RESEARCH BULLETIN 666 MAY, 1958

UNIVERSITY OF MISSOURI COLLEGE OF AGRICULTURE

AGRICULTURAL EXPERIMENT STATION

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Genetic Aspects of Reproduction In Swine

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(Publication authorized May 22, 1958)

COLUMBIA, MISSOURI

ABSTRACT

The genetic aspects of fertility and the physiological environment under which the mammalian embryo is produced and nourished were investigated. Distinct variations were noted in ovulation rate, prenatal mortality, litter size, and uterine capacity between families established by the sires and the dams. These data were indicative of the genetic nature of the reproductive potentialities.

A boar of normal fertility had no influence whatsoever on the performance of gilts mated to him, but his importance was manifested in his ability to transmit his share of inheritance for fertility to his daughters. An optimum second service at about 20 hours after the onset of estrus was found to lower the incidence of the prenatal mortality and significantly increase the embryonic survival at 55 days of gestation. Of all the phenotypic traits studied, the age and weight of the gilts at breeding were found to be more closely associated with reproductive performance. Intra-uterine migration of the fertilized ova was encountered in 30.9 percent of the gilts employed in this investigation. Twice as many fertilized ova migrated from the left to the right horn of the uterus as in the other direction. Morphological abnormalities of the reproductive tracts were of rare occurrence; hence they were regarded as of minor importance in the evaluation of factors influencing the reproductive performance.

The total weight of all corpora per gilt was highly correlated with the litter size ($r = .427$), with a 1 gram increase in corpora weight resulting in a linear increase of 0.705 viable embryos. Results obtained in this study show that prenatal death loss, number of ova shed, and linear capacity of the uterus are important, in that order, and that they largely determine the litter size.

This bulletin reports on Department of Animal Husbandry Research Project 222, "Swine Improvement," and Department of Agricultural Chemistry, 223, "Reproductive Physiology." Animals used in this study were produced with the cooperation of the Regional Swine Breeding Laboratory, AHRD, ARS, U.S. Department of Agriculture.

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Genetic Aspects of Reproduction In Swine

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INTRODUCTION

The study of the physiology of pregnancy is one of the most intriguing and exciting phases of present day research. It is intriguing because biological organisms in their steady and ceaseless efforts to perpetuate their like, require the cooperation and coordination of all their physiological systems; in addition, many complex and yet unknown phenomena may be involved. It is no wonder, then, that these diverse reproductive processes remain difficult to understand and such knowledge has been fragmentary in presentation.

Certainly, any knowledge of the physiological environment under which the mammalian embryo is produced and nourished would be of immense value for practical application in animal breeding. The animal breeder is quite often confronted with the marked variation that exists in the fertility between the females of the same species, breed, and age and even between sibs from the same female. If a portion of this variability could be accounted for or estimated by means of the visible phenotypic traits, selection for fertility would be more accurate and without doubt more successful.

There is a maximal potential fertility for every individual animal and apparently that potentiality is never really exploited in breeding practices. The rate of propagation of any species depends not only on the prolificacy and the frequency of pregnancies but also on the age at which the puberty is attained. It would be worth-while to estimate and if possible, expedite the optimum breeding age by means of the skillful selection of parental stock.

In substance, the primary objectives of this investigation are:

(1) To study the fundamental anatomy and physiology of the reproductive organs during the puberal age and gestational periods.

(2) To determine the genetic and environmental factors which influence ovulation rate, fertilization, intrauterine capacity, embryonic mortality and, ultimately, litter size in swine.

(3) To elucidate the relative importance of these factors of fertility, especially in relation to the litter bearing capacity.

(4) To estimate the portion of the variability in prolificacy that could be accounted for in terms of measurable phenotypic traits.

LITERATURE REVIEW

Inheritance of Fertility and the Factors Affecting Prolificacy

Each race, species or breed is characterized by a certain degree of fertility, both in quality and quantity, which is apparently capable of hereditary transmission. Further, within each breed there are particular strains of related individuals which possess and transmit a higher degree of fertility than the average.

The investigations of Pearson *et al.* (1899) with horses, Rommel and Phillips (1907) with swine, and Nichols (1924) with sheep offered scientific evidence of the hereditary nature of fertility. Winters *et al.* (1935), Lush and Molln (1942), and Bradford *et al.* (1953) indicated that various breeds of swine were characterized by a difference in litter size and that they tend to maintain their relative merit for prolificacy over a period of years. This phenomenon apparently emphasizes the importance of the genetic makeup for fertility.

Effect of Inbreeding

Each 10 percent increase in the inbreeding coefficient has resulted in a reduction of 0.5 to 1.3 pigs per litter (Stewart, 1945). Litter size has usually shown some decline by the time inbreeding has reached 25 to 35 percent (Craft, 1953). Comstock and Winters (1944) estimated that a 10 percent increase in the inbreeding of a dam, independent of the inbreeding of the litter, could cause a reduction of only 0.09 pigs in the litter size at birth. Dickerson *et al.* (1947) recorded a decline of 0.16 pigs per 10 percent increase in inbreeding of the dam, keeping both age of gilt and inbreeding of litter constant.

Phenotypic Traits and General Health

Weight at the time of breeding and gains in weight during gestation were found by Stewart (1945) to be significantly associated with the number of pigs farrowed. He also stated that "Age and weight at mating together provide the most reliable criteria for use in selection for fertility." The longer bodied females were found to be the heaviest at mating (Zeller, 1940) and there were significant differences in fertility between types of swine (Hetzer and Brier, 1940).

Backfat thickness and the number of corpora were found to be significantly correlated ($r = .29$) within breeding groups (Lerner *et al.,* 1957). The same investigators reported an increase of about 1.5 corpora for every 10 mm. increase in backfat deposition. They found the body length of gilts to be significantly associated ($r = .24$) with ovulation rate.

Age of Puberty and Breeding

Stewart (1945) found that litter size at first farrowing increased in a curvilinear fashion with the age of dam up to about 15 months, the relationship being almost linear between the ages of nine and 12 months. An increase of 0.5

pigs for each 10 days increase in age at breeding of gilts was indicated by Squiers *et al.* (1952). Age of gilts at the time of breeding had distinct effects on the ovulation rate and the litter size at farrowing (Craft, 1953).

Ovulation

It is generally accepted that gilts bred at an early heat period have fewer pigs in comparison to those bred at later periods. Ovulation rate is one of the three important factors which control fertility in mammals (Hammond, 1921). Squiers *et al.* (1952) found that number of ova shed was significantly correlated ($r = .47$) with litter size at 25 days of gestation.

Spacing of Ova in Uterus

The curious phenomenon of regular spacing of the ova in the uterus of polytocous mammalian species has always interested investigators but it is not yet completely understood. Whether the mode of migration or transport of the ova down the uterine horns is affected by the activity of the germ chemotaxis, peristalsis (Keye, 1923), or ciliary movement (Mañdl, 1908) is not clearly understood. Even if we knew by which means the ova migrate, this would not explain the reason for the regularly spaced implantations. It was suggested by Mossman (1937) that the implanting ovum may interact in some unknown manner, with the uterine mucosa to create around itself a local refractory zone in which no other ovum can implant. Mouse ova in the anterior chamber of the eye appear capable of developing in close proximity only until the most precocious one among them begins to implant. Thereafter, all, except the implanting ovum, degenerate (Fawcett *et al.*, 1947). This disproves Mossman's assumption that the uterine mucosa participates in the creation of a local gradient of influence around the nidating ovum.

That blastocysts implant in the uterus only at prescribed times in certain pre-determined and especially prepared sites was suggested by Fawcett *et al.* (1947). Bloch (1939) suggested that the uterine epithelial secretion, provoked or induced by the corpus luteum of early pregnancy, seems to migrate into the cells of the blastocysts. The secretion was found only when pre-implantation blastocysts were present in the uterus. Bloch also observed that this secretion could be produced by injection of the corpus luteum hormone in the absence of eggs and that the secretion was rhythmically increasing or decreasing along the length of the uterine horn. Therefore, he postulated that the areas of strong secretion were chemotactically attracting the blastocysts, thus causing implantation in those places.

