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INFLUENCE OF INBREEDING, AGE AND GROWTH RATE OF SOWS ON SEXUAL MATURITY, RATE OF OVULATION, FERTILIZATION AND EMBRYONIC SURVIVAL

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TABLE OF CONTENTS

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INTRODUCTION

Animal husbandmen have long recognized the economic importance of litter size in swine. Under corn belt conditions, a sow must usually wean at least 5 healthy pigs if she is to return feed and labor costs to the producer of market pigs. It is equally well known that losses from farrowing to weaning are likely to equal or exceed 30 per cent. Therefore, a sow must farrow at least 7 pigs if she is to be considered even a marginal producer.

In any swine improvement program, reproductive efficiency must be considered as a means as well as an end, since opportunity for selection is limited by the number of offspring. Inbred lines of swine, in particular, often are characterized by small litters which make maintenance costly and progress slow. Inbreeding both of litter and of dam has been shown to affect litter size adversely. The first effect is usually explained on the basis of lowered viability of embryos. The second could be due to a tendency for inbred sows: (1) to produce fewer ova, (2) to produce ova which are less capable of fertilization, or (3) to have a lower survival of fertilized ova than outbred sows. So far as is known by the authors, no study has been made of the relative importance of these three factors as causes of the decline in litter size associated with inbreeding.

The study presented herein was initiated to determine the relative importance of ovulation rate, efficiency of fertilization, and foetal mortality as factors affecting litter size in swine and particularly, how these components of litter size are influenced by the sow's degree of inbreeding. The females studied were from three inbred strains (two Poland and one Hampshire), the outbred College Duroc herd and their crosses. These stocks were well suited for this investigation because (1) comparison of crosses with parent strains permitted estimates of inbreeding effects on litter size, (2) the genetic diversity between the strains provided a test of the generality of relationships observed, and (3) management was uniform for all stocks and complete pedigree and growth records were available.

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EARLIER STUDIES OF VARIATION IN LITTER SIZE

Influence of Heredity

Rommel (1906) found the average litter size for Poland China sows in the period 1882-1886 to be 7.04 pigs and in the period 1898-1902 to be 7.52 pigs, an increase of 0.48 pigs per litter. Morris and Johnson (1932) also sampling the Poland China breed, found average litter size to be 8.69 in the period from 1918-1921, an increase of more than 1 pig per litter over Rommel's 1902 figure. These findings show an increase of 1.65 pigs, in litter size in the Poland breed during a period of 36 years, indicating either (1) presence of divergent strains from a fertility standpoint within the breed or (2) a substantial gain due to selection or (3) improved environment. In support of the third explanation, Johansson (1929) found that there had been no change in litter size at Bondeson's pig breeding station in Sweden in 35 years, under comparatively uniform systems of feeding and management and Wentworth and Aubel (1916) found no difference in the average litter size of "big-type" and "small-type" Poland China swine.

Rommel and Phillips (1906) reported for Poland China swine a correlation coefficient of $+.06 \pm .008$ between the size of litters in which sows were farrowed and the size of their own litters. The correlation was much higher for yearlings than for older daughters. Johansson (1929) found no repeatability of litter size, but found that the correlation of the mean for the first four litters of sows with the mean for the first four litters of their daughters was $r = +.129 \pm 0.079$. These results indicate that variability in litter size of sows is partly hereditary, but that it is very strongly influenced by environmental influences during growth and development and between successive litters.

Wright (1920) has demonstrated methods of dividing the total variance of a characteristic into genetic and environmental portions. All causes of variation that are not found associated with differences in genotype are classified as environmental. The heritable portion contributes to the resemblance of related animals and when expressed as a fraction of the total variance it is called "heritability." Lush and Molln (1942), in their review, found that heritability estimates for size of litter at birth in swine had ranged from 0.10 to 0.44 and considered their own estimate of 0.17 to be representative. Stewart (1945b) obtained an estimate of 0.14, Cummings *et al.* (1947) reported one of 0.22, and Blunn and Baker (1949) give 0.251 and 0.235 as their estimates by two different methods.

Inbreeding of Dam

The opinion is held by many investigators that inbreeding of the dam affects adversely the size of litter farrowed. Yet few published estimates of the size of this effect have been made. Comstock and Winters (1944) estimated that for 10 per cent increased inbreeding of dam (independent of inbreeding of litter) litter size at birth decreased by only 0.09 pigs. Dickerson *et al.* (1947) compared numbers farrowed by inbred and linecross gilts mated to unrelated boars, and estimated the decline to be 0.16 pigs per 10 per cent increased inbreeding of dam. Stewart (1945a) found that number of pigs farrowed declined about 0.63 per 10 per cent increased inbreeding of dam, if both age of gilt and inbreeding of litter were held constant. Inbreeding of litter was a surprisingly unimportant factor in his data. Blunn and Baker (1949) found the simple regressions of number of pigs farrowed on inbreeding of both dam and litter to be highly significant and about equal in size (–.6 pigs per 10 per cent inbreeding increase) but if age was held constant both relationships lacked significance.

Age of Dam

Studies of the age influence have been of two types. One measures the influence of age at breeding or farrowing on size of first litter. The other estimates the influence of age, previous pregnancy and possibly selection on litter size in successive farrowings. We will consider only age of first farrowing here.

Ellinger (1921), and Krizenecky (1935 and 1942) found little effect of age of breeding upon size of first litter. Johansson (1929) found that litter size increased with age of sow at farrowing up to about 16 months. Olbrycht (1943) found that sows farrowing at 12 months of age produced an average of 1.07 pigs less than those not farrowing until 17 months of age. Stewart (1945a) found that size of the first litter increased in curvilinear fashion with age of dam up to about 15 months, most of the increase taking place between the ages of 9 and 12 months. With inbreeding of both dams and their litters held constant, Stewart calculated the partial regression of total litter size at birth on age of dam in months to be 0.609. Korkman (1947) found a smaller regression (.24 pigs) of litter size at birth on age in months, but in his data most of the gilts farrowed between 11 and 21 months of age.

General Health

It is a well established opinion among animal husbandmen that the physical well-being of a sow prior to and during gestation strongly influences the number and vigor of her offspring. This view has been based largely on the assumption that body weight is indicative of general health, which is undoubtedly true within limits. McKenzie (1928) found a marked relationship of daily gain in weight during the first four weeks after conception with number of pigs farrowed. Hogan and McKenzie (1927) found that sows gaining below the average of their group the first month after breeding, produced litters below the average in size. Zeller *et al.* (1937), and Donald and Fleming (1938) reported similar results. Stewart (1945a) found that age and weight at time of breeding, and gains in weight during gestation were significantly associated with number of pigs farrowed.

Foetal Mortality

During the period from about 1910 to 1920, considerable interest was aroused in the problem of foetal mortality as a cause of reduced fertility, especially among litter bearing animals. This was perhaps largely due to the work of Hammond (1914), who found in 27 sows killed just after ovulation an average of 20 corpora lutea, whereas in the same English breeds the average litter size was 12. This indicated a loss of about 40 per cent of the ova shed.

Corner (1923) reviewed the results of earlier workers concerning foetal mortality in several different species, and reported his own observations in swine. Corner's results were based on the study of 535 reproductive tracts of sows, in various stages of pregnancy, recovered from slaughter houses.

In 10 sows pregnant 10 days or less 104 ova were shed, with recovery of 55 normal and 15 degenerating blastocysts and 10 uncleaved ova. Mortality was 47 per cent if the 24 unrecovered ova were included, but only 31 per cent if it is assumed that mortality among the 24 unrecovered ova was the same as among the 80 recovered.

In 30 sows pregnant from 13 to 21 days, he found 320 corpora, 220 normal and 15 abnormal embryos. Missing and abnormal embryos amounted to 31.3 per cent of all ova shed.

From 127 sows with embryos 8 to 40 mm. long, he counted 1306 corpora and recovered 1035 normal and 9 abnormal embryos; total mortality was 20.8 per cent.

There were 212 pregnancies with embryos 41-150 mm. in length; here 1909 corpora, 1531 normal and 9 abnormal foetuses were found, with total mortality of 19.8 per cent.

Total mortality was 30.1 per cent in 156 sows with pigs 151 mm. or longer at slaughter, based on 1265 corpora and 876 normal and 25 abnormal pigs.

Since these sows were sold for slaughter during pregnancy, they may represent a selected sample of sows. However, Corner's data do indicate important prenatal losses of ova (20 to 30 per cent), most of which leave no trace even at the earliest stages of pregnancy examined. Corner found no evidence of sepsis or of endometrial irregularities.

Gross Anatomical and Physiological Abnormalities

Study of the importance of such abnormalities as could be recognized by inspection of genitalia in sows that failed to conceive after repeated matings has been made by Wilson *et al.* (1949), and Warnick *et al.* (1949). Wilson and associates studied 79 repeat breeders obtained from farmers. When bred again, 53.2 per cent of these sows settled, while the rest showed various abnormalities which they felt accounted for sterility. These abnormalities were tubal aberrations, cystic follicles, and blind or missing portions of the reproductive tract. Among the sows that became pregnant, the discrepancy between number of corpora and number of embryos counted in the uterus at 25 days after breeding accounted for 26 per cent of all ova produced. They thought this discrepancy was due to failure of fertilization or to early embryonic mortality. Warnick and associates concluded from a similar study of 63 repeat-breeding sows and gilts that infertility resulted from failure of fertilization in 53.4 per cent of gilts and 32.6 per cent of sows. Failures of fertilization due to bilateral abnormalities of genitalia amounted to 50.0 per cent among the gilts and 15.8 per cent among the sows. Unaccountable failure of fertilization made up the remaining 3.4 per cent among gilts and 16.8 per cent among sows. They considered embryonic death to be responsible for repeat breeding in 23.9 per cent of the gilts and 67.4 per cent of the sows studied. The remaining 22.7 per cent of the gilts became pregnant.

MATERIALS AND METHODS

The methods used in this study were designed to measure the influence of inbreeding, age and rate of growth on (1) sexual maturity, (2) ovulation rate, (3) efficiency of the fertilization process, (4) embryonic survival to the 25th day of gestation. Incidence of gross anatomical and physiological abnormalities also was observed, and the relative importance of hereditary and environmental influence on ovulation rate was studied.

Experimental Animals

The sows and gilts used in this study were obtained from two inbred lines of Poland China, one of Hampshire, a non-inbred Duroc herd and the six cross-combinations of these four stocks. The three lines mentioned are moderately inbred strains maintained by the Missouri Station in cooperation with the Regional Swine Breeding Laboratory, while the Durocs are part of the College herd. During the period of this study, the percentage of inbreeding was about 45 for line II Poland, 25 for line VI Poland and 30 for line V Hampshire. A total of 278 gilts and 72 sows were studied in four successive seasons. A summary by seasons of number of sows and gilts of respective breeding groups used in each phase of the study is given in Table 1a and Table 1b.

Procedure

Gilts and sows of each strain or cross were bred, whenever possible, to non-related boars, in order to minimize inbreeding of embryos. Alternate gilts of each breeding group, where feasible, were slaughtered 24 hours after the end of estrus to allow counting of ovulation points and recovery of ova from the tubes or uterus for microscopic examination. Remaining gilts and most of the sows were slaughtered on or near the 25th day after breeding to allow counting and examination of corpora and embryos. Efficiency of fertilization was judged by the proportion of ova recovered that were found to be cleaved when examined with a microscope. Mortality to 25 days was determined by comparison of number of functional corpora lutea with number of normal embryos present at 25 days.

Analysis of Data

In analyzing the variation in ovulation rate and litter size at 25 days between breeding groups and seasons, the covariance technique was used to remove variation associated with age of gilt. This was necessary because of highly significant correlations of age with ovulation rate (r = .31) and with litter size (r = .33). The analysis for mortality did not include an age correction, since the correlation between age and mortality was quite low (r = –.11). An estimate of the effect of season was necessary for any comparison between inbreds and crosses, since these groups were available for study mainly in different seasons.

