RESEARCH BULLETIN 615 SEPTEMBER, 1956

UNIVERSITY OF MISSOURI COLLEGE OF AGRICULTURE

AGRICULTURAL EXPERIMENT STATION

J. H. LONGWELL, Director

Genetic and Environmental Factors Affecting Litter Size in Swine

V. RATHNASABAPATHY, J. F. LASLEY, D. T. MAYER

(Publication authorized September 28, 1956)

COLUMBIA, MISSOURI

ABSTRACT

The relative importance of ovulation rate, embryonic or fetal mortality and litter size at mid-pregnancy and some of the genetic and environmental factors associated with litter size were investigated. Although several factors were associated with embryonic or fetal mortality, only a few could be assigned the role of being the immediate cause or causes. A higher ovulation rate did not always result in a larger number of fetuses at mid-pregnancy. Evidence was obtained that overcrowding in the uterus or a primary or secondary uterine deficiency was the most important and immediate cause of fetal mortality. Some other causes of mortality such as nutrition of the dam, presence of bacteria in the reproductive tract, fusion of chorions or innate deficiencies in the embryos and fetuses seemed to be negligible in magnitude as compared to uterine capacity or to possible uterine deficiencies. A significant positive correlation of mortality rate with backfat thickness in gilts at 200 pounds was of interest but may have been a mere association rather than a cause and effect phenomenon.

Families established by sires were significant sources of variation ($P < .05$) in ovulation rate, litter size and fetal mortality. These were still a highly significant source of variation in mortality rate even after adjustments were made for variations in breeding age of the gilts and the number of ova shed. This suggests at least a partial genetic influence on the whole reproductive process.

Measures which should be helpful in the selection of breeding stock with a greater uterine capacity and/or a more desirable uterine environment were discussed.

TABLE OF CONTENTS

Genetic and Environmental Factors Affecting Litter Size in Swine

V. Rathnasabapathy, J. F. Lasley, D. T. Mayer

INTRODUCTION

The swine industry occupies an important place in the livestock world of today. Cost of production on hogs is relatively high due to the use of expensive concentrates for the major part of their subsistence. Cheap roughages are of only of limited value in hog feeding because of the anatomical and physiological peculiarities of their digestive system.

In view of these facts, the success of a swine enterprise is largely governed by the size of the litter delivered at birth and the number of pigs successfully reared to marketable weight. In practice, it is generally considered uneconomical to rear litters of less than seven pigs to marketable age. To rear at least seven pigs from a sow, litter size at birth has to be in excess of that number to offset unavoidable post-partum losses. These lossses reflect the fertility of the sow, her ability to raise pigs and the capacity of the pigs for growth.

Litter size objectives can be accomplished when the physiological factors concerned in reproduction, and the complex relationships of the various hormones associated with genital physiology are ascertained and understood. Further, the application of improved systems of breeding and skillful selection of breeding stock on the basis of such information will be necessary. Genetic progress is dependent, primarily, on the extent to which such characteristics are hereditary and the degree to which hereditary effects can be recognized in the presence of the masking effects of the environment.

The study presented herein was initiated (1) to determine the genetic and environmental factors associated with ovulation, embryonic mortality, and litter size in swine; (2) to ascertain the absolute measure of the relationship of ovulation and related reproductive phenomena with the phenotypic characteristics of the individual, such as body measurements, growth rate, and back fat thickness; (3) to determine and discuss the relative importance of factors that effect litter size; and (4) To suggest, on the basis of the findings, measures that will help to secure a larger litter size.

This bulletin reports on Department of Agricultural Chemistry Research Project 223, "Reproductive Physiology," and Department of Animal Husbandry, 222, "Swine Improvement."

REVIEW OF LITERATURE

In the past two decades much has been accomplished under swine breeding research programs with a major objective of securing a larger litter size. Hammond (1921) indicated that fertility in mammals was largely controlled by (1) the number of ova shed, (2) the number of ova fertilized and (3) the number of embryos which developed normally to birth. He mentioned that the factors controlling the number of eggs which develop to reach birth have the greatest influence in domestic animals. Several investigators, especially Corner (1921, 1923) and Hammond (1914, 1921), have shown that atrophy of embryos in the pig is a common occurrence and may assume considerable proportions. Other workers have demonstrated the causes underlying the embryonic atrophy. Reduced fecundity in the pig can be seasonal (Machens, 1915), can be due to poor management after conception (McKenzie, 1928), or to avitaminosis A (Hughes, Aubel and Lienhardt, 1928), or to age (Sinclair and Syrotuck, 1928).

