347	74.14

*P < .005.

TABLE XXV
ANALYSIS OF VARIANCE OF PROBED BACKFAT IN THE
CROSSBRED POPULATION

Source	Degrees of Freedom	Mean Square	Variance Component	% of Variance
Sires	88	0.0747*	0.0030	11.72
Litters	241	0.0319*	0.0036	14.06
Individuals	900	0.0190	0.0190	74.22

*P < .005.

TABLE XXVI

ANALYSIS OF VARIANCE OF 56 DAY WEIGHT IN THE PUREBRED PIGS
HAVING BOTH 56 DAY WEIGHT AND AVERAGE DAILY
GAIN OBSERVATIONS

Source	Degrees of Freedom	Mean Square	Variance Component	% of Variance
Sires	98	178.25	0.29	0.50
Litters	443	152.92	20.87	35.87
Individuals	2545	37.04	37.04	63.66

TABLE XXVII

ANALYSIS OF VARIANCE OF 56 DAY WEIGHT IN THE CROSSBRED PIGS
HAVING BOTH 56 DAY WEIGHT AND AVERAGE DAILY
GAIN OBSERVATIONS

Source	Degrees of Freedom	Mean Square	Variance Component	% of Variance
Sires	98	282.24	4.32	6.84
Litters	335	155.27	20.30	32.13
Individuals	2136	38.55	38.55	61.03

TABLE XXVIII

ANALYSIS OF VARIANCE OF 56 DAY WEIGHT IN THE PUREBRED PIGS
HAVING BOTH 56 DAY WEIGHT AND PROBES
BACKFAT OBSERVATIONS

Source	Degrees of Freedom	Mean Square	Variance Component	% of Variance
Sires	98	127.64	0.34	0.64
Litters	416	106.63	17.94	34.23
Individuals	1642	34.14	34.14	65.13

TABLE XXIX

ANALYSIS OF VARIANCE OF AVERAGE DAILY GAIN IN THE PUREBRED PIGS
HAVING BOTH AVERAGE DAILY GAIN AND PROBED
BACKFAT OBSERVATIONS

Source	Degrees of Freedom	Mean Square	Variance Component	% of Variance
Sires	98	0.1155	0.0026	6.65
Litters	416	0.0553	0.0062	15.86
Individuals	1642	0.0303	0.0303	77.49

TABLE XXX

ANALYSIS OF VARIANCE OF 56 DAY WEIGHT IN THE CROSSBRED PIGS
HAVING BOTH 56 DAY WEIGHT AND PROBED
BACKFAT OBSERVATIONS

Source	Degrees of Freedom	Mean Square	Variance Component	% of Variance
Sires	88	181.42	4.49	7.64
Litters	241	109.66	21.36	36.39
Individuals	900	32.85	32.85	55.97

TABLE XXXI

ANALYSIS OF VARIANCE OF AVERAGE DAILY GAIN IN THE CROSSBRED PIGS
HAVING BOTH AVERAGE DAILY GAIN AND PROBED
BACKFAT OBSERVATIONS

Source	Degrees of Freedom	Mean Square	Variance Component	% of Variance
Sires	88	0.0991	0.0036	10.47
Litters	241	0.0468	0.0062	18.02
Individuals	900	0.0246	0.0246	71.51

TABLE XXXII
ANALYSIS OF COVARIANCE BETWEEN 56 DAY WEIGHT AND
AVERAGE DAILY GAIN WITHIN THE
PUREBRED POPULATION

Source	Degrees of Freedom	Mean Cross Products	Covariance Component
Sires	98	1.8214	0.0090
Litters	443	1.3981	0.1864
Individuals	2545	0.3629	0.3629

TABLE XXXIII
ANALYSIS OF COVARIANCE BETWEEN 56 DAY WEIGHT AND
AVERAGE DAILY GAIN WITHIN THE
CROSSBRED POPULATION

Source	Degrees of Freedom	Mean Cross Products	Covariance Component
Sires	98	2.9152	0.0277
Litters	335	2.0080	0.2550
Individuals	2136	0.5416	0.5416

TABLE XXXIV
ANALYSIS OF COVARIANCE BETWEEN 56 DAY WEIGHT AND
PROBED BACKFAT WITHIN THE
PUREBRED POPULATION

Source	Degrees of Freedom	Mean Cross Products	Covariance Component
Sires	98	-.07785	-.00161
Litters	416	-.04399	0.00128
Individuals	1642	-.04916	-.04916

TABLE XXXV

ANALYSIS OF COVARIANCE BETWEEN 56 DAY WEIGHT AND
PROBED BACKFAT WITHIN THE
CROSSBRED POPULATION

Source	Degrees of Freedom	Mean Cross Products	Covariance Component
Sires	88	0.52680	0.07093
Litters	241	-.40930	-.08133
Individuals	900	-.11680	-.11680

TABLE XXXVI

ANALYSIS OF COVARIANCE BETWEEN AVERAGE DAILY GAIN
AND PROBED BACKFAT WITHIN THE
PUREBRED POPULATION

Source	Degrees of Freedom	Mean Cross Products	Covariance Component
Sires	98	0.00017	-.00022
Litters	416	0.00422	0.00102
Individuals	1642	0.00009	0.00009

TABLE XXXVII

ANALYSIS OF COVARIANCE BETWEEN AVERAGE DAILY GAIN
AND PROBED BACKFAT WITHIN THE
CROSSBRED POPULATION

Source	Degrees of Freedom	Mean Cross Products	Covariance Component
Sires	88	-.01278	-.00129
Litters	241	0.00436	0.00110
Individuals	900	0.00041	0.00041

VITA

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