All correlation and regression coefficients were computed on a within breeding group and season basis, although seasonal effects did not prove significant for any characteristics studied.

Paternal half-sib and full-sib correlations were the only bases available for estimating heritability of ovulation rate, since these data were not available for dams of the gilts studied. Complete information was available on 267 gilts from 136 litters and by 31 boars. Covariance analysis again was used to adjust for linear regression on age of dam.

RESULTS

Age of Gilts

Since age effects were considered in making all breeding group comparisons, an account of them seems necessary at the outset. The 279 gilts used in this study ranged from 164 to 301 days of age at breeding, with a mean age of 226 days and a standard deviation of 23.2 days within breeding groups and season. Crosses tended to be bred at younger ages than did inbreds and Durocs (206 days and 234 days, respectively) because of the more rapid growth and earlier sexual maturity of the crosses. Hence, adjustment for any age-influence on performance was necessary to avoid bias in comparing crosses with parent lines.

Number of ova shed was significantly correlated (within breeding group and season) with the age at which estrus was observed (r = .31), an increase of 10 days age being associated with a linear increase of 0.35 of an ovum shed. Age was also significantly correlated with litter size at 25 days (r = .33), an increase of 10 days in age at breeding being associated with an increase of 0.5 embryos present. The correlation between age at breeding and total ovum mortality was not statistically significant (r = –.11), but the regression of –0.15 ova lost for 10 days increased age agrees with the first two relationships.

All adjustments for age in group comparisons for ovulation rates, litter size at 25 days, and mortality were made on the basis of the above relationships.

Sexual Maturity

Measurement of sexual maturity was not critical, since checking of gilts for estrus and mating was not begun in several seasons until the mean age was about six months. However, the fact that crosses averaged 28 days younger than the parent lines in age at breeding suggests a definite advantage of at least 13 per cent in age at maturity for the crosses. This difference was partially confounded with any environmental difference between fall and spring farrowed gilts. Analysis of age at breeding of gilts (Table 2a) shows that season was a highly significant source of variation, but the means by seasons for Durocs

TABLE 1a -- NUMBERS OF FEMALES STUDIED BY BREEDING GROUPS AND SEASONS

Season	Breeding Groups	Numbers of Females Studied: At 24 Hours Gilts	At 25 Days Gilts	At 25 Days Sows	For Ovulation Data Only Gilts	For Ovulation Data Only Sows
1948 Spring	Duroc		14	2	2	
	Line V			7	8	2
	Line VI		2	9	3	
	Line II		2	6		1
	II x V				13	
	II x VI		3		6	
	V x VI				5	
	All		21	24	37	3
1948 Fall	Duroc	9	8	8		
	Line V	15	9	4	1	
	Line VI	12	13	2	5	
	Line II		5	1	4	2
	All	36	35	15	10	2
1949 Spring	Duroc	6	4	1		
	Line V		2	1		
	Line II	1	2			
	II x V	2	7		1	
	II x VI	6	5		1	
	V x VI	3	4		1	
	V x D	4	4			
	II x D	2	3		1	
	VI x D	5	3		1	
	All	29	34	2	5	
1949 Fall	Duroc	2	19	7		
	Line V		18	6		
	Line VI		6	7	2	
	Line II	10	14	4		2
	All	12	57	24	2	2

TABLE 1b -- NUMBERS OF FEMALES STUDIED IN ALL SEASONS

Season	Breeding Groups	At 24 Hours Gilts	At 25 Days Gilts	At 25 Days Sows	For Ovulation Data Only Gilts	For Ovulation Data Only Sows	Total
All Seasons	Duroc	17	45	18	2		82
	Line V	15	29	18	9	2	73
	Line VI	12	21	18	10		61
	Line II	11	23	11	4	5	52
	II x V	2	7		14		23
	II x VI	6	8		7		21
	V x VI	3	4		6		13
	V x D	4	4				8
	II x D	2	3		1		6
	VI x D	5	3		1		9
	All	77	147	65	54	7	350

indicated no advantage for fall as compared with spring breeding (Table 2b). Crosses were bred only in the spring seasons, while most of the parent-line gilts were bred in the fall (Table 1a). Hence, the significant variation between breeding groups within seasons (Table 2a) indicates mainly differences among parent lines or among crosses, whereas the even more significant difference between all breeding groups also includes differences between crosses and parent lines. The paired comparisons of crosses with means of their parent lines (Table 3), ignoring seasons, indicate a highly significant advantage of 30 days in age at breeding for crosses, or of 13 days for each 10 per cent of inbreeding of the lines crossed.

TABLE 2a -- ANALYSIS OF VARIATION IN AGE AT BREEDING AMONG GILTS BETWEEN BREEDING GROUPS AND SEASONS

Component	Degrees Freedom	Mean Square	F
Between Breeding Groups Within Season	20	1950.4	3.6*
Between Seasons Within Breeding Groups	14	2029.9	3.7*
Within Season and Breeding Groups	253	541.7	
Between Breeding Groups	9	6004.3	11.1*

* Significant at .01 level.

TABLE 2b -- MEAN AGE AT BREEDING BY SEASONS FOR DUROC GILTS

Season	No. Gilts	Age Bred in Days
1948 Spring	16	255.8
1948 Fall	17	212.6
1949 Spring	10	212.4
1949 Fall	20	234.5

Ovulation Rate

It is apparent that the number of ova shed by a sow determines the upper limit of her litter size for any particular gestation, barring the occurrence of identical twins. Likewise, the average number of ova shed per estrus in a particular breeding group provides a basis for predicting average litter size to be expected in that group, other factors being constant.

In this study, ovulation rate was determined by counting the number of new corpora present on the ovaries of each female slaughtered from a given breeding group, on the assumption that ordinarily only one ovum was shed per corpus. The new corpora were readily differentiated from the old by color

TABLE 3 -- COMPARISON OF CROSSES WITH MEAN OF THE PARENT LINES FOR AGE AT BREEDING IN GILTS

Breeding	No. Gilts	Mean % Inbr.	Age at Breeding in Days: Mean	Difference Total	(Cross-Parents) Per 10 % Inbreeding Parent Lines
II and VI	38 + 43	36.5	232.6		
(II x VI) Cross	20	9.0	220.0	+12.6	4.58
II and V	38 + 53	35.7	239.1		
(II x V) Cross	24	0.0	203.9	+35.2	9.86
V and VI	53 + 43	28.9	234.9		
(V x VI) Cross	13	0.0	202.5	+32.4	11.21
II and D	38 + 63	21.6	233.1		
(II x D) Cross	6	0.0	197.0	+36.1	16.70
VI and D	43 + 63	14.8	229.6		
(VI x D) Cross	9	0.0	191.0	+38.6	26.08
V and D	53 + 63	14.0	234.9		
(V x D Cross	8	0.0	208.3	+26.6	19.00
All	277		226.0	30.25	12.7

and size and, in most cases, were quite easy to count. For all gilts, the mean ovulation rate determined in this manner was 11.46 with a standard deviation of 2.53. For sows it was 15.32 with a standard deviation of 3.40. Both standard deviations are based on variation within season and breeding group.

Results of the analysis for breeding group and season differences among gilts in number of ova shed per estrus are given in Table 4a. It will be noted that differences both between breeding groups within season, and between breeding groups ignoring season, were highly significant, while season differences within breeding groups were small and non-significant. The smaller mean square between groups within seasons than between groups ignoring season

TABLE 4a -- ANALYSIS OF VARIATION IN OVULATION RATE OF GILTS BETWEEN BREEDING GROUPS AND SEASONS

Component	Degrees Freedom	Age Adjusted Mean Square	F
Between Breeding Groups Within Season	20	13.5	2.25*
Between Seasons Within Breeding Groups	14	8.3	1.38
Within Breeding Groups and Season	253	6.4	
Between Breeding Groups	9	20.0	3.33*

* = Highly significant

was largely because crosses and inbreds were observed for the most part at different seasons (see Table 1a). Comparisons within season were mainly between females of the different parent stocks or between different crosses. If season is ignored, on the basis of the non-significant seasonal effect, the comparison then includes differences between crosses and parent groups. A similar analysis on sow data (Table 4b) did not show between group differences to be significant, but here no crosses were involved.

TABLE 4b -- ANALYSIS OF VARIATION IN OVULATION RATE OF SOWS BETWEEN BREEDING GROUPS

	Degrees Freedom	Mean Square
Between Breeding Groups	3	9.0
Within Breeding Groups	68	10.6
Total	71	10.6

A comparison of the age-adjusted breeding group means is presented in Table 5 for gilts and in Table 6 for sows. Line II gilts, the most highly inbred group, had significantly lower performance than any other group. Crosses in general had higher ovulation rates than did parent strains. This tendency is best illustrated in Table 7, in which performance of crosses is compared with mean performance of parent strains. The mean difference of 1.19 ova in favor of crosses, is highly significant. This superiority in the ovulation rate of the

TABLE 5 -- GROUP COMPARISONS OF OVULATION RATE IN GILTS‡

No. Gilts	Mean Corpora	Breeding Group	Mean % Inbr.	Differences in Favor of Horizontal Groups: D	V	VI	II	VxVI	IIxVI	IIxV	VxD	IIxD	VIxD
63	11.85	D	0.0							0.70	1.63	0.77	
53	11.43	V	28.1	0.42					0.25	1.12	2.05*	1.19	0.20
43	11.03	VI	29.7	0.82	0.40			0.21	0.65	1.52*	2.45**	1.59	0.60
38	9.74	II	43.3	2.11**	1.69**	1.29**		1.50	1.94*	2.81**	3.74**	2.88**	1.89*
13	11.24	VxVI	0.0	0.61	0.19				0.44	1.31	2.24*	1.38	0.39
20	11.68	IIxVI	9.0	0.17						0.87	1.80	0.94	
24	12.55	IIxV	0.0								0.93	0.07	
8	13.48	VxD	0.0										
6	12.62	IIxD	0.0								0.86		
9	11.63	VIxD	0.0	0.22					0.05		1.85	0.99	
277	11.44	All		0.41	-0.01	-0.41	-1.70	-0.20	0.24	1.11	2.04	1.18	0.19

‡Means are adjusted to the mean age of 225 days.
** = Highly significant, * = Significant, based on mean square for error = 6.0, and standard error mean difference = $\sqrt{6 \cdot \frac{n_1+n_2}{n_1 n_2}}$, where n_1 and n_2 are numbers of observations in groups 1 and 2.

crosses amounts to 0.55 ova for each 10 per cent of inbreeding for the parent strains.

TABLE 6 -- GROUP COMPARIONS OF OVULATION RATE IN SOWS

Number Sows	Mean Corpora	Breeding Group	Differences in Favor of Horizontal Groups[1] D	V	VI	II
18	16.11	D				
20	14.85	V	1.26		0.98	
18	15.83	VI	0.28			
16	14.63	II	1.48	0.22	1.20	
72	15.36	All	0.75	-0.51	0.47	-0.73

1/ Differences are not significant, based on mean square for error = 10.6, and standard error mean difference $= \sqrt{(10.6)\,\frac{(n1+n2)}{(n1\ n2)}}$

TABLE 7 -- COMPARISON OF CROSSES WITH MEAN OF THE PARENT LINES FOR OVULATION RATE IN GILTS

Breeding	No. Gilts	Mean% Inbr.	Number of Cropora Mean[1]	Number of Cropora Difference Total	(Cross-Parents) Per 10% Inbreeding Parent Lines
II and VI	38 + 43	36.5	10.38		
(II x VI) Cross	20	9.0	11.68	+1.30	+ .47
II and V	38 + 53	35.7	10.58		
(II x V) Cross	24	0.0	12.55	+1.97	+ .55
V and VI	53 + 43	28.9	11.23		
(V x VI) Cross	13	0.0	11.24	+0.01	0
II and D	38 + 63	21.6	10.80		
(II x D) Cross	6	0.0	12.62	+1.82	+ .84
VI and D	43 + 63	14.8	11.44		
(VI x D) Cross	9	0.0	11.63	+0.19	+ .13
V and D	53 + 63	14.0	11.64		
(V x D) Cross	8	0.0	13.48	+1.84	+1.31
all	277		11.44	+1.19[2]	+0.55

1/. Means have been adjusted for age to a 225 day basis.
2/. Mean difference is highly significant ($P < .01$)

Efficiency of Fertilization

The gross standard deviation in number of ova shed was 2.53 among all 277 gilts, and 2.66 among the 147 gilts observed at about the 25th day of gestation. The larger standard deviation of 3.26 in pig (embryo) numbers present in the uterus at 25 days, indicates important variation in survival of ova. One source could well be variation in the proportion of ova shed which are fertilized. In this study, efficiency of fertilization was determined in the following manner:

1. Gilts were bred according to a mating plan (modified factorial design) which tended to distribute any boar and line of boar effects equally among different breeding groups of gilts and thus allow statistical removal of boar effects. As it happened this procedure was not necessary since no sizable boar effects were found.