Heredity

The constancy of litter size in different breeds of swine, reported by several workers, gives at least a partial explanation of this phenomena, although it is strongly influenced by environmental conditions. Heritability estimates of litter size ranging from 10 to 44 percent, but most of them lying between 10 and 20 percent, have been cited in reports from the various swine breeding research projects in the United States (Craft, 1953).

Type

There are conflicting reports in the literature on the use of type as a measure of predictability for litter size. To arrive at a clear decision, litter size needs to be correlated with type based on actual measurements of the body rather than with type measured on an arbitrary scale such as large, medium, and small.

Breeding Age

Stewart (1945) demonstrated that the size of the first litter increased in a curvilinear fashion with the age of the dam to about 15 months, with most of the increase taking place between the ages of 9 to 12 months. Wiggins *et al.* (1950) observed that gilts which conceived at the third heat period farrowed 1.4 more pigs than gilts which conceived at the second heat and 2.5 more pigs than those which conceived at the first heat. There is, apparently, an optimum age to breed young animals for the first time, which is likely to vary from breed to breed.

Number of Services

Weaver and Bogart (1943) found more pigs per litter in gilts bred twice during the heat period than in gilts bred only once. But Squiers, *et al.* (1952) reported results that gave little indication that a second service, 24 hours after the first, would increase the size of the litter, although it raised the conception rate by 23 percent.

Uterine Capacity

Overcrowding of embryos or primary or secondary uterine deficiencies have been considered as the chief causes of embryonic mortality by several workers. Corner (1921, 1923) thought that overcrowding was an important, but not the only factor, in causing embryonic mortality in the pig and his view was supported by Burger (1952).

Cumulative evidence from work at the Missouri station (Squiers, *et al.*, 1952; Lerner, 1951) shows that embryonic mortality, the major factor which governs the litter size, is due to a multiplicity of causes. It is a question of the relative importance of each cause rather than any one being absolutely responsible.

MATERIALS AND METHODS

Experimental Animals

The 95 gilts and 8 boars used in this study were maintained at the Missouri experiment station, in co-operation with the swine breeding laboratory. The gilts were crosses between Landrace and Poland breeds (Figure 1). The boars were Landrace x Poland crossbreds, purebred Duroc, or Landrace. The animals used for the study of litter size were born during the period between February 28 and March 27, 1954. Tables 1 to 3 list the number of animals used at different stages in different groups.

Fig. 1—Some of the Landrace x Poland gilts used in this study.

TABLE 1 -- NUMBER OF GILTS STUDIED AT DIFFERENT STAGES OF THE EXPERIMENT

Stage	Number of gilts studied
At maturity	24
At 55 days of gestation	44
At parturition	27
TOTAL	95

TABLE 2 -- FEMALES STUDIED AT THE 55TH DAY OF GESTATION BY SIRE GROUPS

Sire group	Number of gilts studied
Landrace 3	3
Landrace 5	2
Landrace 8	4
Landrace 105	3
Landrace 333	3
Landrace 149	4
Poland 92	4
Poland 93	3
Poland 175	4
Poland 295	6
Poland 296	4
Poland 305	2
Total	42

TABLE 3 ---FEMALES STUDIED AT 55 DAYS OF GESTATION BY SERVICE GROUPS

No. of services*	Number of gilts studied
Single	25
Two at an interval of 24 hours	17
Total	42

*Dependent on the number of days in heat.

Procedure

The methods used in this study were designed to determine the exact age at puberty, to measure the genetic and environmental influences on litter size at 55 days of gestation, and to estimate the embryonic mortality from 55 days to parturition. Hence, the experiment was conducted in three stages: (1) at maturity, (2) at mid-term, and (3) at farrowing.

The first group of gilts were killed when they reached approximately 200 pounds, live body weight. Their reproductive organs were examined for signs of maturity. Gilts which had ovulation points or freshly formed corpora were classified as mature. The pubescent age was calculated from the birth date and the maturity date. In addition, the reproductive organs were measured to determine the changes effected as a result of maturity.