Prenatal Mortality

Bischoff (1842) was the earliest worker to postulate a theory of prenatal mortality, based upon observations in the rabbit. He indicated that in polytocous mammals the number of corpora lutea generally corresponds to the number of embryos. However, occasionally he did notice the presence of fewer embryos than corpora lutea, particularly in the later stages of pregnancy. He interpreted this discrepancy by the death accompanied by absorption, resorption, or abortion of some of the embryos.

Hammond (1921) found 32.6 percent embryonic mortality in 21 sows which were slaughtered between the fourteenth to sixtieth day of gestation. Corner (1923) obtained data on 535 reproductive tracts of sows, in different stages of gestation, and observed that only about 70 percent of the ova were represented at term by living pigs. The work of Lerner, Mayer, and Lasley (1957) with gilts of different breeds showed mortality rates of 25.07 percent at 17 days and 33.63 percent at 25 days of gestation. The extensive investigation of Squiers, Dickerson, and Mayer (1952) revealed a pre-natal loss of 35 percent at 25 days of gestation. Embryonic mortality of 31.3 percent at 55 days of gestation was reported by Rathnasabapathy, Lasley, and Mayer (1956).

Imbalanced or unbalanced hormonal availability for the maintenance of pregnancy could result in higher embryonic losses. The hormones may act directly on the blastocysts (Corner, 1928; Bloch, 1939) or, by their actions on the uterine tissue, they may indirectly affect the intrauterine environment. Van de Horst and Gillman (1942) reported the existence of restricted areas in the uterine horn of the elephant shrew and all the fertilized eggs other than those that reached these implantation sites degenerated.

Corner (1921) thought that overcrowding was an important but not the only factor responsible for embryonic deaths, especially during the latter half of gestation. Warwick *et al.* (1943), on the basis of their investigation with rabbits, concluded that the embryonic deaths were due either to a primary or secondary uterine deficiency rather than any defects in the ova. Engle (1927) also stated that intrauterine crowding was the cause of embryonic death but he later postulated a deficiency of progesterone. Since that time several workers have tried to increase litter size by the use of gonadotrophic material, but in general these trials have been unsuccessful. However, Warwick *et al.* (1943) and Burdick (1942) indicated that progesterone and estrogen played an important part in improving uterine environment.

MATERIALS AND METHOD

Experimental Animals

The 117 gilts and nine boars used in this study were obtained from the Missouri Agricultural Experiment Station herd which is maintained in cooperation with the Regional Swine Breeding Laboratory U. S. Department of Agriculture. Gilts used in 1955 tests were from reciprocal crosses among Landrace (L), Poland China (P) and Duroc (D) breeds; those used in 1956 were from Landrace and Poland China breeds. Tables 1 and 2 show the number and breed of animals used in this investigation.

TABLE 1--GILTS EMPLOYED FOR THE STUDY OF SEXUAL MATURITY AT DIFFERENT LIVE BODY WEIGHTS

Stage of Growth	1956 No. of Gilts (L x P)†	1955 No. of Gilts (L x P x D)††	1955 No. of Gilts Poland	Total
100 pounds live body weight	4			
150 pounds live body weight	5			
200 pounds live body weight	3	22	7	
250 pounds live body weight	3			
Estrus	2			
Anestrus	3			
Total	20	22	7	49

†Landrace x Poland.
††Landrace x Poland x Duroc.

TABLE 2--FEMALES STUDIED AT 55 DAYS OF GESTATION BY SIRE GROUPS

1955 Spring Sire Group	1955 Spring No. of Gilts (L x P x D)†	1956 Spring Sire Group	1956 Spring No. of Gilts (L x P)††	1956 Spring Sire Group	1956 Spring No. of Gilts (Duroc)	Total
Landrace x Poland 256	6	Landrace 194	2	Duroc 46	3	
Landrace x Poland 394	4	Landrace 203	1	Duroc 355	1	
Landrace x Poland 428	10	Landrace 256	2	Duroc Honor Ace	3	
Duroc 157	6	Landrace 308	2			
Duroc 350	1	Poland 43	1			
Duroc 355	3	Poland 183	1			
Duroc 500	12	Poland 217	1			
Duroc Velvet King	9					
Total	51		10		7	68

†Landrace x Poland x Duroc.
††Landrace x Poland.

All the gilts employed in this study were weighed at weekly intervals. As soon as they attained 200 pounds of live body weight, some of the phenotypic traits, including body length, heart girth, flank girth and subcutaneous deposition of fat on the shoulder, hip and ham were measured and recorded. The mature gilts were then checked with boars for the detection of estrus two or three times each day.

All females were bred to nonrelated boars to avoid inbreeding of the embryos. They were slaughtered on or as near to the 55th day after breeding as possible. The entire reproductive tracts were removed immediately for a detailed laboratory examination and the following observations were made: (1) Length of vagina, cervix, body of the uterus, gravid horns and fallopian tubes; (2) viable embryos in each horn; (3) intra-uterine spacing of the embryos; (4) weights of the intact gravid uteri; (5) weights of the individual embryos; (6) length of the embryos; (7) sex ratio of the embryos; (8) nipple number on each embryo; (9) weight of the ovaries; (10) number of corpora lutea present on each ovary and corpora weights; (11) presence of any gross physiological and anatomical abnormalities of the embryos and the pregnant uterus; (12) efforts were made to isolate bacteria of any pathological significance from different regions of the gravid uteri and vaginas.

In an attempt to explore the possible extent of association between the measurable phenotypic traits and the reproductive performance, each of the characteristics listed below were studied in relation to ovulation rate, linear capacity of the uterus, prenatal mortality and litter size: (1) Birth weight; (2) weaning weight; (3) 154-day weight; (4) age at breeding; (5) weight at breeding; (6) weight at 55 days of gestation; (7) body length, heart girth and flank girth at 200 pounds body weight; (8) subcutaneous deposition of fat over the regions of shoulder, hip and ham; (9) growth rate from weaning to 200 pounds body weight; (10) growth rate from weaning to slaughter.

RESULTS AND DISCUSSION

Sexual Maturity

Seven Poland and 22 Landrace x Poland x Duroc gilts were employed in 1955 and 20 Landrace x Poland gilts in 1956 for investigating the relative growth of the reproductive organs during pre-puberal, puberal, and post-puberal stages. Efforts were made to estimate the age of puberty in these breeds and crosses.

Of the 22 Landrace x Poland x Duroc gilts, 13 had either ovulation points or freshly formed corpora lutea and thereby were classified as mature animals. Their reproductive tracts exhibited definite signs of maturity with marked growth associated with an apparent increase in the vascularity and water content. The age of these mature gilts varied from 165 to 217 days with a mean of 186 $\pm$ 16.4 days. The mean number of corpora lutea was 12.0 $\pm$ 2.6 per gilt. The remaining nine gilts were considered to be approaching maturity and their ages varied from 157 to 207 days with a mean of 169 $\pm$ 10.2 days.

Of the seven Poland gilts studied, only two gilts, at a mean age of 204 days, were classified as mature. These gilts had a mean number of 14 corpora per gilt. Landrace x Poland x Duroc gilts matured 18 days earlier than the purebred Polands, which indicates a definite advantage of crosses in age at maturity.

The age of maturity in Landrace x Polands was 178 $\pm$ 6.0 days with an average of 15 $\pm$ 2.1 corpora per gilt. This difference in age at maturity between Landrace x Poland and Landrace x Poland x Duroc gilts was partly confounded due to the uncontrollable environmental and other variations between the years 1955 and 1956.

Although considerable variation exists between seasons and between individuals within season under the conditions of this investigation, it could be said that Poland, Landrace x Poland, and Landrace x Poland x Duroc breeds attain sexual maturity around 204.0 ± 24.2, 178 ± 12.0 and 186 ± 32.8 days, respectively.