2. Gilts were slaughtered 24 hours after the end of estrus, as nearly as possible, and reproductive tracts were recovered. It was found that the ova were usually in the Fallopian tubes at this time and could be recovered by flushing.

3. Fluid was stripped from the Fallopian tubes onto a microscope slide and the ova were examined under the objectives of a compound microscope. A magnification of 20X was found to be sufficient for locating ova and counting cleavage segments, but higher magnification was needed for detecting spermatozoa in the *zona pellucida.* Rather early in the study of fertilization rate, the investigators occasionally noted "ghost" ova in flushings from the Fallopian tubes. These appeared to consist of a *zona pellucida* whose cellular content was absent. Later, their true nature was discovered, quite by accident. In attempting to observe a cleaved ovum under the "high dry" objective of the microscope, a cover slip was placed lightly over the cell. A break appeared in the *zona pellucida* and the cellular contents flowed out into the medium. The *zona* then closed the gap and the remaining structure resembled a "ghost" ovum. After this experience, the flushing technique was modified so that less pressure was applied, and although the ova were recovered less effectively, very few "ghost" cells appeared. Unfortunately many of the earlier ones had been classified as "unfertilized ova" without noting their "ghostly" nature, and hence could not be reclassified as "undetermined." Thus the recorded efficiency of fertilization (95 per cent) may be somewhat lower than would otherwise have been the case.

4. Ova were classified as fertilized if two or more blastomeres were present. In a few cases, usually among those recovered from the uterine horn, ova were subdivided into a group of particles resembling cells but lacking organization. These were classified as unfertilized ova. However, spermatozoa were observed in the *zona* of some of these abnormal ova and they may represent dead or dying fertilized ova.

5. All ova recovered were examined for the presence of sperm in the *zona pellucida.* These were not always easily found, even in cleaved ova, but it is of some interest that uncleaved ova surrounded by *zona* containing many spermatozoa were recovered from several sows along with cleaved ova having 4 to 8 cells. This observation could be interpreted to mean that certain ova (1) were incapable of activation and cleavage even though penetrated by spermatozoa,

(2) were not penetrable or (3) were penetrated by a "defective" spermatozoon, preventing fertilization by viable ones.

6. Fertilization efficiency for any group was defined as the proportion of all recovered eggs classified as fertilized.

Although 24 hours after the end of heat was found to be the most favorable time for recovery of ova, in several cases it proved to be too early or too late. When gilts were slaughtered too early, none of the ova were beyond the 2-cell stage and ova that had not completed first cleavage could not be classified as unfertilized. When gilts were slaughtered too late, part or all of the ova were in the uterine horn and incomplete recovery often resulted.

A summary of fertilization data is given in Table 8. It will be noted that all ova were cleaved in 37 out of the 52 cases in which some cleaved ova were present. Of the 20 gilts in which complete failure of fertilization occurred, 18 had been bred to young boars with no previous record of fertility, and with low concentrations of spermatozoa. In interpreting the data, these 20 complete failures of fertilization were considered comparable to returns to heat in the usual breeding program (which do not affect average litter size). Thus the figure for per cent of ova fertilized (94.9 per cent) in Table 8 is the proportion

TABLE 8 -- SUMMARY FOR EFFICIENCY OF FERTILIZATION OF OVA RECOVERED

a. Classification of Gilts by Propertions of Ova Fertilized

% Ova Cleaved	0	60-69	70-79	80-89	90-99	100	Cleavage Incomplete2/	Total
No. of Gilts	20 1/	2	2	7	4	37	5	77 2/

b. Gross Efficiency of Recovery and of Fertilization

	Recovery of Ova					Fertilization of Ova 3/	
			Mean Number/Gilt				
No. Gilts	No. Corpora	No. Ova Recovered	Ovulation Points	Ova Recovered	% Recovery	No. Gilts	%
77	866	695	11.2	9.0	80.3	52	94.9

c. Percentage of Ova Fertilized in Fertile Matings, by Breeding Groups 3/

Breeding Group 4/	Duroc	V	VI	II	IIxV	IIxVI	VxVI	VxD	IIxD	VIxD
No. Gilts	11	9	9	8	1	3	1	4	2	4
% Ova Cleaved	97.3	96.7	86.8	96.7	100.	95.8	100.	95.3	100.	100.

1/ 18 of 20 gilts in which complete failure of fertilization occurred were bred to boars with no previous record of fertility.

2/ Including 5 cases of premature slaughter, in which the only cleaved ova were in the 2-cell stage and others showed signs of dividing, so that proportion fertilized could not be determined.

3/ Omitting 20 completely infertile matings and the 5 cases of incomplete cleavage.

4/ Group differences in efficiency of fertilization were not significant.

of cleaved ova for the 52 gilts classified as pregnant. This high fertilization percentage indicates that partial failure of fertilization was not an important factor affecting litter size in the population sampled, provided cleavage is an accurate criterion of fertilization. However, complete non-fertilization was an important cause of returns to heat, probably because some immature boars of questionable fertility were used. Group differences in proportion of ova fertilized were not significant, although line VI females had fewer eggs fertilized than did those of other groups.

Survival of Fertilized Ova to the 25th Day of Gestation

General. As has been pointed out earlier, litter size after 25 days of gestation was determined by counting the number of normal and undeveloped or degenerating embryos recovered. The difference between number of normal embryos recovered and number of corpora lutea is considered to represent total ovum mortality, on the presumably valid assumption that one ovum was shed for each corpus present at 25 days. Total mortality can be divided into portions due to non-fertilization and to loss of fertilized eggs. If losses due to non-fertilization do not exceed 5 per cent on the average, then most of the discrepancy between numbers of ova shed and numbers of pigs present at 25 days must be due to factors causing the early loss of part of the fertilized eggs. This early loss amounted to about 35 per cent of all ova shed, in both gilts and sows (see Table 9). Early losses of fertilized eggs have been partitioned further

TABLE 9 -- MEAN OVULATION RATE, EMBRYONIC MORTALITY AND LITTER SIZE AT 25 DAYS OF GESTATION

No. Animals	No. Corpora	No. Normal Embryos	Ova Lost		Mortality of Ova: Unfertile‡		Other Early		Degenerating	
			No.	%	No.	%	No.	%	No.	%
147 Gilts	11.3	7.3	4.0	35.4	.57	5.0	2.63	23.3	.80	7.1
65 Sows	15.3	10.0	5.3	34.6	.77	5.0	3.83	25.0	.70	4.6

‡ Using the mean percentage non-fertilized ova from Table 8.

into those accounted for by the dead or degenerating embryos recovered and those of which no trace remains at 25 days. The very early losses are many times as large as those represented by abnormal embryos at 25 days in both gilts (23.3 vs. 7.1 per cent) and sows (25.0 vs. 4.6 per cent).

The discrepancy between number of corpora lutea counted on the ovaries and number of normal embryos found in the uteri was quite great, often as high as 100 per cent. In some cases all that remained of the products of conception was one or two undeveloped and partially resorbed embryos. In other cases nothing could be found except areas of stimulation on the uterine wall, together with some rather amorphous lumps of uterine tissue, quite similar to those which appeared at either end of the chorionic fields of normal 25-day embryos. These observations, together with the fact that these gilts had not returned to heat during the 25 days or more since breeding, suggested that complete embryonic resorption is not uncommon. These cases have been treated as returns to heat on the premise that they eventually would have done so and thus would not have affected average litter size.

Breeding Groups. Analyses of variation between seasons and breeding groups among gilts is given in Table 10a for litter size on the 25th day of gestation and in Table 11 for total mortality to 25 days. Seasonal effects did not prove significant in either case. Variation between breeding groups, ignoring season, was significant for litter size of gilts at 25 days, but that between breeding groups within seasons was not. This apparent discrepancy arose because the intra-season comparisons are largely inbreds with inbreds or crosses with crosses, since spring litters consisted largely of parent lines and the fall litters were mainly crosses. Only the Durocs were available in comparable numbers in all four seasons covered by the study, although line II was represented in all four seasons and lines V and VI in three of the four. This means that the inbred lines did not differ significantly in litter size among themselves or from the Durocs, but they did differ from the crosses. Similarly, it would seem that variability among crosses was not significant, but the number of crossbreds observed at the 25-day period was perhaps too small to justify this conclusion.

TABLE 10 -- ANALYSIS OF VARIATION IN NUMBER OF NORMAL EMBRYOS AT 25 DAYS OF GESTATION

a. Among Gilts

Component	Degrees Freedom	Age Adj. Mean Square	F
Between Breeding Groups Within Season	17	9.76	0.95
Between Seasons Within Breeding Groups	11	3.45	0.34
Within Seasons and Breeding Groups	123	10.27	
Between Breeding Groups	9	20.22	1.97*

* P = .05

b. Among Sows

Component	Degrees Freedom	Mean Square
Between Breeding Groups	3	14.6
Within Breeding Groups	61	15.4
Total	64	15.4

Differences between sows of the four strains likewise were negligible compared with those within strains (Table 10b).

The comparison of breeding group means for litter size at 25 days in Table 12, shows that litters from outbred Durocs and from several of the crosses were significantly larger on the 25th day of gestation than litters from inbred line II gilts.

TABLE 11 -- ANALYSIS OF VARIATION AMONG GILTS IN TOTAL MORTALITY OF OVA TO THE 25TH DAY OF GESTATION

Component	Degrees Freedom	Mean Square	F
Between Breeding Groups Within Season	17	7.52	0.75
Between Seasons Within Breeding Groups	11	12.60	1.25
Within Seasons and Breeding Groups	124	10.02	
Between Breeding Groups	9	2.84	0.28*

*P $\leq$ .05 that variation between breeding groups less than within season and breeding groups.

TABLE 12 -- GROUP COMPARISON OF LITTER SIZE (NORMAL EMBRYOS) AT 25 DAYS GESTATION AMONG GILTS

				Differences in Favor of Horizontal Groups 2/									
Number Gilts	Mean Number Pigs 1/	Breeding Group	Mean Per Cent Inbreeding	D	V	VI	II	VxVI	IIxVI	IIxV	VxD	IIxD	VIxD
44	8.03	D	0.0					0.68		0.93	1.56	0.47	
28	6.73	V	31.3	1.30				1.98	1.03	2.23	2.86	1.77	1.00
21	6.47	VI	26.8	1.56	0.26			2.24	1.29	2.49	3.12	2.03	1.26
23	5.52	II	42.6	2.51**	1.21	0.95		3.19	2.24	3.44*	4.07*	2.98	2.21
4	8.71	VxVI	0.0							0.25	0.88		
7	7.76	IIxVI	9.0	0.27				0.95		1.20	1.83	0.74	
8	8.96	IIxV	0.0								0.63		
4	9.59	VxD	0.0										
3	8.50	IIxD	0.0					0.21		0.46	1.09		
3	7.73	VIxD	0.0	0.30				0.98	0.03	1.23	1.86	0.77	
145	7.80	All		0.23	-1.07	-1.33	-2.28	0.91	-0.04	1.16	1.79	0.70	-0.07

1. Means are adjusted to the mean age of 229 days.
2. * = Significant, ** = Highly significant, based on mean square for error = 10.3, and standard error of mean difference = $\sqrt{(10.3)\frac{(n1+n2)}{(n1\ n2)}}$.