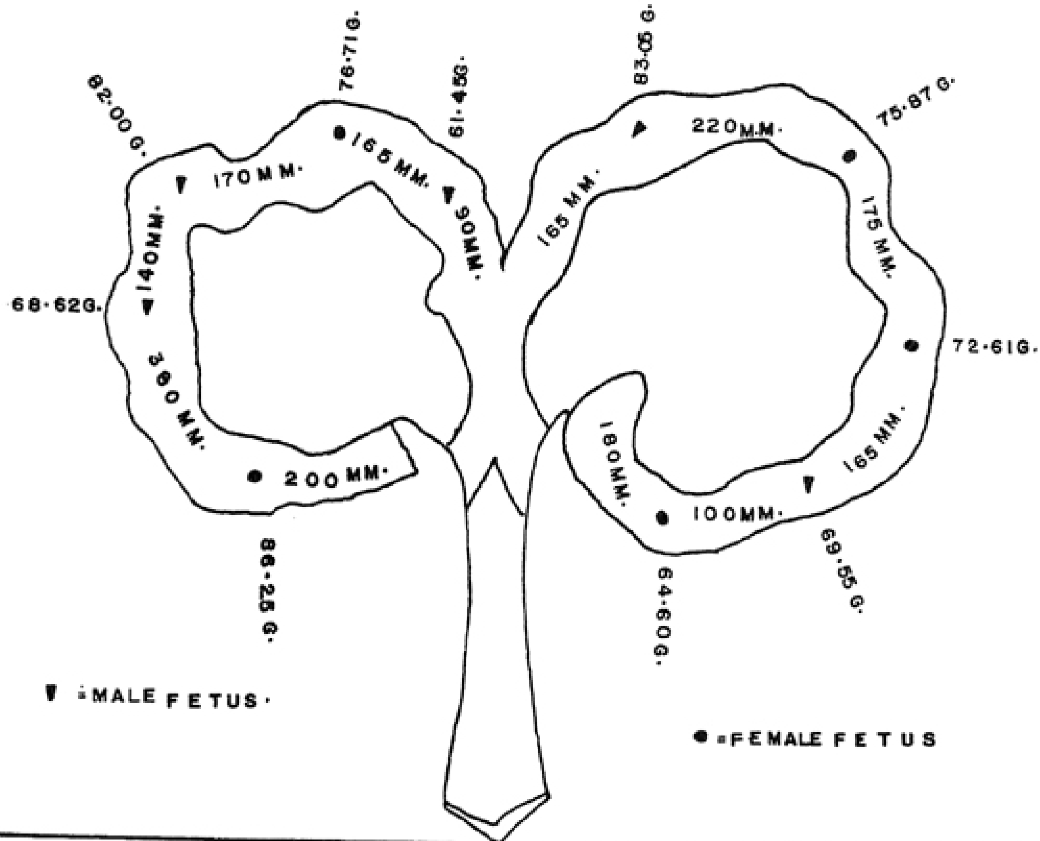
The second group received the maximum treatment in this study. After they had attained 200 pounds of live body weight, they were turned out with the boars, once daily, to check for estrus and to main-

GROUP NO. I TREATMENT. NIL

NO. OF SOW AND BREEDING. LANDRACEX POLAND 272

DATE BRED. 9-8-1954.

DATE SLAUGHTERED. 11-3-1954.



	I	II	III
LENGTH OF VAGINA INSIDE	435 MM.		
OVARY RIGHT	8.56 G.		
OVARY LEFT	4.62 G.		
CORPORA RIGHT	8	5.38 G.	
CORPORA LEFT	3	2.14 G.	
EMBRYOS VIABLE RIGHT	5		
EMBRYOS VIABLE LEFT	5		
EMBRYOS DEGENERATING RIGHT	—		
EMBRYOS DEGENERATING LEFT	—		

FIG. 2. RECORD SHEET FOR THE STUDY OF REPRODUCTIVE ORGANS OF GILTS.

Fig. 2—Record sheet for the study of reproductive organs of gilts.

tain breeding records. Those which did not repeat the heat period for a second time were slaughtered on or near the 55th day of gestation for a study of litter size. In those gilts which repeated the heat period, the gestation period was calculated from the time of the last fertile mating. The gilts which did not settle during two heat periods were slaughtered and observations were made for possible abnormalities.

Soon after slaughter the reproductive tracts were examined to provide the following information: (1) length of vagina, (2) length of right and left horns of the gravid uterus, (3) length of the right and left fallopian tubes, (4) weights of the ovaries, (5) number and individual weights of corpora lutea in each ovary, (6) viable embryos in each horn, (7) length and weight of individual embryos, and (8) distance between the embryos. To assure accuracy the corpora were dissected out separately. Every gilt was assigned a chart and the full information was recorded as shown in Figure 2 for further critical studies.