The results obtained in this study therefore disagree with the findings of the earlier workers (Corner, 1921; Marshall and Hammond, 1937; Asdell, 1938) who indicated that the age of onset of puberty was at four months. The minimum age at which puberty occurred in this study was 168 days (five and one-half months) and that was observed in only two individuals.

The fundamental morphology and the magnitude of the growth and distention of the reproductive organs are summarized in Tables 3, 4 and 5. Analysis of that data distinctly suggests a marked increase in growth of the reproductive organs just prior to the first oestrus period. On the basis of the evidence obtained in this study, it would appear that live body weight does not necessarily reflect the functional stage of the reproductive organs. On the other hand, age of the gilts provides a more reliable picture of the reproductive development.

During estrus the linear capacity (footnote, Table 3) of the uterus was

TABLE 3--LINEAR CAPACITIES AND WEIGHTS OF THE REPRODUCTIVE TRACTS IN POLAND GILTS BEFORE AND AT OR AFTER MATURITY DURING 1955†

Part of the Reproductive Tract	Before Maturity (Around 196 Days)	At or After Maturity (Around 204 Days)	Percent Growth
Vagina	263.4 mm.	289.5 mm.	9.9
Right Horn	336.0 mm.	583.0 mm.	73.5
Left Horn	326.4 mm.	572.5 mm.	75.4
Uterus (Length)	662.2 mm.	1155.6 mm.	74.5
Uterus (Weight)	160.5 gms.	321.8 gms.	100.5
Rt. Fallopian Tube	195.6 mm.	241.0 mm.	23.2
Lt. Fallopian Tube	193.2 mm.	230.0 mm.	19.0
Right Ovary	1.89 gms.	2.36 gms.	24.9
Left Ovary	2.20 gms.	2.49 gms.	13.2

†Linear capacity = combined length of both the uterine horns.

TABLE 4--LINEAR CAPACITIES AND WEIGHTS OF THE REPRODUCTIVE TRACTS IN LxPxD GILTS BEFORE AND AFTER MATURITY DURING 1955

Part of the Reproductive System	Before Maturity (Around 169 Days)	At or After Maturity (Around 186 Days)	Percent Growth	At 55 Days of Pregnancy	Percent Distention
Vagina	292.3 mm.	317.5 mm.	8.6	464.0	46.1
Right Horn	367.8 mm.	587.4 mm.	59.7	1291.8	119.9
Left Horn	398.9 mm.	622.3 mm.	56.0	1306.3	109.9
Uterus (Length)	766.5 mm.	1209.9 mm.	57.8	2598.2	114.7
Uterus (Weight)†	152.9 gms.	263.4 gms.	72.3	5134.8	1849.4
Rt. Fallopian Tube	210.0 mm.	239.2 mm.	13.9	271.4	13.5
Lt. Fallopian Tube	224.5 mm.	242.8 mm.	8.2	287.4	18.4
Right Ovary	1.99 gms.	2.66 gms.	33.7	6.89	159.0
Left Ovary	2.28 gms.	2.99 gms.	31.1	7.85	162.5

†Weight of the uteri at 55 days gestation excludes the weights of the embryos.

TABLE 5--RELATIVE GROWTH OF REPRODUCTIVE ORGANS IN LxP GILTS THROUGH PREPUBERAL, PUBERAL AND GESTATIONAL PERIODS DURING 1956

Stage of Growth: Weight in Pounds	Stage of Growth: Age in Days	Vagina (mm.)	Right Horn (mm.)	Left Horn (mm.)	Length of Uterus (mm.)	Weight of the Genital Tract (gm.)	Right Ovary (gm.)	Left Ovary (gm.)
108.5	107.8	210	258.8	272.5	531.2	95.2	1.53	2.04
158.0	148.0	250	349.6	364.2	713.8	157.9	2.92	2.94
Percent Growth		19	35.1	33.6	34.4	65.8	90.8	44.1
212.6	160.0	274	346.0	363.3	709.3	142.2	2.16	2.32
Percent Growth		10						
215†	178.0	281	556.0	533.0	1089.0	320.1	1.68	2.26
Percent Growth††		2	60.7	46.8	53.5	125.0		
250	195.6	259	374.0	367.0	741.3	153.0	2.59	3.54
Percent Growth††		-6	8.1	1.1	4.5	7.6	19.90	52.60
55 Days Gestation		410	1283.6	1326.5	2610.1	4804.8	6.58	7.54
Percent Growth††		50	270.9	265.1	270.0	3278.9	204.6	225.0

†Gilts in estrus.

††Percent growth in relation to the measurements at 200 pounds body weight.

1089.0 mm. in contrast to 709.3 mm. at 200 pounds body weight. This difference represents a 53.5 percent increase from the non-estrus to the estrus state. There was a marked distention of the uterus at 55 days of gestation as evidenced by its linear capacity of 2610.1 mm. and a 270 percent growth increase in relation to the uterine capacity at 200 pounds live body weight. Similarly, the weight of the reproductive tract showed a 2½-fold increase during estrus and a 33-fold increase during the first 55 days of pregnancy, in comparison with its weight at 200 pounds live body weight.

It is interesting to observe that the left uterine horn was longer and the left ovary was heavier than their counterparts at 100 days of age; they maintained that superiority all through the several phases of growth and also at 55 days gestation.

Heredity and Reproductive Potentiality

Fertility in swine is greatly confounded by a multiplicity of factors; it is, therefore, a difficult task to estimate the influence of sires and dams of the families on the fertility of a limited number of daughters. The ability of the different sires and dams of the families to transmit the genetic make-up for fertility can be assessed to a certain extent by a comparison of the performance of the daughters from different families. The primary components of fertility, such as age at breeding, ovulation rate, prenatal mortaility and litter size, classified by the sire groups of the families, are presented in Table 6.

TABLE 6--MEANS AND COEFFICIENTS† OF VARIATION OF AGE AT BREEDING, OVULATION RATE, LITTER SIZE, AND PRENATAL MORTALATIES CLASSIFIED BY SIRE GROUPS OF THE FAMILIES DURING 1955

Sire Group	No. of Gilts	Age at Breeding in Days		Ovulation Rate		Litter Size		Prenatal Mortality	
		Mean	C.V.	Mean	C.V.	Mean	C.V.	Mean	C.V.
Landrace x Poland 256	6	195.5	.080	11.50	.284	7.00	.326	4.50	.640
Landrace x Poland 394	4	203.0	.093	10.25	.167	8.00	.306	2.25	1.169
Landrace x Poland 428	10	191.7	.260	12.70	.148	7.90	.346	4.80	.527
Duroc 157	6	195.3	.165	11.00	.223	7.83	.285	3.17	.612
Duroc 350	1	209.0	---	10.00	---	8.00	---	2.00	---
Duroc 355	3	209.3	.183	11.67	.247	9.33	.446	2.33	.657
Duroc 500	12	196.8	.081	12.00	.167	8.25	.333	3.75	.781
Duroc Velvet King	9	196.1	.055	15.00	.705	9.44	.150	5.56	1.751

†Coefficients of variation are expressed as fractions of 1, taking 100 percent variation as unit 1.

Age of Gilts at Breeding.

Age at breeding in Landrace x Poland x Duroc gilts ranged from 169 to 256 days, with a mean of 197.9 ± 17.9 days. Analysis of variance (Table 7) re-

TABLE 7--ANALYSIS OF VARIATION IN AGE AT BREEDING TIME AMONG LxPxD GILTS

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Squares	F
Sires of the Families	6	3,359.1	559.85	5.62***
Dams of the Families	16	27,110.2	1,694.38	16.99***
Breeding Groups of the Families	1	43.5	43.5	.44
Individuals	19	1,894.9	99.73	
Total	42	32,407.7		

***Very highly significant; $P < .005$

veals that the sires of the families as well as the dams of the families differ significantly in relation to the performance of their offspring. Furthermore, these data show that the age at breeding was influenced by the dams of the families to a larger extent than by the sires of the families. This confirms the general opinion that the age at breeding is affected by the maternal influence to a great degree.

Ovulation Rate.