Comparisons of mean litter size at 25 days for sows of the four lines are shown in Table 13. None of these differences was large enough for statistical significance.

TABLE 13 -- GROUP COMPARISON OF LITTER SIZE (NORMAL EMBRYOS) AT 25 DAYS GESTATION IN SOWS

No. Sows	Mean Number Pigs	Breeding Group	Differences Favoring Horizontal Groups[1] D	V	VI	II
18	11.22	D				
18	9.05	V	2.17		0.89	0.49
18	9.94	VI	1.28			
11	9.54	II	1.68		0.40	
65	9.94	All	1.28	-0.89	0.00	-0.40

1. Differences lack significance, based on mean square for error = 15.4, and standard error mean difference $=\sqrt{(15.4)\frac{(n_1+n_2)}{n_1 n_2}}$.

Heterosis. When 25-day litter size of each cross was compared with that for the two parent lines (Table 14), a highly significant mean advantage of 1.85 embryos was found. This advantage seems to be largely due to the higher ovulation rate for crosses (+1.19 ova, Table 7). However, crossbred gilts tended to lose about .81 fewer embryos by the 25th day of gestation than did

TABLE 14 -- COMPARISON OF CROSSES WITH THE MEAN OF PARENT LINES FOR LITTER SIZE AT 25 DAYS GESTATION AMONG GILTS

Breeding	No. Gilts	Mean Inbr. %	Mean[1] Litter Size	Differences (Cross-Parent) for Litter Size	Gain/10% Inbreeding of Parents
II and VI	23 + 21	34.7	5.99		
(IIxVI) Cross	8	9.0	7.76	+1.77	+0.69
II and V	23 + 28	36.9	6.13		
(IIxV) Cross	7	0.0	8.96	+2.83	+0.77
V and VI	28 + 21	29.1	6.60		
(VxVI) Cross	4	0.0	8.71	+2.11	+0.73
II and D	23 + 44	21.3	6.78		
(IIxD) Cross	3	0.0	8.50	+1.72	+0.81
VI and D	21 + 44	13.4	7.25		
(VIxD) Cross	3	0.0	7.73	+0.48	+0.36
V and D	28 + 44	15.6	7.38		
(VxD) Cross	4	0.0	9.59	+2.21	+1.42
All	145		7.27	+1.85[2]	+0.80

1. Means were adjusted to the mean age of 230 days.
2. The mean difference is highly significant.

the gilts of the parent strains (Table 15). This mean difference has a 5 per cent probability of chance occurrence. If this difference is real, it must be attributed to superiority in the uterine environment provided by crossbred dams, since a deliberate attempt was made to avoid inbreeding of litters. Out of 116 total matings in the parent strains, only 16 were within-line (inbred) matings. The average loss to 25 days in these 16 matings was 4.2 pigs as compared to the mean loss of 4.0 pigs, for all gilts.

TABLE 15 -- COMPARISON OF CROSSES WITH THE MEAN OF PARENT STRAINS FOR MORTALITY TO 25 DAYS OF GESTATION

Breeding	No. Gilts	Mean Inbr. %	Mean[1] Mortality Per Litter	Differences (Cross-Parent) Mortality	Gain/10 Per Cent Inbreeding of Parents
II and VI	23 + 21	34.7	4.15		
(IIxVI) Cross	8	9.0	3.38	-0.77	+0.30
II and V	23 + 28	36.9	4.19		
(IIxV) Cross	7	0.0	2.04	-2.15	+0.58
V and VI	28 + 21	29.1	4.13		
(VxVI) Cross	4	0.0	3.04	-1.09	+0.37
II and D	23 + 44	21.3	4.26		
(IIxD) Cross	3	0.0	4.37	+0.11	-0.05
VI and D	21 + 44	13.4	4.20		
(VIxD) Cross	3	0.0	3.89	-0.31	+0.23
V and D	28 + 44	15.6	4.23		
(VxD) Cross	4	0.0	3.56	-0.67	+0.43
All	145		3.79	-0.81[2]	+0.33

1. Means were adjusted to the mean age of 230 days.
2. Mean differences approaches .05 level of significance.

Effect of Two Services at 24-Hour Intervals

The results from experimental slaughter of gilts at 24 hours and at 25 days after breeding indicated that fertilization of ova was largely an "all or none" process. Among the gilts showing any fertilized (i.e., cleaved) ova at 24-hour slaughter, the proportion of ova fertilized was 95 per cent. However, a rather large number of matings (20 of 77) showed no ova fertilized. This could have resulted from the fact that some boars were used when relatively immature (i.e., 5 to 8 months old). It also could have been due to faulty timing of service in relation to ovulation. To test this point, gilts from each of 9 lines of breeding were divided into two groups in the 1949 Fall breeding season. Gilts of one group were bred only once when estrus was first observed. Gilts of the other group were bred once when estrus was first observed and then rebred 24 hours later. Alternate gilts coming into estrus in each line were assigned to the one service and the two service groups, as nearly as usage of the boars permitted. An outbreak of influenza in the herd about 10 days after breeding was started complicated this experiment. Breeding was suspended for 7 to 10 days in several of the lines most affected. A few of the boars were sick, but neither boars nor gilts were mated if either was noticeably sick.

Conceptions (Table 16). The percentage of matings resulting in pregnancy was higher by 23 per cent from two services than from a single service

TABLE 16 -- EFFECT OF TWO SERVICES AT 24 HOUR INTERVALS ON PERCENTAGE OF MATINGS‡ RESULTING IN PREGNANCY

a. Means

Strain	One Service: No. of Matings (n_1)	One Service: % Pregnant (X_1)	Two Services: No. of Matings (n_2)	Two Services: % Pregnant (X_2)	Diff. (X_2-X_1) (D)	Weighting $W=\frac{n_1 n_2}{n_1+n_2}$
II Poland	12	67	13	85	18	6.24
VI Poland	14	50	9	89	39	5.48
Ia. Poland	3	100	3	100	0	1.50
S. Poland	3	100	2	100	0	1.20
M. Duroc	3	67	3	100	33	1.50
T. Duroc	2	100	4	100	0	1.33
V Hamp.	4	50	3	100	50	1.71
C. Hamp.	3	33	3	67	34	1.50
Ia. Landr.	4	75	5	80	5	2.22
Total or Wt'd. Avg.	50	66.0	48	89.1	23.1	22.68

‡Some of the gilts which returned to estrus after the first mating were rebred.

b. Test for Significance

Source	Degrees of Freedom	Sum of Squared Deviations	Mean Square	%
Weighted Mean Diff. (X_2-X_1)	1	$\frac{(\Sigma wD)^2}{\Sigma w}$	12067	t=4.015 P= .002*
Diff. x Line	8	$\Sigma(wD^2) - \frac{(\Sigma wD)^2}{\Sigma w}$	749	

95% Confidence Interval = $23.1 \pm (2.3)\sqrt{\frac{749}{22.68}} = 23.1 \pm 13.27 = 9.8$ to 36.4

*One-half the tabular probability for t - 4.015 with 8 d.f. since it is not considered possible that a second service would reduce likelihood of pregnancy.

(89 and 66 per cent, respectively). In 95 per cent of repeated trials of this size, the advantage would be expected to vary between 10 and 36 per cent. An advantage for two services as large as the 23 per cent found due solely to sampling error would be expected only once in 500 trials. This 23 per cent advantage may be an overestimate, because of the possibility that more of the single service matings were by boars affected by influenza or in marginal health

for other reasons. A few of the single-service matings occurred simply because the boar used for the first service would not work the following day. However, it seems reasonable to attribute most of the advantage of two services to the presence of fresher sperm in the reproductive tract of the female during middle and latter part of the estrus period.

Size of Litters (Table 17). There was little indication that a second service 24 hours after the first increased the size of litters farrowed. An advantage as large as the .51 pigs found in this experiment would be expected about once in six experiments of this magnitude even if there was no real benefit from the second service. However, the 95 per cent confidence limits (0 to 1.54 pigs) are so wide that this experiment does not preclude the possibility of an important

TABLE 17 -- EFFECT OF TWO SERVICES AT 24 HOUR INTERVALS ON LITTER SIZE AT BIRTH AMONG GILTS PREGNANT

a. Means

Strain	One Service: No. of Gilts (n_1)	One Service: Litter Size (X_1)	One Service: No. of Gilts (n_2)	One Service: Litter Size (X_2)	Diff. (X_2-X_1) (D)	Weighting $W=\frac{n_1 n_2}{n_1+n_2}$
II Poland	8	7.87	11	8.27	.40	4.63
VI Poland	7	7.57	8	7.50	- .07	3.73
Ia. Poland	2*	6.00	3	4.67	-1.33	1.20
S. Poland	3	6.33	2	8.50	2.17	1.20
M. Duroc	2	5.00	3	7.67	2.67	1.20
T. Duroc	2	6.50	4	6.00	- .50	1.33
V Hamp.	2	4.00	3	7.00	-3.00	1.20
C. Hamp.	1	12.00	2	7.50	-4.50	.67
Ia. Landr.	3	6.33	4	8.00	1.67	1.71
Total or Wt'd. Avg.	30	6.98	40	7.49	.51	16.87

*1 of 3 pregnant aborted.

b. Test for Significance

Source	Degrees of Freedom	Mean Square	
Weighted Mean Diff. (X_2-X_1)	1	4.3623	t=.98 P=.16‡
Diff. x Line	8	5.2724	N.S.
Within Subclasses	52	4.4796	
Pooled Error	60	4.5855	

95% Confidence Interval = $.51 \pm (2.0)\sqrt{4.5855\left(\frac{1}{30}+\frac{1}{40}\right)} = .51 \pm 1.03 = -.52$ (or 0‡) to 1.54.

‡One-half of the tabular probability for t=98 with 60 d.f., since it is not considered possible that a second service would reduce litter size.

real effect. It would require about 2.75 times as many animals as were used for the observed advantage of .51 pigs to be significant at the 5 per cent level, but an advantage of .85 pigs would have been significant at this level in the present experiment. If the true advantage were 1.0 pigs, about 108 gilts would be needed on each of the two treatments for a 95 per cent probability of obtaining a positive difference significant at the 5 per cent level.

Foetal Mortality from 25 Days to Parturition

It has already been shown that only about 65 per cent of the ova produced are represented by apparently normal embryos at the 25th day of gestation in both gilts and sows. In order to learn the extent of embryonic mortality after 25 days, the 1949 Spring gilts in each of four strains were divided into two groups; one to be slaughtered 25 days after breeding, the other to farrow litters in the Spring of 1950 (see Table 18). The gilts retained to farrow litters were

TABLE 18 -- COMPARISON OF LITTER SIZE AT 25TH DAY OF GESTATION AND AT BIRTH WITHIN STRAINS FOR GILTS BRED IN THE FALL OF 1949

a. Means

	At 25 Days					At Birth					
Strain	No. Gilts (n_1)	Age Bred in Days	154 Day Wt. in Lbs.	Normal Embryos Act.	Normal Embryos Adj.‡	No. Gilts (n_2)	Age Bred in Days	154 Day Wt. in Lbs.	No. Pigs Born	Diff. $X_{25}-X_b$ (D)	$\frac{n_1 n_2}{n_1+n_2} = w$
II Poland	14	231	119	5.79	8.12	19	252	146	8.10	.02	8.06
VI Poland	6	226	139	6.17	9.30	15	260	168	7.53	1.76	4.29
V Hamp.	16	238	111	7.06	8.28	13	255	117	7.00	1.28	7.17
Duroc	18	231	---	8.67	10.04	12	253	---	7.25	2.79	7.20
Total or Wt'd. Avg.	54	232	120	6.97	8.87	59	254	140	7.48	1.385	26.72

b. Test of Significance

Source	Degrees Freedom	Mean Square	
Weighted Mean Diff. ($X_{25}-X_b$)	1	51.22	t = 2.49 P = .008*
Diff. x Strain	3	10.00	N.S.
Within Subclasses	105	8.34	
At 25 Days	50	12.96	F = 3.13 P ∠∠ .01
At Birth	55	4.14	

$$t = \frac{1.38}{\sqrt{\frac{12.96}{54} + \frac{4.14}{59}}} = 2.49$$

* One half of the tabular probability for t = 2.49, with 53 and 58 d.f., because litter size at 25 days in reality cannot be smaller than litter size at birth.