The following characteristics were studied in relation to ovulation, fetal mortality, and litter size: (1) birth weight, (2) weaning weight, (3) 154 day weight, (4) weight at 55 days of gestation, (5) body measurements (length, chest, and flank) at 200 pounds and at 55 days of gestation, (6) back fat (shoulder, hip and ham) at 200 pounds and at mid-pregnancy, (7) age at breeding, (8) average daily gain from weaning to 200 pounds and from 200 pounds to the time of slaughter, (9) weight of corpora, (10) weight of ovaries, (11) length of uterus and (12) spacing of embryos in the uterus.

The third group of gilts was allowed to go to term and, from the litter size obtained, an estimate of the fetal mortality from 55 days to parturition was calculated.

Measurements

The length of body was measured along the back from the base of the ears to the base of the tail. The heart girth was measured around the body in the region of the axilla and the flank girth, around the body in the region of the flank. The measurements were taken in millimeters by a steel tape. Back fat thickness was taken in two places on either side of the vertebral column in the region of the shoulder (about the third or fourth costo-vertebral junction), hip (in front of the aitch bone) and ham (mid-way between the aitch bone and base of the tail). Averages for each region and total back fat averages were used for calculations.

Explanation of Terms

In the present study, ovulation rate is always based on the number of functional corpora present in both ovaries, litter size on the number of apparently normal and healthy fetuses with no signs of atrophy, and fetal mortality on the number of corpora lutea that are not represented by live fetuses. Uterine space occupied by the fetus is the sum of the distances half way between the fetus in question and the one in front and half way between the former and the one behind. The fetuses at the extreme ends of the horns were not used in this phase of the study.

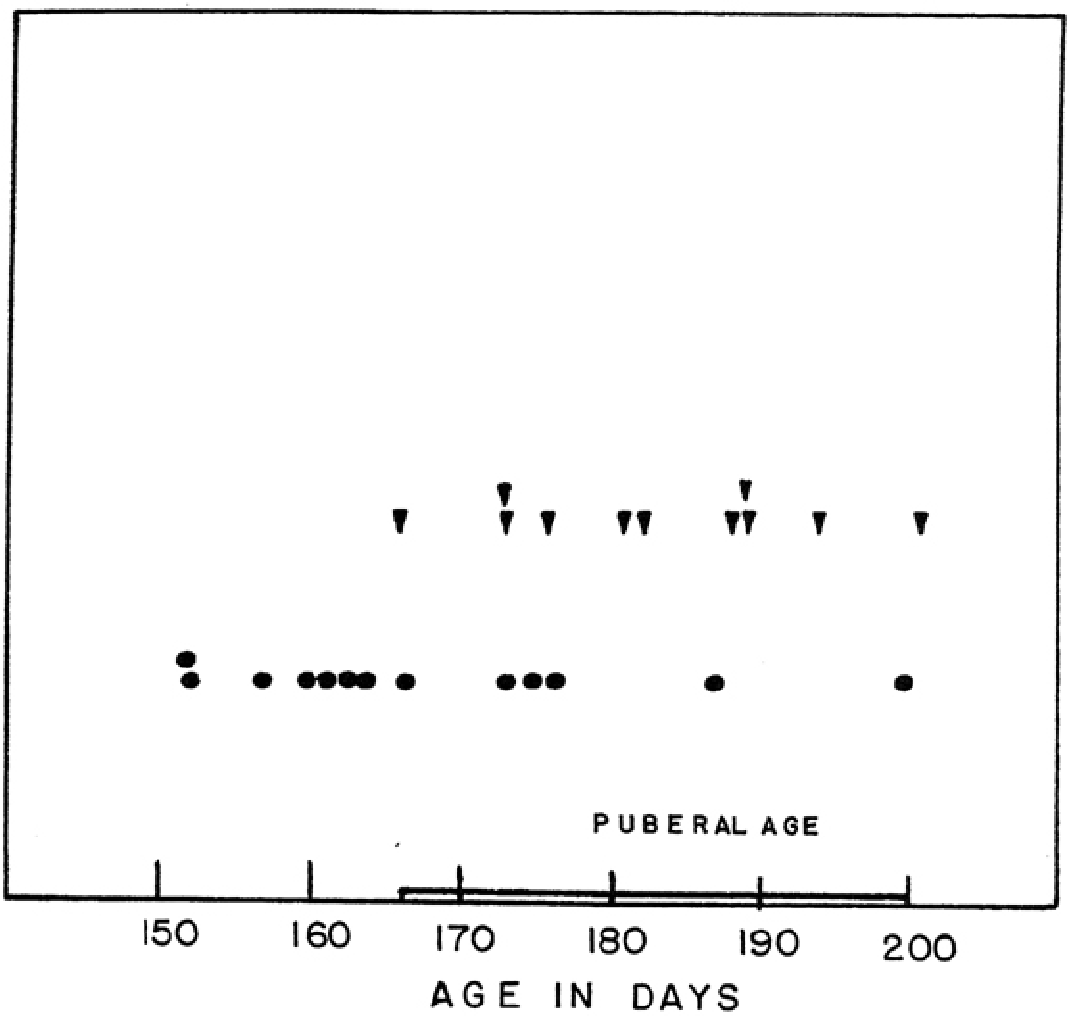
Analysis of Data

Group comparisons, correlations, regression coefficients, analysis of variance and covariance, and tests of significance were worked out by methods described by Snedecor (1950).