The ovulation rate in each female was based on the valid assumption that the number of new corpora present on the ovaries at the time of slaughter represented the number of ova shed. One of the primary reasons for selecting the 55th day of gestation for the study of embryonic death loss was to minimize the experimental error in counting the corpora lutea. They are prominent at that stage of gestation and are distinctly larger than the corpora lutea of estrus and possess a characteristic fleshy color.

The ovulation rate in Landrace x Poland x Duroc gilts ranged from 8 to 17 with a mean of 11.69 ± 2.12. The ovulation rates classified by sires of the families are presented in Table 6. Statistical treatment of these data (Table 8) demon-

TABLE 8--ANALYSIS OF VARIATION IN OVULATION RATE AMONG LxPxD GILTS

Source of Variation	Degrees of Variation	Sum of Squares	Mean Squares	F
Sires of the Families	6	50.40	8.40	3.12**
Dams of the Families	16	52.25	3.89	1.45[1]
Breeding Groups	1	.25	.25	
Individuals	19	51.15	2.69	
Total	42	164.05		

**Highly significant with $P < .03$.

[1] $P < .25$.

strates that sires of the families were a significant source of variation ($P < .01$); whereas the dams of the families failed to vary significantly, although they did exhibit a tendency for genetic variation in relation to the ovulation rate of their offspring.

In view of the highly significant association of ovulation rate with the age of breeding ($r = .564$) the data were subjected to analysis of covariance with the means of ovulation rate adjusted for the variation in the age at breeding (Table 9). This technique brought an increase in the significance of variations

TABLE 9--ANALYSIS OF COVARIATION IN OVULATION RATE AMONG LxPxD GILTS AND TEST OF SIGNIFICANCE OF MEANS ADJUSTED FOR AGE AT BREEDING

Source of Variation	Degrees of Freedom	Sum of Squares & Products: Sum of x^2	Sum of xy	Sum of y^2	Errors of Estimate: Sum of Squares	Degrees of Freedom	Mean Square	F
Total	42	32,497.7	1035.5	164.05				
Sires of the Families	6	3,359.1	783.9	50.40				
Dams of the Families	16	27,110.2	966.3	62.25				
Individuals	20	1,938.4	-714.7	51.40	-212.24	19	-11.17	
Sires + Individuals	26	5,297.5	69.2	101.80	101.02	25		
Difference for testing adjusted sire group means					313.26	6	52.21	4.67***
Dams + Individuals	36	29,048.6	251.6	113.65	111.47	35		
Difference for testing adjusted dam group menas					323.71	16	20.23	1.81[1]

***Very highly significant with $P < .005$.

[1] $P < .10$.

(P<.005) in ovulation rate among the sires of the families. Although dams did not vary as much as sires there still was enough evidence to suggest a genetic explanation of this phenomenon.

Prenatal Mortality at 55 Days of Gestation.

The number of unaccounted ova at 55 days of gestation was considered as prenatal death loss, the accuracy of which depends to some extent upon the efficiency of fertilization. Individual prenatal mortality rates ranged from 0 to 11 with a mean of 3.49 ± 2.49. The high coefficient of variation of 71.3 percent indicated pronounced individual variation in prenatal mortality rate. The sires and the dams of the families were not significant sources of variation in the mortality rate (Table 10). However, analysis of covariance with means adjusted for con-

TABLE 10--ANALYSIS OF VARIATION IN PRENATAL MORTALITY RATE AMONG LxPxD GILTS

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Squares	F
Sires of the Families	6	50.23	8.37	1.24[N]
Dams of the Families	16	90.40	5.65	.84
Breeding Groups	1	12.06	12.06	1.78[1]
Individuals	19	128.11	6.74	
Total	42	280.8		

[N]Not statistically significant.
[1]$P < .25$.

stant breeding age and ovulation rate (Tables 11 and 12) demonstrated that the sires of the families were a major contributing source of variation (P<.025). The differences among dams approached significance when the mean mortality rates were adjusted for variation in the ovulation rate (Table 12).

Embryonic Survival Up to 55 Days of Gestation.

"Litter size" at 55 days of gestation was determined on the basis of the number of viable embryos recovered from the uterus at that stage. The mean embryonic survival in the 51 Landrace x Poland x Duroc gilts was 8.2 ± 2.38 with a range of 3 to 14. Here again, it appears as though there were no family variations in relation to the embryonic survival (Table 13). But with analysis of covariance for age of breeding, distinct family differences due to both the sires and the dams were found (Table 14) revealing the genetic nature of this primary component of fertility.

Breed Variations in Components of Fertility.

Table 15 presents a comparative picture of some of the reproductive potentialities and performances of the Landrace x Poland and Duroc breeds studied during 1956. No comparisons with the Landrace x Poland x Durocs are included in Table 15 since, in the author's opinion, there exists a possibility of

TABLE 11--ANALYSIS OF COVARIATION IN PRENATAL MORTALITY AMONG LxPxD GILTS AND TEST OF SIGNIFICANCE OF MEANS ADJUSTED FOR AGE AT BREEDING

Source of Variation	Degrees of Freedom	Sum of Squares & Products: Sum of x^2	Sum of xy	Sum of y^2	Errors of Estimate: Sum of Squares	Degrees of Freedom	Mean Square	F
Total	42	32,407.7	- 4.05	280.8				
Sires of the Families	6	3,359.1	126.85	50.2				
Dams of the Families	16	27,110.2	81.25	90.4				
Breeding Groups	1	43.5	- 22.85	12.1				
Individuals	19	1,894.9	-181.20	128.1	110.77	18	6.15	
Sires + Individuals	25	5,254.0	- 54.35	178.3	177.74	24		
Difference for testing adjusted sire group means					76.97	6	12.83	2.09[a]
Dams + Individuals	35	29,005.1	99.95	218.5	218.16			
Difference for testing adjusted dam group means					107.39	16	6.71	1.10
Breeding Groups + Individuals	20	1,938.4	204.05	140.2	118.72	34		
Difference for testing adjusted dam group means					7.95	1	7.95	1.29

[a]Approached significance with $P \ngtr .05$ and $< .10$.

TABLE 12--ANALYSIS OF COVARIATION IN PRENATAL MORTALITY RATE AMONG LxPxD GILTS AND TEST OF SIGNIFICANCE OF MEANS ADJUSTED FOR OVULATION RATE

Source of Variation	Degrees of Freedom	Sum of Squares & Products			Errors of Estimate			
		Sum of x^2	Sum of xy	Sum of y^2	Sum of Squares	Degrees of Freedom	Mean Square	F
Total	42	164.05	151.8	280.8				
Sires of the Families	6	50.40	19.4	50.2				
Dams of the Families	16	62.25	23.6	90.4				
Breeding Groups	1	.25	1.8	12.1				
Individuals	19	51.15	107.0	128.1	-95.7	18	-5.32	
Sires + Individuals	25	101.55	126.4	178.3	20.1	24		
Difference for testing adjusted sire group means					115.8	6	19.30	3.63**
Dams + Individuals	35	113.40	130.6	218.5	68.1	34		
Difference for testing adjusted dam group means					163.8	16	10.24	1.92[a]
Breeding Groups + Individuals	20	51.40	108.8	140.2	-90.1	19		
Difference for testing adjusted breeding group means					5.6	1	5.6	1.05

**Highly significant with $P < .025$.

[a]Approached significance with $P > .05$ and $< .10$.