95% Confidence Interval = 1.38 ± (2.00) (.557) = .27 to 2.50.

‡Adjusted to same mean age at breeding and 154 day weight as the gilts farrowed in that strain (see text).

a selected sample chosen to represent these strains in testcrosses because of superiority in their own rate of growth and conformation and in their dams' productivity. Growth records were not available for the Durocs, but for the other three lines the gilts retained to farrow litters averaged 20 pounds heavier at 154 days of age than the gilts slaughtered. Also, the gilts slaughtered were bred when about three weeks younger than the gilts allowed to farrow. Analysis of earlier data indicated that the partial regression of 25-day litter size on age in days, holding constant 154-day weight was .0606 pigs, and that the partial regression of 25-day litter size on 154-day weight holding constant age at breeding was .0374. These partial regressions were used to adjust the mean 25-day litter size for each line to the same mean age at breeding and mean 154-day weight as the gilts retained to farrow litters in that line (Table 18).

The results indicate that mortality of embryos from 25 days to birth amounted to about 1.38 pigs. A loss of this size would be expected solely from sampling error only about once in 125 trials with the numbers used in the present comparison. The wide 95 per cent confidence limits (.27 to 2.50 pigs) indicate that a much larger experiment would be necessary for a reasonably precise estimate of losses during the last 90 days of pregnancy.

The intra-strain standard deviation in litter size was nearly twice as large at 25 days (3.6) as at birth (2.04), and the probability of this large a difference solely from sampling error is much less than 1 per cent. The larger intra-strain standard deviation in age bred for gilts slaughtered than for gilts kept to farrow (22.4 days and 15.7 days, respectively with $P < .01$) was partly responsible. However, the fact that gilts slaughtered were about 20 pounds lighter at 154 days of age but were bred when about 3 weeks younger indicates that they were nearer the threshold of sexual maturity and hence might be expected to vary more in litter size than the older growthier gilts of the same lines. The tendency for the embryonic loss between 25 days and parturition to vary between strains was not significant at the 5 per cent level. For this reason, the variance within strains was used for testing significance of the difference in litter size between 25 days and parturition.

Causal Relations Among Factors Influencing Litter Size at 25 Days

To obtain a more complete understanding of the relative importance of, and the interrelationships between, factors causing variation in litter size at the 25th day of gestation, a multiple regression analysis was made. The simple correlations and regressions are given in Table 19. A diagram of the causal relationships with the corresponding path coefficients is shown in Figure 1.

It is not surprising that age of gilt should be associated with both ovulation rate, mortality, and with their difference, litter size at 25 days. The relative size of these relationships is, however, of some interest. On the basis of calculated regression coefficients, an increase of 10 days in age of gilt when bred was associated with an increase of 0.5 pigs in litter size. This was made possible by an increase of 0.35 of an ovum shed and a decrease of 0.15 in total ovum mortality. It is apparent that litter size is completely determined by ovulation rate and total mortality.

TABLE 19 -- MEANS, STANDARD DEVIATIONS AND SIMPLE CORRELATIONS[1/] FOR LITTER SIZE AT THE 25TH DAY OF PREGNANCY AND RELATED VARIABLES

Variables X	Y	No. of Observations	Correlation r_{XY}	Regression b_{XY}	Mean of X	Mean of Y	Standard Deviation X	Standard Deviation Y
Age in Days at Estrus or Conception	Lit. Size[2/]	145 G[3/]	+.33*	+.050	2.29	7.29	22.2	3.26
	Ovulation Rate	277 G	+.31*	+.035	2.26	11.46	23.2	2.53
	Mortality	145 G	-.11	-.015	2.29	4.00	22.2	3.16
Ovulation Rate	Lit. Size	147 G	+.47*	+.60	11.29	7.29	2.66	3.26
	Lit. Size	65 S	+.49*	+.57	15.32	9.98	3.40	4.03
	Mortality	147 G	+.34*	+.40	11.29	4.0	2.66	2.14
	Mortality	65 S	+.38*	+.43	15.32	5.33	2.40	3.80
	% Mort.[5/]	147 G	+.08	+.01	11.29	35.3	2.66	24.7
Weight at 154 Days	Ovulation Rate	224 G	+.10	+.01	140.6	11.27	21.7	2.65
	Mortality	105 G	-.05	-.006	130.8	3.92	20.7	2.50
	Age (Days)	224 G	-.27*					
	Litter Size	105 G	.12					
Mortality[4/]	Lit. Size	147 G	-.67*					
Inbreed. of Indiv.	Ovulation Rate	133 G	-.02		33.0		5.4	
	Mortality	133 G	+.08		33.0		5.4	

* = Highly Significant, P < .01
1/ All computations were based on variation within breeding groups and seasons.
2/ Litter Size = Number of normal embryos present at 25 days after conception.
3/ G = Gilts, S = Sows
4/ Mortality = Number of corpora not represented by normal embryos at 25 days.
5/ % Mortality = % of corpora not accounted for by normal embryos at 25 days.

The relationship between ovulation rate and total mortality ($r_{OM} = +.34$ in gilts) is almost entirely automatic. This is apparent from the very slight relationship between ovulation rate and per cent mortality ($r_{OM} = +.076$ in gilts). Thus, although the actual number of pigs (ova) lost during the first 25 days of gestation increased by .40 with each additional ova shed, the proportionate loss increased very little (i.e., by the difference between .4 and mean total loss, .354, Table 9).

The simple correlation between growth rate and number of ova shed ($r_{GO} = +.10$) would be larger except for the rather strong tendency of faster growing gilts to be bred at an earlier age. If the relationship is studied holding age constant, the partial correlation coefficient ($r_{GO.A} = .20$) is highly significant.

When viewed in terms of standard partial regression (path) coefficients (Figure 1), difference in mortality had a slightly greater effect on variation in litter size in gilts than did differences in ovulation rate. Age at breeding, in turn accounted for somewhat more of the variability in both ovulation rate

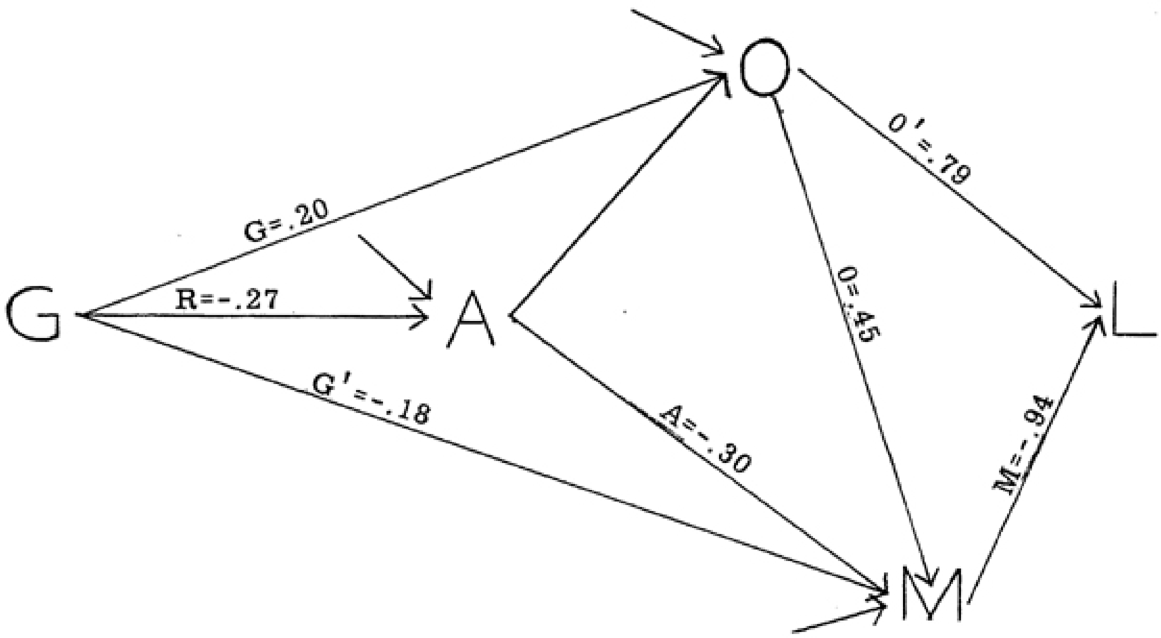

Fig. 1.—Path coefficient diagram showing relationship among factors affecting litter size to 25 days. L = number of normal pigs at 25 days; O = number ova shed (corpora); M = total pigs (ova) lost to 25 days; G = 154-day weight (lbs.); A = age (days) at breeding.

and mortality than did growth rate to 154 days. This does not mean, of course, that body weight at time of breeding, a function of both growth and age, might not be a more accurate determinant than either one. Unfortunately, data bearing on this possibility are incomplete because the animals could not be weighed during some breeding seasons.

The partial regression coefficient (computed from path OM, Figure 1) describing the direct influence of ovulation rate on mortality was found to be 0.53, a slightly higher value than the simple regression coefficient (b_{MO} = 0.40). The difference may be explained by the fact that both faster growth rate and older age at breeding increase ovulation rate but decrease the proportion of ova lost (Figure 1). The difference again suggests a tendency for percentage mortality to rise slightly with increased ovulation rate. The mean loss was only .354 per ova shed (Table 9) compared with the direct effect of .53. The direct effect of increasing age by one day, independent of growth rate, was .042 more ova shed, .019 fewer ova lost and .061 more embryos at 25 days; the direct effect per pound of increased 154-day weight was .024 more ova shed, .013 fewer ova lost and .037 more embryos at 25 days.

Heritability of Ovulation Rate

The chief results from this part of the study are shown in Table 20. The mean square between sire progenies is so small as to suggest no heritable differences in ovulation rate. However, the mean square between dams within sire progenies approaches significance and indicates some degree of maternal influence. The latter is substantiated by the finding of a significant mean square between reciprocal crosses within breeding groups and season.

TABLE 20 -- ANALYSIS OF VARIANCE IN OVULATION RATE WITHIN SEASON AND BREEDING GROUP

Source of Variation	Degrees Freedom	Age Adj. Mean Square	F
Between Sire Progenies	37	5.82	.93
Between Reciprocal Crosses	6	15.6	2.50**
Between Sire Progenies Within Reciprocals	31	4.06	.65
Between Litters Within Sire Progenies	75	6.23	1.34*
Pigs Within Litters	131	4.63	

** = Significant, $P < .05$
* = Approaches significance at .05 level

The extremely low mean square for sire differences suggested some sort of bias operating to reduce differences between the sire progenies. Retention of a larger proportion of the inbred and Duroc gilts for replacements in the breeding project from the better sire progenies may have acted to reduce differences between sire progenies among those remaining gilts assigned to the present study. Consequently, the analysis was made using only information on crossbred gilts, none of which had been kept for breeding. This resulted in the finding of a mean square for between sires of 2.80 and for an error of 3.60.

Variation associated both with age and with 154-day weight was then removed, resulting in a proportionately even smaller mean square between sires. One interesting point shown by this approach, however, was that about 25 per cent of the variation in ovulation rate, both between sire progenies and between dams within sire progenies, was linearly associated with age and growth, whereas only about 9.0 per cent of the variance between litter mates was related to these two variables ($R_{O.AG}$ = .2495, .2487 and .09, respectively). Similarly, if age is held constant, a significant partial correlation coefficient is obtained for the relationship between growth rate and number of ova shed between sire progenies ($r_{OG.A} = .40$) and between dam progenies within sires ($r_{OG.A} = .31$) but not between litter mates ($r_{OG.A} = .12$). This suggests that an important association between ovulation rate and rate of growth exists, arising either from maternal or transmitted influences or both, on the two characters.

Gross Abnormalities

Remarkably few gross reproductive abnormalities were found in the population of 359 females studied. Of those found, "cystic" ovaries were the most common (Figure 2). A total of 15 females had one or more persistent follicles. Five of these were classified as "very cystic" in that both ovaries were literally masses of cysts. Three of the five "very cystic" females were pregnant; the most interesting case being one in which only one corpus luteum could be found and one normal foetus was present (Figure 3). The right and left ovaries of this sow measured 3½ and 4 inches in diameter, respectively, and yielded more than 200 cc. of follicular fluid.

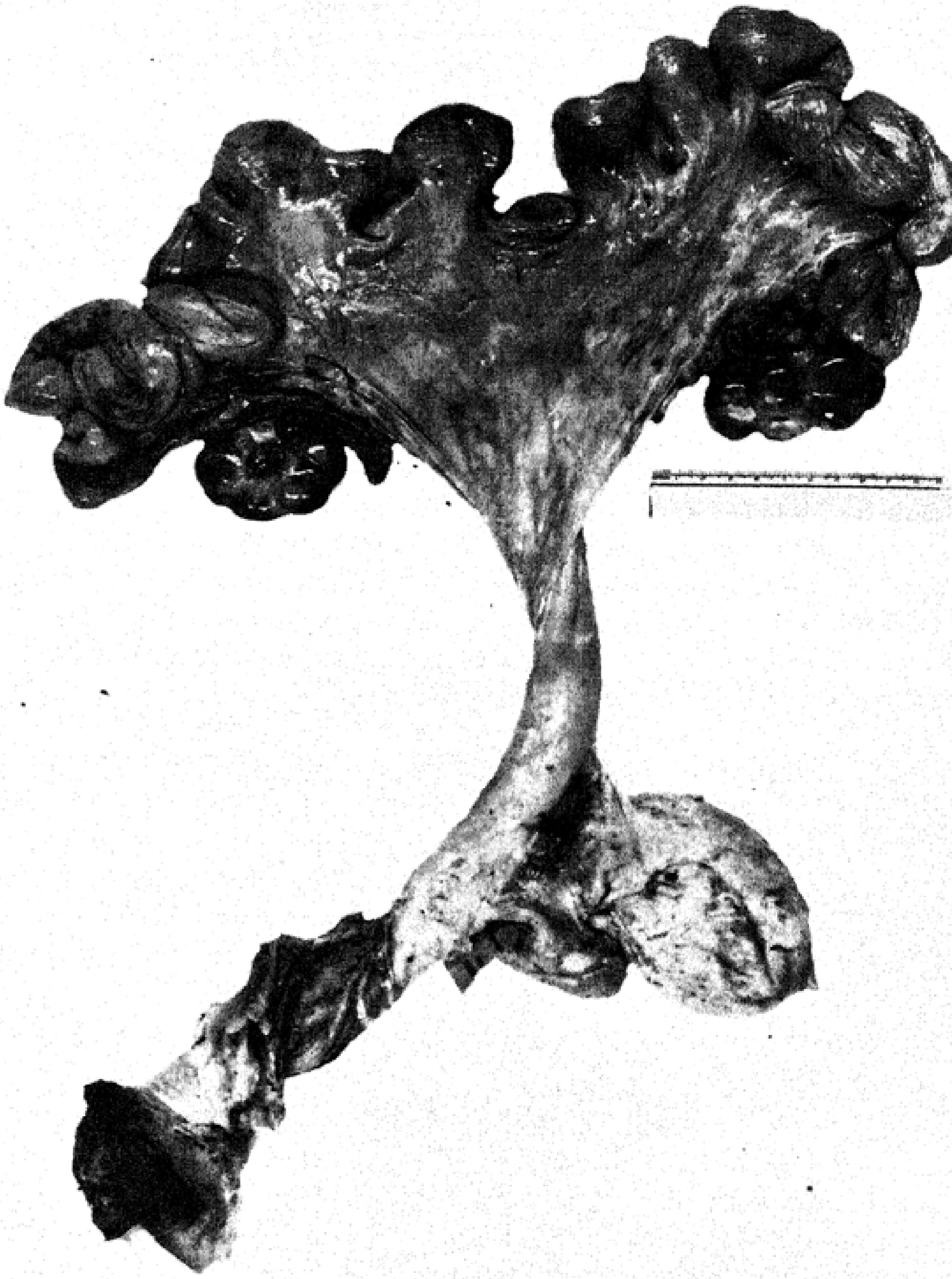

Fig. 2.—Completely cystic ovaries.

Fig. 3.—Line V Hampshire gilt. Both ovaries cystic; one corpus luteum; one pig.

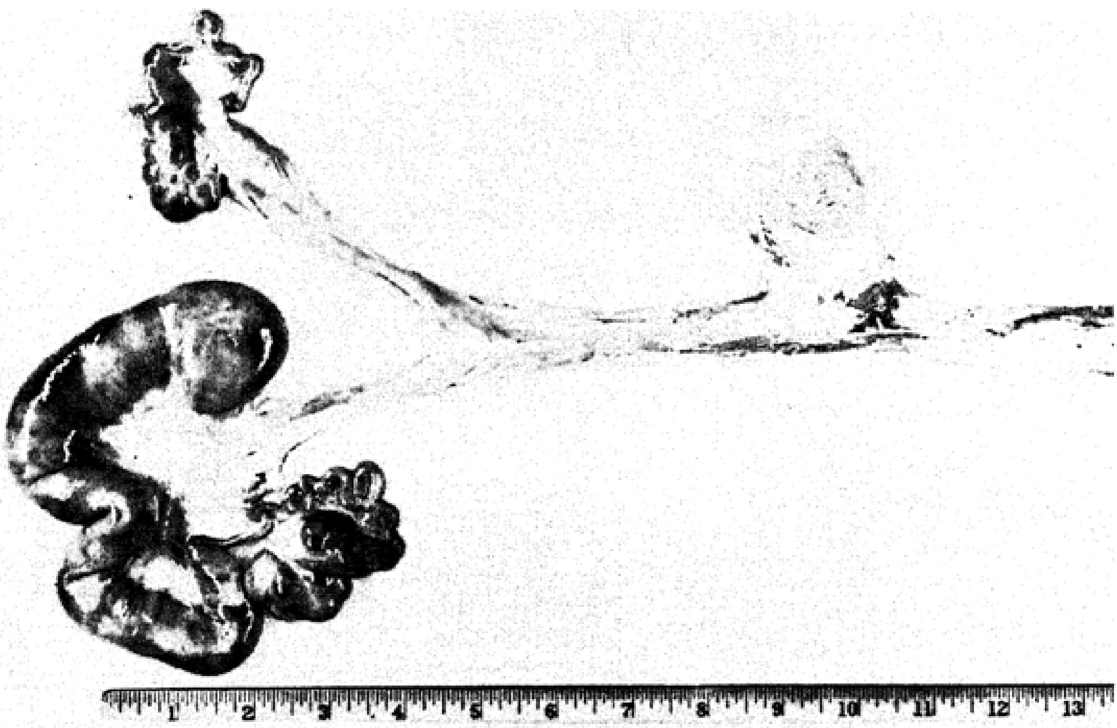

Fig. 4.—Incomplete development of Mullerian ducts.

In five females, segments of the reproductive tract were missing or incompletely developed (Figure 4). In two of these cases only one uterine horn was involved and the remaining horn contained the foetuses (Figure 5). It may be of some significance that 4 of these 5 females were from Poland line VI and the other was a line VI Poland x line II Poland cross.

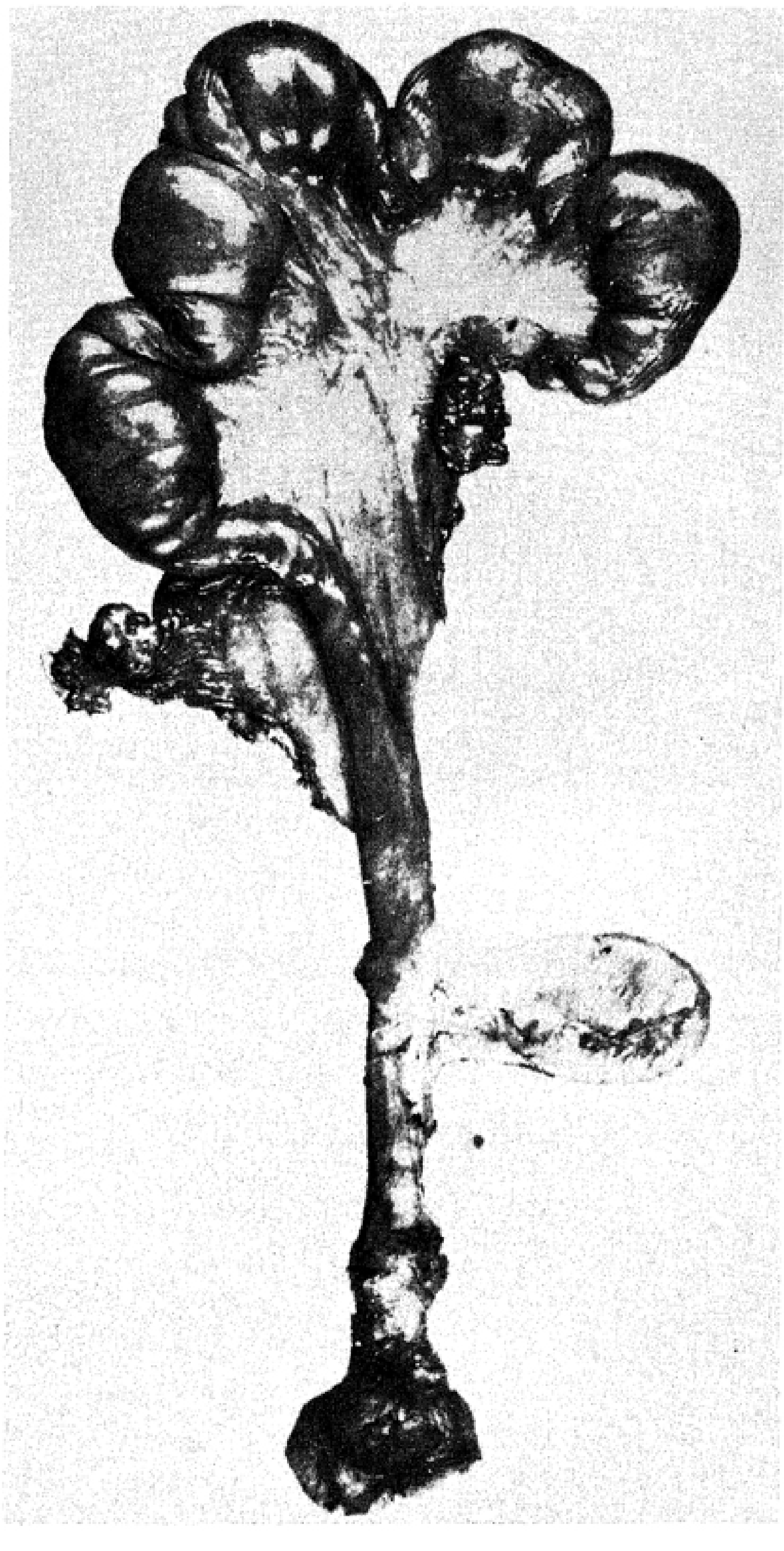

Fig. 5.—Line VI sow. One uterine horn missing, other horn gravid.