TABLE 13--ANALYSIS OF VARIATION IN LITTER SIZE AMONG LxPxD GILTS

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Squares	F
Sires of the Families	6	38.6	6.43	.663
Dams of the Families	16	8.3	.52	.054
Breeding Groups	1	8.7	8.70	.897
Individuals	19	185.6	9.77	
Total	42	241.2		

TABLE 14--ANALYSIS OF COVARIATION IN LITTER SIZE AMONG LxPxD GILTS AND TEST OF SIGNIFICANCE OF MEANS ADJUSTED FOR AGE AT BREEDING

Source of Variation	Degrees of Freedom	Sum of Squares & Products			Errors of Estimate			
		Sum of x^2	Sum of xy	Sum of y^2	Sum of Squares	Degrees of Freedom	Mean Square	F
Total	42	32,407.7	1039.6	241.2				
Sires of the Families	6	3,359.1	657.3	38.6				
Dams of the Families	16	27,110.1	885.3	8.3				
Individuals	20	1,938.4	-503.0	185.6	55.0	19	2.89	
Sires + Individuals	26	5,297.5	154.3	224.2	217.7	25		
Difference for testing adjusted sire group means					162.7	6	27.11	9.38***
Dams + Individuals	36	29,048.6	382.3	193.9	188.9	35		
Difference for testing adjusted dam group means					133.9	16	8.37	2.90**

***Very highly significant with $P < .005$.

**Highly significant with $P < .01$.

TABLE 15--MEANS OF SOME COMPONENTS OF FERTILITY WITH BREED OR CROSS VARIATIONS

Trait	Breed or Cross: Duroc	Landrace x Poland
Ovulation Rate	8.7 ± .75	10.3 ± 1.34
Mortality Rate	2.1 ± 1.07	2.4 ± 1.84
Litter Size	6.6 ± 1.51	7.9 ± 1.66
Linear Capacity of the Uterus (mm.)	2396 ± 370	2610 ± 442
Weight of the Reproductive Tract (gms.)	6668 ± 1690	5445 ± 1163

confounded effects on the performance of Landrace x Poland x Duroc gilts investigated during 1955 due to seasonal variations.

Ovulation: The ovulation rate in Duroc gilts was 8.71 ± 0.75, whereas, Landrace x Poland had an average ovulation rate of 10.3 ± 1.34. Thus, a mean difference of 1.59 ova per gilt was statistically significant with $P<.05$ (Table 16). The mean ovulation rate in Landrace x Poland x Duroc gilts was 12.46 which indicates the possibility that heterosis was involved in the expression of this major component of fertility.

TABLE 16--MEAN SQUARES FROM ANALYSIS OF VARIANCE AND TEST OF SIGNIFICANCE BETWEEN LANDRACE x POLAND AND DUROCS

Trait	Mean Squares: Between	Within	F
Ovulation Rate	10.4	1.30	8.00*
Mortality Rate	.2	2.49	.08
Litter Size (55th Day Gestation)	7.3	2.57	2.84[a]
Linear Capacity of the Uterus	187,993	171,988	1.09
Weight of the Reproductive Tract	6,156,007	1,954,011	3.15[1]

*Significant with $P < .05$.

[a]Approached P at .10.

[1]Probability < .10.

Mortality: The mean mortality rate of 2.1 in Duroc gilts was not much lower than the loss of 2.4 pigs in Landrace x Polands. Nevertheless, this slightly lower rate of prenatal mortality coupled with lesser variation within the Durocs (S.D. 1.07) does indicate a tendency of lower incidence of embryonic death loss in the Duroc breed.

Litter size: The litter size in Duroc gilts was only 6.6 ± 1.51 as against 7.9 ± 1.66 in Landrace x Polands at the 55th day of gestation. This difference of 1.3 pigs per gilt was not statistically significant (Table 16). However, this observation lends confirmation to the superiority of crossbreds over purebreds in relation to litter size.

Capacity of the Uterus and Weight of the Reproductive Tract: Uteri of the Duroc gilts were more capacious and apparently more vascular than either those of the

Landrace x Polands or the Landrace x Poland x Durocs. The somewhat shorter uteri in Durocs with a mean linear capacity of 2396 ± 370 mm. compared to the mean capacity o 2610 ± 442 mm. in the crosses is contrary to the opinion that Durocs generally possess a more distended and more voluminous uterus than the Landrace x Poland and Landrace x Poland x Durocs. The relative weights of the reproductive tracts confirm the above observation. The mean weight of the reproductive tracts in Durocs was 6668 ± 1690 grams compared to a mean weight of 5445 ± 1663 grams in Landrace x Polands.

A close scrutiny of the data above suggests that the families established by the sires as well as the dams were significant sources of variation in relation to several components of fertility such as ovulation rate, mortality rate, and litter size. Furthermore, variations in ovulation, mortality, and litter size between breeds were observed in this study. Therefore, it would appear logical to conclude that physiological components of fertility are influenced and controlled by the genetic makeup of the animal. This observation is in agreement with those of earlier workers like Winters *et al.* (1935), Lush and Molln (1942) and Bradford *et al.* (1953) who indicated that the different breeds of swine were characterized by differences in litter size and that each breed tended to maintain its relative merit for prolificacy. These results emphasize the importance of the genetic factors as determinants of fertility in swine. This observation should be an important consideration in the evaluation of the results of anatomical, physiological or endocrinological investigations of reproductive processes.

Phenotypic Traits and the Reproductive Performance.

In order to explore the possibility and the extent of association between the measurable phenotypic traits and the reproductive potentialities and performance, simple and partial regression analyses were employed in this study.

Tables 17 and 18 summarize the means, standard deviations, simple correlations and regressions.

The ovulation rate was associated with the age at breeding as well as with the weight at breeding, with correlation values of 0.564 and 0.352 respectively, both values being highly significant. Also, age of gilts was highly correlated with litter size at 55 days of gestation ($r_{AL} = .310$); an increase of 10 days in age being associated with linear increases of 0.67 ova shed and 0.41 viable embryos at 55 days of gestation. The influence of age on the litter size was considerably minimized when ovulation rate was kept constant mathematically. It appears that the high association between age of gilts and litter size is primarily due to the age influence on the ovulation rate. However, the partial correlation and regression values ($r_{AL.O} = .125$; $b_{AL.O} = .019$) indicate that older gilts have a tendency to farrow larger litters irrespective of ovulation rate, which might be due to a better uterine environment.

Growth rate from 154 days of age to breeding time was negatively correlated with ovulation rate ($r = -.246$). The possibility that this association might be

TABLE 17--MEANS, STANDARD DEVIATIONS AND GROSS CORRELATION COEFFICIENTS FOR OVULATION RATE, EMBRYONIC MORTALITY AND LITTER SIZE AT 55 DAYS OF GESTATION IN LxPxD GILTS

Variables x	y	Correlation r_{xy}	Regression b_{xy}	Mean of x	Mean of y	Standard Deviation x	Standard Deviation y
Weight at 154 days (lb.)	Ovulation rate	.098	.010	173.2	11.69	21.21	2.12
	Mortality rate	.156	.018	173.2	3.49	21.21	2.49
	Litter size	.077	.009	173.2	8.20	21.21	2.38
Weight at breeding (lb.)	Ovulation rate	.352**	.047	206.0	11.69	15.96	2.12
	Mortality rate	.110	.017	206.0	3.49	15.96	2.49
	Litter size	.196	.029	206.0	8.20	15.96	2.38
Rate of gain from 154 days to breeding time (lb.)	Ovulation rate	-.246[a]	- .796	0.71	11.69	0.33	2.12
	Mortality rate	-.205	-1.576	0.71	3.49	0.33	2.49
	Litter size	.107	.781	0.71	8.20	0.33	2.38
Body length (mm.)	Ovulation rate	.038	.002	1053.8	11.69	35.81	2.12
	Mortality rate	-.074	- .005	1053.8	3.49	35.81	2.49
	Litter size	.111	.007	1053.8	8.20	35.81	2.38
Heart girth (mm.)	Ovulation rate	-.127	- .012	996.1	11.69	22.97	2.12
	Mortality rate	-.211	- .023	996.1	3.49	22.97	2.49
	Litter size	.107	.011	996.1	8.20	22.97	2.38

[a]Approaches significance.