The only other gross abnormalities noted were two cases of adhesion involving the infundibulum, ovaries, and uterine horn; one case in which the cervix was blocked (Figure 6), and one "infantile" reproductive tract (Figure 7).

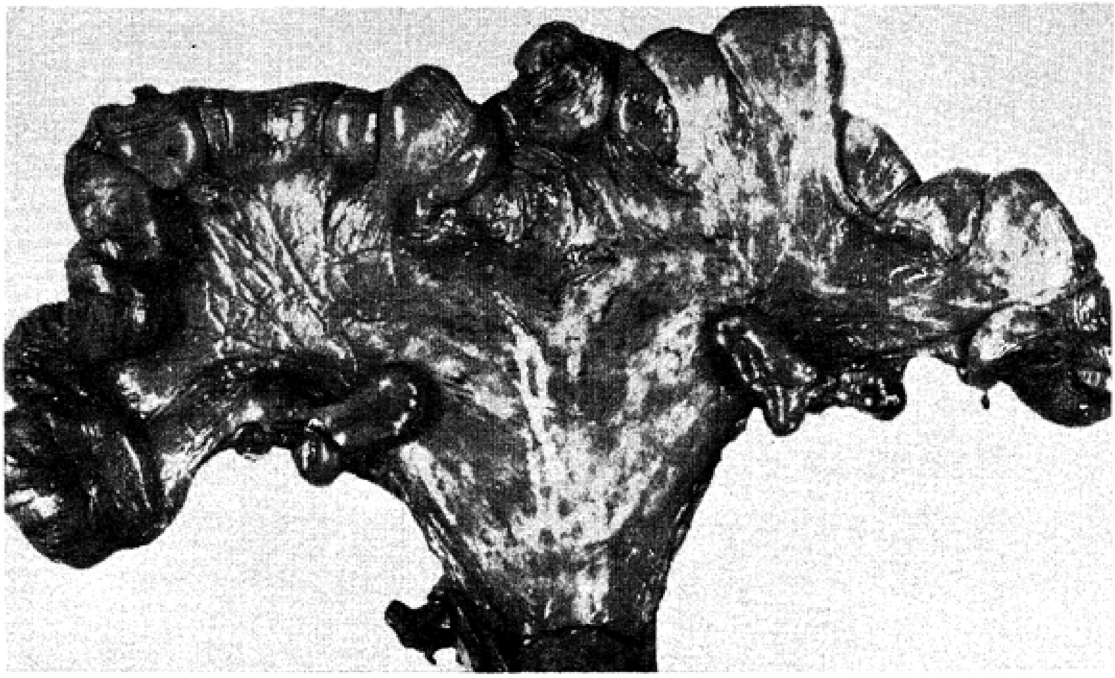

Fig. 6.—Blocked cervix with fluid in uterine horns and tubes.

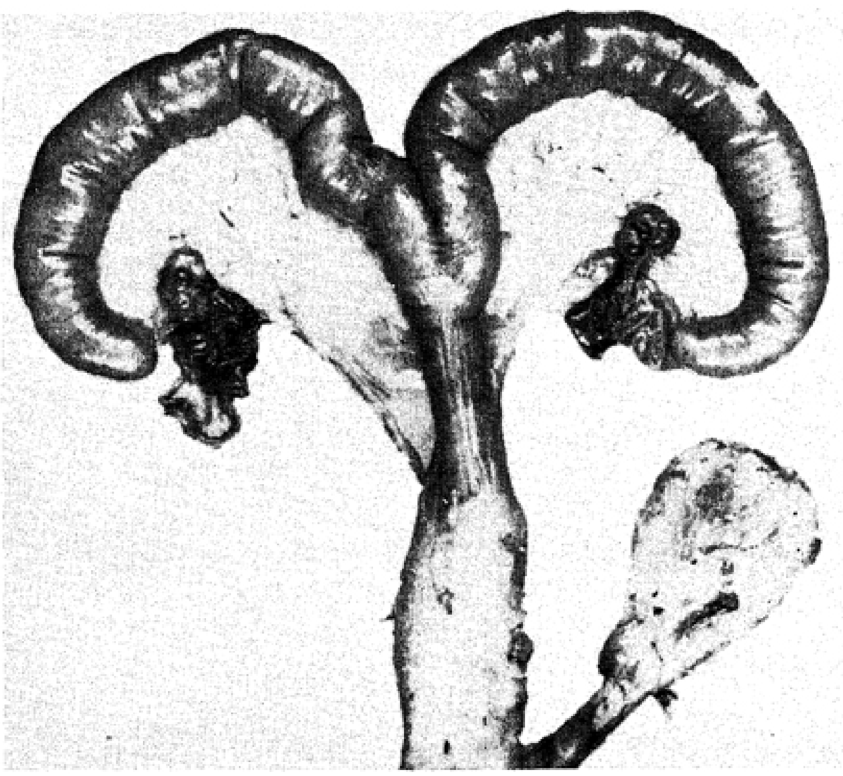

Fig. 7.—Infantile reproductive tract.

DISCUSSION OF RESULTS

Physiological Components of Fertility

Hammond (1941) states that, in any analysis of factors affecting fertility of animals, it is necessary first of all to relate those factors to the phase of the reproductive process which they affect. He recognizes three sets of factors or components which, from this viewpoint, control the effectiveness of the reproductive process in animals:

1. Factors affecting the number of ova shed; these being regulated mainly by the gonadotrophic hormones of the anterior pituitary.
2. Factors affecting the number of ova fertilized; these including, in general, not only the number of spermatozoa produced by the male, but also the time relations between mating and ovulation, the conditions influencing the viability of the spermatozoa in the female tract, and variations in fertilizability of ova.
3. Factors affecting the number of embryos developing normally to birth, including (a) progestin, which is secreted from the corpus luteum, and is necessary for attachment of the embryo and the maintenance of pregnancy, and (b) genetic factors causing foetal atrophy.

In the present study, an attempt was made to: (1) estimate the relative importance of these three sets of factors in the determination of litter size in swine; (2) determine to what extent these three components of fertility are influenced by degree of inbreeding and by difference between breeding groups; (3) estimate the degree of interrelationship among the three components of fertility and note the effect of such relationships upon litter size at 25 days; (4) study the effects of growth rate and age at breeding on each of the three components; (5) determine to what extent ovulation rate is inherited, in the hope that this character, measured in related females, would be helpful in breeding for larger litters; and (6) note the incidence of gross anatomical and physiological abnormalities. The results obtained in this study are evaluated below as they relate to the six objectives enumerated.

Relative Importance of Ovulation, Fertilization and Viability

The relative importance of these factors in the population observed in this study can perhaps best be expressed by summarizing briefly some of the data shown in Table 9 and in Figure 1. The average gilt was found to have shed 11.3 ova of which 10.7 or about 95 per cent were fertilized (as judged by cleavage). After 25 days of gestation, 7.3 normal embryos were present, representing 65 per cent of all ova shed, judging by number of corpora counted. An average of 0.80 degenerating embryos (or "mummies") were found, accounting for about 7 per cent of all ova shed. Thus among the 147 gilts studied at 25 days, about 35 per cent of the total ova shed were lost, about 5 per cent being accounted for by non-fertilization and about 30 per cent by non-development or early death of the fertilized eggs. Although more ova were shed by older sows (15.3) the proportion surviving to 25 days was about the same.

Estimated mortality of embryos between the 25th day of gestation and parturition in the present experiment amounted to 1.38 pigs from about 12.5 ova shed per gilt. This was about 11 per cent or less than one-third as great as mortality before the 25th day. However, total intra-uterine mortality was very large, amounting to about 46 per cent of all ova shed.

On the basis of standard partial regression coefficients shown in the path diagram in Figure 1, a change of one standard deviation in number of ova shed is associated with a change of about 0.8 standard deviation units in pig numbers at 25 days, if total mortality is held constant. Similarly, if ovulation rate is held constant, an increase of one standard deviation in total mortality (total ova lost through non-fertilization + early death) leads to a decrease in litter size of about 0.94 standard deviation units. Mortality seems to be slightly more important than ovulation rate in determining variation in litter size at 25 days.

Variation in proportion of ova fertilized was unimportant among pregnant animals, but did account for a rather high incidence of completely infertile matings (20 of 77) when immature boars were used. The experiment comparing conception rate and litter size from one and from two services indicated that a second service 24 hours after the first increased the conception rate by 23 per cent (from 66 to 89 per cent), but its effect on litter size among the gilts which became pregnant was small and uncertain (.51 ± .52 pigs). Results of this sort might be expected if all ova were shed at nearly the same time, but the timing of ovulation with reference to onset of estrus varied between individuals or between cycles. A second service would provide spermatozoa capable of fertilizing ova during a longer period, thus increasing conception rate, but fertilization would be effective for all normal ova if spermatozoa capable of fertilization were present in the oviducts.

The 35 per cent loss of ova to 25 days and the 46 per cent loss to parturition may be compared with Corner's (1923) finding that loss of ova varied from about 19 per cent to 35 per cent and with Hammond's (1914) estimate of a 40 per cent loss during the gestation period. It may also be compared with results of Wilson *et al.* (1949) who found a discrepancy of about 26 per cent between total corpora and viable embryos at 25 days among pregnant sows with a history of "shy breeding."

Observations made in this investigation, in agreement with those of earlier workers, yielded no evidence of sepsis in the uteri of sows in which embryonic death and resorption were occurring. There was no pus, odor or other evidence of putrifactive change in the degenerating embryos studied. The changes taking place in these embryos were much more suggestive of autolysis than of the action of micro-organisms. In most cases in which degenerating embryos were found, death had evidently occurred quite early, for they were usually small by comparison with the 25-day embryos. Occasionally larger dead embryos were found. Many of these were soft and flaccid and were surrounded by "bloody" amnionic fluid. A few embryos were found which were normal in appearance, but were surrounded by "bloody" amnionic fluid.

Like earlier observers, the authors were unable to assign causes for the high incidence of early mortality. If the embryo's own genetic makeup is entirely responsible, then a rather large number of genetic factors must be involved, for even in the least affected breeding groups the incidence was quite high. If nutritional deficiencies in the sow's ration are involved, they must exist even in pasture supplemented breeding rations, since the experimental animals used in this study during fall seasons had access to pasture from about 3 weeks of age until slaughtered. In addition, the analysis for seasonal effect gave negative results. An interaction between the sow's nutrition and the individual embryo's requirement for certain nutrients may, of course, exist. Such an interaction might possibly explain the occurrence of blighted embryos with vigorous neighbors on either side, but one hesitates to accept this explanation without more concrete evidence. The cause may be one of endocrine imbalance. If so, the effect must express itself through interaction with genetic makeup or age of embryos, because otherwise it is difficult to explain why hormone imbalance affects some embryos in the same uterus in which others thrive.

Inbreeding Effects and Strain Differences

Ovulation Rate. Among gilts, breeding group differences both within season and between season were highly significant, but seasonal variation within strains was negligible. This means, in effect, that significant difference existed both among all strains studied and between parent strains and crosses, since the strains were, for the most part, studied in different seasons than their crosses. When performance of the crosses was compared with the mean performance of their respective parent strains, it was found that crosses had a highly significant advantage of 1.19 ova. This advantage of crosses over parent lines amounts to .55 ova per 10 per cent of inbreeding of the parent lines. The within-group regression of number of ova shed on degree of inbreeding did not prove significant, probably due to the small variation in degree of inbreeding within strains. The large inbreeding and strain differences in rate of ovulation among gilts indicated there would be an important source of variation in litter size. The ovulation rates of older crossbred sows were not measured in this study, but strain differences among older sows were neither important nor significant.