**Highly significant with $P < .01$.

TABLE 18--MEANS, STANDARD DEVIATIONS AND GROSS CORRELATION COEFFICIENTS FOR OVULATION RATE, EMBRYONIC MORTALITY AND LITTER SIZE AT 55 DAYS OF GESTATION IN LxPxD GILTS

Variables x	y	Correlation r_{xy}	Regression b_{xy}	Mean of x	Mean of y	Standard Deviation x	Standard Deviation y
Average subcutaneous fat deposition (mm.)	Ovulation rate	.014	.007	37.23	11.69	4.62	2.12
	Mortality rate	.150	.082	37.23	3.49	4.62	2.49
	Litter size	-.145	-.175	37.23	8.20	4.62	2.38
Flank girth (mm.)	Ovulation rate	.063	.004	995.2	11.69	36.35	2.12
	Mortality rate	-.137	-.009	995.2	3.49	36.35	2.49
	Litter size	.201	.013	995.2	8.20	36.35	2.49
Age at breeding (days)	Ovulation rate	.564**	.067	197.9	11.69	17.89	2.12
	Mortality rate	.412**	.026	197.9	3.49	17.89	2.49
	Litter size	.310**	.041	197.9	8.20	17.89	2.38
Ovulation rate	Mortality rate	.481**	.572	11.69	3.49	2.12	2.49
	Litter size	.380**	.427	3.49	8.20	2.12	2.38
Mortality rate	Litter size	-.626**	-.593	3.49	8.20	2.49	2.38
Weight of ovaries (mm.)	Mortality rate	.003	.001	13.75	3.49	2.36	2.49
	Litter size	.056	.095	13.75	8.20	2.36	2.38
Weight of corpora	Ovulation rate	.511**	.757	6.50	11.69	1.44	2.12
	Mortality rate	.013	.023	6.50	3.49	1.44	2.49
	Litter size	.427**	.705	6.50	8.20	1.44	2.38

**Highly significant with $P < .01$.

due to the fact that the faster growing gilts were bred at an earlier age was ruled out by standard partial correlation and regression techniques. This procedure elaborated the extent and the nature of such an association ($r_{GO.A} = -.923$; $b_{GO.A} = -1.135$) which seems to indicate the desirability of controlled feeding and growth prior to the breeding period of the gilts. Even though significant correlation and regression coefficients cannot be demonstrated between body length, heart girth and flank girth and the components of fertility, such an association has a positive trend, with flank girth appearing to have more relative importance.

Total weight of all corpora per gilt was highly correlated with litter size ($r = .427$) and a 1-gram increase in corpora weight was associated with a linear increase of 0.705 viable embryos. On the basis of the standard partial correlation and regression coefficients ($r_{CL.O} = .293$; $b_{CL.O} = .520$) with mathematical adjustment for variation in the ovulation rate, it may be theorized that the heavier corpora lutea might be secreting greater amounts of progesterone and creating conditions conducive to lesser embryonic death loss and greater litter size. This observation is in agreement with the biochemical investigation of Gawienowski and Mayer (1956) who reported a significant correlation (+ .522) between the weight of the corpora and their progesterone content.

Relative Importance of the Components of Fertility.

It is logical that litter size was found to be highly associated with the number of ova shed ($r_{LO} = .380$) and the prenatal mortality rate ($r_{LM} = -.626$). Litter size was also correlated with the linear capacity of the uterus ($r_{LU} = .165$). However, these simple correlations carry the confounding effect due to the interrelationship among the number of ova shed, prenatal death loss and linear capacity of the uterus. As such, these simple correlations fail to reveal the relative merits of each of the primary components of fertility in their contribution to prolificacy in a polytocous mammal. Multiple regression analysis yielded the following results:

$b_{LO.MU} = .9798$
$b_{LM.OU} = .9965$
$b_{LU.OM} = .0006$

L = litter size; O = ovulation rate; M = mortality rate; U = linear capacity of the uterus.

βeta coefficient $b_{LO.MU} = .882$
βeta coefficient $b_{LM.OU} = -.1029$
βeta coefficient $b_{LU.OM} = .134$

An estimating equation for litter size would then become:

$$L = -1.3232 + .9798O - .9965M + .0006U$$

The above βeta-coefficients apparently show that prenatal death loss, number of ova shed and linear capacity of the uterus are important in that order and that they largely determine the litter size at 55 days of gestation.

Effect of the Number of Services on Fertility.

The 51 Landrace x Poland x Duroc gilts employed in this phase of the study during 1955 were served at or near the zero hour of their estrus. Forty-one of the gilts were allowed a second service within an interval of 16 to 20 hours after the first service. Fourteen of these 41 gilts were mated a third time about 16 hours after the second service. Through this procedure, 10 gilts were serviced once, 27 gilts were mated twice and 14 were mated three times. Each boar was assigned to a certain number of gilts at random and the subsequent services were repeated with the same boar.

Attention should be directed to the fact that the duration of estrus was not an influencing factor in determining the number of services, with the exception of 6 gilts in the three-services group which remained in heat for three and one-half days. As the prolificacy in a gilt is to a considerable extent dependent upon the number of ova shed, it is of considerable importance to show whether the selection of the gilts in each group has been truly random. Table 19 gives the numbers of ova shed, classified by the number of services during the heat period.

TABLE 19--MEANS AND COEFFICIENTS OF VARIATION IN OVULATION RATE, LITTER SIZE AND MORTALITY IN LxPxD GILTS CLASSIFIED BY SERVICE GROUPS

No. of Services	No. of Gilts Studied	Ovulation Rate		Litter Size		Mortality	
		Mean	C.V.	Mean	C.V.	Mean	C.V.
1	10	11.30	.145	6.80	.352	4.50	.482
2	27	11.52	.180	8.33	.233	3.18	.808
3	14	12.29	.203	8.86	.310	2.59	.755

The means of ovulation rate were 11.30 ± .145, 11.52 ± .180 and 12.29 ± .203 in one, two- and three-service groups, respectively. Variance analysis shown in Table 20 points to no significant differences in the ovulation rate between service groups, although there is a slight edge for the three-service group.

TABLE 20--ANALYSIS OF VARIATION IN OVULATION RATE AMONG LxPxD GILTS BETWEEN SERVICE GROUPS

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Squares	F
Number of Services	(2)	(7.03)	3.01	.66[N]
Single vs. Two and Three	1	1.87	1.87	.41[N]
Between Two and Three Services	1	5.16	5.16	1.14[N]
Individuals	48	217.96	4.54	
Total	50	224.99		

[N]Not statistically significant.

The mean prenatal mortality rate was 4.50 ± .48 in the single-service group, whereas the correseponding figures were 3.18 ± .81 and 2.59 ± .76 in the two- and three-service groups (Table 19). Variance analysis in Table 21 shows that this difference was not statistically significant. Nevertheless, a smaller prenatal

TABLE 21--ANALYSIS OF VARIATION IN PRENATAL MORTALITY AMONG L x P x D GILTS SERVICE GROUPS

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Squares	F
Number of Services	(2)	(12.72)	6.36	1.01[N]
Single vs. Two and Three Services	1	12.20	12.20	1.94[N]
Between Two and Three Services	1	.52	.52	.08
Individuals	48	302.03	6.29	
Total	50	314.75		

[N]Not statistically significant.

death loss of 1.32 and 1.91 pigs in two- and three-service groups over the single-service group would be of considerable economic value to the animal breeder. Further, statistical control of the variation in mortality due to the differences in age at breeding and ovulation rate (Tables 22, 23, 24 and 25) would seem to provide additional evidence of the superiority of two and three services over a single service during the estrous period.

Referring back to the litter size presented in Table 19, attention is drawn to a distinct advantage of 1.53 and 2.06 pigs per litter in two- and three-service groups, respectively, in relation to the single-service group. Variance analysis (Table 26) shows this difference was significant at the 5 percent level. However, theorizing as to the factors underlying this phenomenon, it might be that the significant difference in litter size is induced partly by the variations in age at breeding and in the ovulation rate among different service groups. Relevant statistical treatments appearing in Tables 27, 28, 29 and 30 illustrate the independent influence of a second service at an optimum period during estrus.

McKenzie and Miller (1930b) and McKenzie (1932) stated that matings made too early in the estrous period might be barren and recommended double services to procure larger litters. Haring (1937) recommended the second day, or about 24-40 hours after the beginning of estrus as the optimum period to breed sows. On the other hand, Krallinger and Schott (1933) concluded that there is no optimum service period in swine.

There certainly exists a higher probability of synchronization of the availability of fresh spermatozoa in the genital tract and the liberation of the ova in the two service group, when the second service is spaced 20 hours after the first service as was done in this investigation. However, this does not adequately explain the necessity of such synchronization, although the results suggest the desirability of an optimally-spaced second service.

Examination of the mean prenatal mortality rate (4.50 pigs) in the single service at zero hours estrus and a comparison with the mean prenatal mortality in two- and three-service groups (3.18 and 2.59 pigs, respectively) suggests a rational possibility that a good part of these embryonic death losses could have been due to failure of fertilization in the single service group. At the time of

TABLE 22--ANALYSIS OF COVARIATION IN PRENATAL MORTALITY AMONG LxPxD GILTS BETWEEN SIRES AND NUMBER OF SERVICES AND TEST OF SIGNIFICANCE OF MEANS ADJUSTED FOR AGE

Source of Variation	Degrees of Freedom	Sum of Squares & Products: Sum of x^2	Sum of xy	Sum of y^2	Errors of Estimate: Sum of Squares	Degrees of Freedom	Mean Square	F
Total	50	16,006.1	12.6	314.8				
Sire Groups	4	2,833.3	-211.6	29.9				
Service Groups	2	2,284.7	- 29.5	12.7				
Individuals	44	10,887.9	253.7	272.2	266.3	43	6.20	
Sires + Individuals	48	13,721.2	4.21	302.1	302.099			
Difference for testing adjusted sire group means					35.799	4	8.95	1.44
Services + Individuals	46	13,172.8	224.2	284.9	281.1			
Difference for testing adjusted services					14.3	2	7.15	1.15

TABLE 23--ANALYSIS OF COVARIATION IN MORTALITY AMONG LxPxD GILTS AND COMPARISONS BETWEEN THE NUMBER OF SERVICES WITH ADJUSTMENT FOR AGE AT BREEDING

Source of Variation	Sum of Squares of Products: Sum of x^2	Sum of xy	Sum of y^2	Errors of Estimate: Sum of Squares	Degrees of Freedom	Mean Square	F
Service Groups	(2,284.9)	(-29.5)	(12.7)				
Single vs. Two and Three Services	318.9	-62.3	12.2				
Two vs. Three Services	1,966.0	32.8	.5				
Individuals	10,887.9	253.7	272.2	266.3	43	6.20	
Single vs. Two and Three Services + Individuals	11,206.8	191.4	284.4	280.8			
Difference for Testing Adjusted Single vs. Two and Three Services				14.2	1	14.2	2.29[1]

[1] $P > .10$ and $< .25$.

TABLE 24--ANALYSIS OF COVARIATION IN PRENATAL MORTALITY AMONG LxPxD GILTS AND TEST OF SIGNIFICANCE OF MEANS ADJUSTED FOR OVULATION RATE

Source of Variation	Degrees of Freedom	Sum of Squares & Products			Errors of Estimate			F
		Sum of x^2	Sum of xy	Sum of y^2	Sum of Squares	Degrees of Freedom	Mean Square	
Total	50	224.99	129.2	314.8				
Sire Groups	4	22.00	18.4	30.3				
Service Groups	2	7.23	-3.0	12.7				
Individuals	44	195.76	113.8	271.8	205.6	43	4.78	
Sires + Individuals	48	217.76	132.2	302.1	211.9			
Difference for testing adjusted sire group means					16.3	4	4.08	.85
Services + Individuals	46	202.99	110.8	284.5	224.0			
Difference for testing adjusted service groups					18.4	2	9.20	1.92

TABLE 25--ANALYSIS OF COVARIATION IN PRENATAL MORTALITY RATE AMONG LxPxD GILTS AND TEST OF SIGNIFICANCE OF MEANS ADJUSTED FOR OVULATION RATE

Source of Variation	Sum of Squares & Products			Errors of Estimate			F
	Sum of x^2	Sum of xy	Sum of y^2	Sum of Squares	Degrees of Freedom	Mean Square	
Service Groups	(22.00)	(18.4)	(30.3)				
Single Service vs. Two and Three Services	1.87	-4.7	12.2				
Two vs. Three Services	20.13	23.1	18.1				
Individuals	195.76	113.8	271.8	205.6	43	4.78	
Single Service vs. Two and Three Services + Individuals	197.63	109.1	284.0	223.8			
Difference for Testing Adjusted Single vs. Two and Three Services				18.2	1	18.20	3.81[a]

[a] Approached significance at 5 percent level.

TABLE 26--ANALYSIS OF VARIATION IN LITTER SIZE AMONG LxPxD GILTS BETWEEN SERVICE GROUPS

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Squares	F
Number of Services	(2)	(26.09)	13.09	2.46[N]
Single vs. Two and Three Services	1	23.87	23.87	4.49*
Between Two and Three Services	2	2.22	2.22	.42
Individuals	48	255.32	5.32	
Total	50	281.41		

[N]Not significant

*Significant with $P < .05$.

TABLE 27--ANALYSIS OF COVARIATION IN LITTER SIZE AMONG LxPxD GILTS BETWEEN NUMBER OF SERVICES AND TEST OF SIGNIFICANCE OF MEANS ADJUSTED FOR AGE

Source of Variation	Degrees of Freedom	Sum of Squares & Products			Errors of Estimate			F
		Sum of x^2	Sum of xy	Sum of y^2	Sum of Squares	Degrees of Freedom	Mean Square	
Total	50	16,006.1	620.2	281.4				
Sire Groups	4	2,833.3	199.7	15.6				
Service Groups	2	2,284.9	157.2	26.1				
Individuals	44	10,887.9	263.3	239.7	233.4	43	5.43	
Sires + Individuals	48	13,721.2	463.0	255.3	239.7			
Difference for testing adjusted sire group means					6.3	4	1.58	.26[N]
Services + Individuals	46	13,172.8	420.5	265.8	252.4			
Difference for testing adjusted service group					19.0	2	9.50	1.75[1]

[N]Statistically not significant.

[1]$P < .25$.

TABLE 28--ANALYSIS OF COVARIATION IN LITTER SIZE AMONG LxPxD GILTS AND COMPARISONS BETWEEN THE NUMBER OF SERVICES WITH ADJUSTMENT FOR AGE AT BREEDING

Source of Variation	Sum of Squares of Products: Sum of x^2	Sum of xy	Sum of y^2	Errors of Estimate: Sum of Squares	Degrees of Freedom	Mean Square	F
Service Groups	(2,284.9)	(157.2)	(26.1)				
Single vs. Two and Three Services	318.9	86.7	23.6				
Two vs. Three Services	1,966.0	70.5	2.5				
Individuals	10,887.9	263.3	239.7	233.4	43	5.43	
Single vs. Two and Three Services + Individuals	11,206.8	350.0	263.3	252.4			
Difference for Testing Adjusted Single vs. Two and Three Services				19.0	1	19.00	3.5[a]
Two vs. Three Services + Individuals	12,853.9	333.8	242.2	233.53			
Difference for Testing Adjusted Two vs. Three Services				.13	1	.13	.02

[a] $P < .10$ and $> .05$.

fertilization the spermatozoa introduced at the onset of estrus must have been 24 to 36 hours old, if not older, and their fertilizing capacity may have been impaired due to 'staleness' associated with partial loss of motility, resulting in the lower litter size of 6.80 pigs per gilt. On the other hand, a second service at about 16 to 20 hours after the onset of estrus apparently provided sufficient fresh spermatozoa to insure larger litter size (8.33 pigs per gilt). This increase in litter size could be due either to a higher rate of fertilization or lesser embryonic death loss or both.

The fact that there was no significant difference in the fertility between two and three services suggests that a third service would not be necessary provided the second service was permitted about 20 hours after the onset of estrus.

Effect of Boar on Fertility of Gilts Bred to Him.

Statistical treatments of the fertility as recorded in Tables 22, 24, 27 and 29 clearly demonstrate that the boar does not influence the prenatal death loss or the litter size of the litters he sires. This observation is in agreement with the findings of earlier workers (Oestermeyer, 1934; Langlet, 1934; Schmidt, 1937). These observations and other evidence referred to show that the importance of the boar lies in his ability to transmit factors requisite for good fertility to his daughters, and that a boar of normal fertility has no influence whatsoever on the performance of the gilt or sow mated to him.