Fertilization Rate. There was little indication from this study that either the strain or the degree of inbreeding of sows influenced the proportion of their ova fertilized, when completely infertile matings are excluded. The average fertilization rate of 95 per cent leaves little room for an influence of inbreeding or strain of sow.

Total Mortality. In view of the apparently small (5 per cent) average reduction of litter size at 25 days due to failure of fertilization, it was decided that for purposes of comparing breeding groups, total ovum mortality to 25 days would be used (i.e., number of active corpora minus number of normal embryos for each pregnant female). Variation between the four parent strains in total mortality proved to be entirely non-significant, but when performance of each cross was compared with the mean performance of the parent lines for gilts on an age corrected basis, a barely significant ($P = .05$) advantage of .81 pigs for crosses was obtained. This amounts to .33 fewer pigs lost by crossbred sows for each 10 per cent inbreeding of the lines crossed. Increased heterozygosity of the crossbred dams appears to be associated with less intrauterine mortality, but this conclusion must be tentative in view of the large sampling error of the difference and the fact that seasonal influences may have contributed to the difference between crosses and parent lines.

Litter Size at 25 days. Differences among breeding groups of gilts in litter size at the 25th day of gestation were statistically significant but were proportionately smaller than the differences in ovulation rate. This is due to (1) the large part of the variability in litter size associated with mortality of fertilized ova and (2) the tendency for breeding group to influence ovum mortality much less than ovulation rate. Differences in litter size at 25 days between older sows of the four parent stocks were no larger than expected from sampling error alone.

The paired comparisons of crosslines with parent lines indicated a highly significant advantage of 1.85 pigs in litter size at the 25th day of gestation. This superiority of the more heterozygous crossbred gilts amounts to .80 pigs for each 10 per cent inbreeding of the parent lines. Inbreeding of litters was not a factor because inbred litters were avoided. This figure is smaller by .08 than the sum of the estimated increases of 0.55 ova shed and of 0.33 in ovum viability per 10 per cent of inbreeding for the parent lines crossed. The discrepancy occurred because many non-pregnant gilts for which ovulation data were available provided no information about 25-day litter size or mortality of ova.

This estimate of an 0.8 pig advantage of crossbred gilts in litter size at 25 days for each 10 per cent inbreeding of the lines crossed is higher than any previous estimate of inbreeding effect on litter size at farrowing. It is an overestimate because it includes the advantage in heterozygosity of crossbreds over purebreds in addition to the advantage of purebreds over the inbred parent lines, whereas the calculated inbreeding difference includes only the latter. Previous estimates of the rise in litter size per 10 per cent lower inbreeding of dam based on regression within line and season are .63 by Stewart *et al.* (1945) holding constant age of gilt and inbreeding of litter, and .09 by Comstock and Winters (1944) holding constant only inbreeding of litter. In the latter study the correlation between inbreeding of dam and litter was .45, so that the partition of the effects of inbreeding of dam and litter has a large sampling error. From a comparison of non-inbred litters from linecross and inbred dams of the same Poland lines, Dickerson, *et al.* (1947) obtained an estimate of only .16 pigs larger litters for each 10 per cent less inbreeding of dam. However, earlier estimates of the increased litter size from crossbred compared with non-inbred sows of parent breeds are 1 to 2 pigs by Winters *et al.* (1936), and 1.4 pigs by Lush *et al.* (1939).

Relationships Between Ovulation Rate, Total Mortality, Growth Rate and Age at Breeding

As shown in Figure 1, litter size at 25 days is completely determined by ovulation rate and total mortality among ova shed. Mortality is partly determined by ovulation rate as shown by a path coefficient of +0.45. An increase of one standard deviation in ovulation rate is thus associated with a 0.45 standard deviation increase in mortality. This relationship is, however, largely automatic, since proportionate mortality increased only slightly with larger numbers of ova shed. Evidently, crowding of embryos in the uterus cannot be considered an important factor in early mortality. This is in agreement with the general observation in this study, as well as by Hammond (1914) and by Corner (1923), that deteriorating embryos are found quite often in the uterine horn which is least populated, and with no closely competing neighbors.

Growth rate (154-day weight) and age at breeding influence litter size at 25 days through both direct and joint effects upon ovulation rate and mortality. Each acts directly to increase ovulation rate and reduce mortality. Part of this favorable effect was masked in the present study by a significant tendency for the faster growing gilts to be bred at a younger age ($r_{AG} = -.27$) and by the tendency for increased ovulation rate to be associated with greater total, although only slightly greater proportionate mortality. However, the combined effects of age and growth rate are not large. Most of the variability in ovulation rate and mortality, and thus in litter size, is determined by causes whose nature is not apparent from this study. Because of the much greater breeding group differences in ovulation rate than in mortality or litter size itself, selection between breeding groups based on ovulation rate rather than litter size alone would seem to offer hope of more rapid genetic improvement.

In the present data on gilts bred at a mean age of 226 days (standard deviation of 23 days), litter size at 25 days increased .61 pigs for each increase of 10 days in age with 154-day weight held constant. This is much larger than the regression of .20 pigs obtained by Stewart (1945a). The difference probably is due partly to the older age range among gilts studied by Stewart and partly to the fact that growth rate was not held constant in his calculation.

Heritability of Ovulation Rate

Since breeding group differences were relatively large for ovulation rate, it seemed worthwhile to attempt an estimate of heritability based on the correlation between paternal half-sibs and between full-sibs.

Covariance technique was used to adjust for regression on age of gilt. Unfortunately, no effect of sire upon ovulation rate of his daughters was evident from the results obtained, but differences between litters within sires were nearly significant and differences between reciprocal crosses were highly significant. These results indicate a strong maternal influence on ovulation rate, but provide no basis for an estimate of heritability based on the transmitted influence of the sire. These results were unexpected, since Lush and Molln (1942), Stewart (1945), Cummings *et al.* (1947), Blunn and Baker (1949) and others have found that litter size at birth has a low but definite degree of heritability. The small volume of data, or the fact that gilts of the parent lines were those not considered good enough for use as breeders, may account for the small sire influence obtained.

On the basis of partial correlation holding age constant, ovulation rate was found significantly associated with 154-day weight when the relationship was computed between sire groups or between litters within sires, but not when computed for differences between litter mates. This suggests that the association between 154-day weight (growth rate) and ovulation rate arises from either maternal or transmitted influences, or both, on the two characters.

Incidence of Gross Abnormalities

The incidence of gross reproductive abnormalities in the population of gilts and sows studied was not high amounting to less than 7 per cent of all females studied. In agreement with the results of Wilson *et al.* (1949) and Warnick *et al.* (1949), the most common abnormalities noted were ovarian cysts of either single or multiple nature. The principal effect of these cysts seemed to be a reduction in total number of ova shed rather than any adverse effect on the embryos present, since there was no greater discrepancy between number of corpora and number of embryos in cystic than in non-cystic cases.

Of special interest was one sow, both of whose ovaries were a mass of cysts, in which only one corpus was present and a single normal embryo was found in the uterus (Figure 8). Evidently this single corpus had produced enough progesterone for implantation of the single embryo. Other abnormalities included missing segments, adhesions, a blocked cervix and one "immature" tract.

SUMMARY AND CONCLUSIONS

Gilts and sows of two inbred Poland China, one inbred Hampshire and one non-inbred Duroc strains and gilts of the six crosses were used to determine sexual maturity, rate of ovulation, efficiency of fertilization and extent of embryonic mortality, and to study the influence of inbreeding, age and rate of growth on these components of litter size in swine, as follows:

1. Number of ova shed (i.e., active corpora counted) per estrus averaged 11.5 for 277 gilts of all groups at a mean age of 225 days and 15.4 for 72 older sows of the four strains. Standard deviations within season and strain or cross were 2.53 ova for gilts and 3.40 for sows.

2. Among 77 gilts bred once early in estrus to boars 6-8 months of age, and slaughtered 24 hours after end of estrus, some fertilized (cleaved) ova were

recovered from 52, 20 yielded no fertilized ova, and 5 were slaughtered too soon for determination of cleavage. In the 52 fertile matings, 95 per cent of all ova were cleaved and in 37 cases 100 per cent of the ova were cleaved. Fertilization appeared to be largely an "all or none" process.

3. Among 147 pregnant gilts bred once in early estrus and slaughtered approximately 25 days later, a mean of 11.3 ova were shed but only 65 per cent were represented by normal embryos at 25 days. The 35 per cent loss was ascribed 5 per cent to infertile ova, 23 per cent to fertile ova of which no trace remained and 7 per cent to degenerating embryos recovered. For 65 sows, a mean of 15.3 ova were shed, of which 35 per cent were lost; 5 per cent were infertile, 25 per cent had disappeared and 5 per cent were degenerating. Standard deviations within season and strain were 3.14 pigs or 24.7 per cent in total mortality and 3.26 in litter size at 25 days for gilts; and 3.80 and 4.03 pigs for mortality and for litter size, respectively, in sows.

4. Comparison of litter size at 25 days for 54 pregnant gilts with litter size at parturition for 59 gilts of the same four strains indicated an additional loss of 1.4 embryos or 11 per cent, or an average total loss from ovulation to parturition of about 46 per cent.

5. Comparison of 50 gilts of 9 strains bred once on the first day of estrus with 48 gilts of the same strains bred twice at 24-hour intervals indicated that the second service increased conception rate by 23 per cent (from 66 to 89 per cent, $\pm$ 5.7, $P = .002$), but increase in litter size was small and uncertain ($+ .51 \pm .52$ pigs, $P = .16$).

6. For each increase of 10 days in age at conception among gilts (mean 226 days, $\pm$ 23.2 days) .35 more ova were shed, .15 fewer ova were lost and .50 more normal embryos were present at 25 days after conception. Weight of gilts at 154 days of age also was associated with higher ovulation rate and lower mortality of ova, but with younger age at conception ($r = -.27$). The partial regressions describing the independent effects of age in days and of 154-day weight in pounds, respectively, were .042 and .024 for ova shed, –.019 and –.013 for ova lost, and .061 and .037 for number of normal embryos at 25 days.

7. Variation in litter size 25 days after conception was determined more largely by mortality of ova ($r = -.67$, $\beta = -.94$) than by number of ova shed ($r = .47$, $\beta = .80$). The partial regression of mortality on number of ova shed (age and growth constant) was .53 in contrast with the simple regression of .40 and the mean proportion lost of .35, indicating a slight tendency for proportion of ova lost to increase with number of ova shed.

8. Intra-season variation between the four strains or between the six crosses, after adjusting for regression on age, was highly significant for number of ova shed but not for 25-day litter size or number of ova lost. Variation between seasons within breeding groups was only slightly and not significantly greater than within breeding group and season for number of ova shed and for

number lost, but was significantly smaller than within group and season for 25-day litter size, suggesting a negative association between seasonal effects on numbers of ova shed and on mortality of ova.

9. Paired comparisons of crosses with the mean of the two parent lines for gilts, ignoring the negligible seasonal variation, indicate advantages for crosses of 30 days earlier sexual maturity ($P < .01$, 277 gilts), and after adjustment for age bred of 1.19 more ova shed ($P < .01$, 277 gilts), .81 fewer ova lost to 25 days ($P = .05$. 147 gilts) and 1.85 more pigs per litter at 25 days ($P < .01$, 147 gilts). For each 10 per cent of inbreeding of the parent lines, these advantages for crosses amounted to 13 days earlier maturity, .55 more ova shed, .33 fewer ova lost and .80 more embryos per gilt 25 days after conception. These advantages include crossbreeding effects (in 5 of the 6 crosses) as well as reduction of inbreeding effects within a breed.

10. Gross abnormalities of the reproductive tract were found in only 7 per cent of the 359 females examined; 15 had cystic or persistent follicles, 5 had discontinuous or undeveloped uterine horns, 2 had adhesions involving the infundibulum, 1 had a blocked cervix and 1 had an "infantile" tract.

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