TABLE 29--ANALYSIS OF COVARIATION IN LITTER SIZE AMONG LxPxD GILTS AND TEST OF SIGNIFICANCE OF MEANS ADJUSTED FOR OVULATION RATE

Source of Variation	Degrees of Freedom	Sum of Squares & Products: Sum of x^2	Sum of xy	Sum of y^2	Errors of Estimate: Sum of Squares	Degrees of Freedom	Mean Square	F
Total	50	224.99	95.8	281.41				
Sire Groups	4	22.00	3.6	15.56				
Service Groups	2	7.23	10.3	26.11				
Individuals	44	195.76	81.9	239.74	205.48	43	4.78	
Sires + Individuals	48	217.76	85.5	255.30	221.73			
Difference for testing adjusted sire group means					16.25	4	4.06	.85
Services + Individuals	46	202.99	92.2	265.85	223.97			
Difference for testing adjusted service group means					18.49	2	9.24	1.93

TABLE 30--ANALYSIS OF COVARIATION IN LITTER SIZE AMONG LxPxD GILTS AND TEST OF SIGNIFICANCE OF MEANS ADJUSTED FOR OVULATION RATE

Source of Variation	Sum of Squares & Products: Sum of x^2	Sum of xy	Sum of y^2	Errors of Estimate: Sum of Squares	Degrees of Freedom	Mean Square	F
Service Groups	(7.23)	(10.3)	(26.11)				
Single vs. Two and Three Services	1.87	6.6	23.60				
Two and Three Services	5.36	3.7	2.51				
Individuals	195.76	81.9	239.74	205.48	43	4.78	
Single vs. Two and Three Services + Individuals	197.63	88.5	263.34	223.71			
Difference for Testing Adjusted Single vs. Two and Three Service Groups				18.23	1	18.23	3.81[a]

[a]Approached significance at the 5 percent level.

Migration of Fertilized Ova.

The fertilized ova are distributed somewhat equally within the available intra-uterine space. This fairly equal distribution of ova is accomplished by the peristaltic action of the uterine musculature. Both uterine horns might act as a continuous tube to facilitate the migration of ova in either direction.

Migration of the fertilized ova has a highly beneficial value in the polytocous mammals, more so in swine. It is imperative that the individual embryos of the large litters shall find a fair share of the space within the uterus, apparently to assure adequate nutrition for the developing embryo. Migration of the fertilized ovum from one horn to the other is assumed if the number of embryos carried in any one horn exceeds the relative number of corpora on the corresponding ovary. Such an assumption can be confounded by the existence of polyovular follicles or twinning. But, such phenomena are very rare and seldom occur in sufficient numbers to provide an explanation for the high frequency of migration.

Table 31 illustrates the number of fertilized ova which migrated, the direction of migration, and the frequency of such migrations. Of the total population of 68 pregnant gilts employed in this study, migration was recorded in 21 instances (30.9 percent). There is a preponderance of migration from the left to the right horn as assessed by this happening in 16 of 21 gilts (76.2 percent) whereas, in only five instances did the ova migrate from the right to the left horn. Examination of Table 31 shows that migration in some instances appears to have assumed considerable proportions involving as many as 4 and even 5 embryos.

Abnormalities of the Reproductive Tracts.

Relatively few reproductive tracts with abnormalities were encountered in a population of 145 females employed in this study. Two cases of cystic ovaries were observed; there was only one embryo in the right horn of one of these gilts, probably representing the one corpus luteum adjacent to a big cyst present on the right ovary of this female. In the other gilt the right horn was without any embryos although there were six corpora lutea on the right ovary. In this case the cysts were of a small, diffused type and appeared to exert an adverse effect on the function of the corpora lutea as judged by their morphological features.

Two cases of adhesions involving ovaries, Fallopian tubes and uterine horns were observed. Two gilts failed to come into estrus over a long period of observation. On slaughter, it was revealed that one possessed infantile genitalia; the other had a considerable hypermia and congestion of the entire reproductive tract, particularly the Fallopian tubes and the ovaries. The only other abnormality encountered in this study was a single case of blocked cervix.

TABLE 31--MIGRATION OF THE FERTILIZED OVA

	Right Uterine Horn			Left Uterine Horn		
Gilt No.	No. of Embryos in Excess of No. of C.L.	C.L. No.	No. of Embryos	No. of Embryos	C.L. No.	No. of Embryos in Excess of No. of C.L.
			Landrace x Poland x Duroc			
80	1	0	1	2	9	-
533	5	1	6	3	8	-
94	-	12	3	2	0	2
391	3	1	4	4	10	-
543	-	7	4	6	4	2
454	2	2	4	3	11	-
544	4	0	4	5	9	-
541	2	1	3	5	11	-
51	2	4	6	5	7	-
6	4	3	7	5	10	-
93	1	5	6	3	6	-
400	1	3	4	6	10	-
532	2	1	3	4	8	-
53	-	11	2	4	1	3
340	-	8	5	6	5	1
452	1	4	5	3	6	-
110	3	1	4	5	9	-
			Landrace x Poland			
223	1	1	2	2	10	-
252	2	1	3	4	9	-
380	1	4	5	3	5	-
			Duroc			
73	-	7	3	3	1	2

CONCLUSIONS

The variations in ovulation, mortality, litter size and other related reproductive phenomenon between breeds and families within breeds were given thorough consideration in this study. Results suggested that the physiological components of fertility were greatly influenced by the genetic make-up of the animal. This observation should be an important consideration for the future evaluation of physiological, biochemical and endocrinological investigations of the complex reproductive process.

Live body weight does not necessarily reflect the functional stage of the reproductive organs; age of the gilts provides a more reliable picture of the reproductive development. Age at breeding is affected by the maternal influence to a great degree. Three or more services during the heat period served no useful purpose provided the second service was permitted about 20 hours after the onset of the estrus. Controlled feeding and controlled gains in weight of gilts prior to breeding operations contributed to more efficient reproductive performance. Embryonic mortality was the major factor limiting the reproductive performance and a therapeutic approach to this problem may not be beyond the realm of modern scientific progress.

APPLICATION OF RESULTS

Litter size at farrowing is one of the most important economic traits in swine. For this reason a study was made of some of the factors responsible for small litter size in gilts of various breeds and crosses.

Several points of practical interest are suggested by the results of this study and certain recommendations may be made to swine breeders for improving litter size in swine. It is not advisable to breed gilts too young because in this study an increase in 10 days in age resulted in 0.67 more eggs shed and in 0.41 more embryos present in the uterus at mid-pregnancy. Older gilts also tended to have larger litters, even when adjustments were made to remove variations due to ovulation rate. Possibly older gilts supply a more suitable uterine environment for their offspring than younger gilts.

Gilts should not gain rapidly in weight just prior to breeding. In the study, those which made faster gains tended to shed fewer eggs. Limited feeding and slower gains just prior to breeding may be desirable, although under no circumstances should gilts be placed on a starvation diet at this time.

Two services, 16 to 20 hours apart, are recommended to the swine breeder. In this study, a second service within 16 to 20 hours after the first srevice resulted in an increase of 1.53 pigs per litter at mid-pregnancy. A third service 16 hours after the second improved litter size very little and did not seem justifiable.

Results obtained in this study do not support the claims of breeders that some boars sire larger litters than others. In this investigation it was found that a boar of normal fertility had no influence on the reproductive performance of gilts mated to him, but his importance is manifested in his ability to transmit the genetic make-up for fertility to his daughters.

Distinct family differences in some components of fertility due to both the sires and the dams were found showing the genetic nature of reproductive potentialities. Crossbreds were superior to purebreds in relation to litter size.

Embryonic mortality was found to be the major limiting factor of prolificacy. Therapeutic approach at certain critical stages of gestation to improve the intra-uterine environment and the practice of family selection are recommended for further research.

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