RESULTS

Age at Puberty

Twenty-four Landrace x Poland gilts provided data for this study. Of the twenty-four, 13 had no visible ovulation points or corpora lutea



● = IMMATURE GILT; ▼ = MATURE GILT.

Fig. 3—Diagram illustrating the puberal age in Landrace x Poland gilts.

in their ovaries: the reproductive tracts being normal without any sign of maturity. The age of these gilts ranged from 152 to 200 days with a mean of 168 and a standard deviation of 13.4. The ovaries of the remaining 11 gilts had either ovulation points or freshly formed corpora, which were judged to be from one to four days old from their morphological appearance. The uterus was larger and longer in these gilts, with an apparent increased water content and the endometrium was a rosy red color marked with streaks of capillaries. The number of corpora averaged 8.6 ± 2.3 per gilt. The age of these mature gilts ranged from 166 to 201 days with a mean of 182.9 and a standard deviation of 10.4.

Figure 3 illustrates the distribution of the mature and immature gilts on the age scale. When the overlapping of the ages of these two groups is taken into consideration, the pubescent age lies between 166 and 200 days with a mean of 183 days.

Growth Following Puberty

The reproductive organs showed an enormous growth following maturity. The data on the length of the reproductive tract; the weight of the ovaries before puberty, immediately following puberty, and at mid-term of pregnancy; and the relative growth of the ovaries in comparison to the premature stage appear in Table 4. The average length of the vagina, which was 284.8 mm. before maturity, measured 321.8 mm. immediately after maturity and 463.0 mm. at 55 days of gestation, representing an increase of 13.0 percent and 62.6 percent during the two periods. Corresponding increases in growth for the right and left horn of the uterus and the whole uterus were 104.7 percent, 106.9 percent, and 105.8 percent respectively, following puberty and were 282.5 percent, 300.9 percent and 291.8 percent respectively, at 55 days of gestation.

TABLE 4 -- MEASUREMENTS OF THE REPRODUCTIVE TRACTS OF LANDRACE X POLAND GILTS BEFORE AND AFTER MATURITY

Protion of the tract	Before maturity (around 168 days)	After maturity (around 183 days)	Increase percent	At 55 days of gestation	Increase percent
Vagina	284.8 mm.	321.8 mm.	13.0	463.0 mm.	62.6
Right horn	368.0 mm.	753.8 mm.	104.7	1407.5 mm.	282.5
Left horn	373.5 mm.	772.7 mm.	106.9	1497.3 mm.	300.9
Uterus	741.5 mm.	1525.9 mm.	105.8	2904.8 mm.	291.8
Right ovary	2.54 G.	4.14 G.	63.0	7.96 G.	213.4
Left ovary	2.96 G.	4.80 G.	62.0	8.75 G.	195.6

The right and left ovaries weighed 2.54 gm. and 2.96 gm. before maturity, 4.14 gm. and 4.80 gm. after maturity, and 7.96 gm. and 8.75 gm. at 55 days of pregnancy. The percentage increases were 63.0 and 62.0 during the mature non-pregnant stage and 213.4 and 195.6 during mid-pregnancy.

The left horn of the uterus, which was longer than the right before maturity, maintained its superiority even after maturity and also at the 55th day of pregnancy. This was also true for the weight of the left ovaries.

Age at Breeding

Age at breeding for the 42 Landrace x Poland gilts ranged from 176 to 240 days, with a mean of 202.1 ± 16 days. The age for the different sire groups is given in Table 5. Analysis of age at breeding (Table 6) shows that neither the sires nor the breed groups of sires were a significant source of variation.

TABLE 5 -- MEAN AGE AT BREEDING OF LANDRACE X POLAND GILTS BY SIRE GROUPS

Sire group	Number of gilts studied	Mean age at breeding in days
Landrace 3	3	206.0
Landrace 5	2	202.5
Landrace 8	4	197.0
Landrace 105	3	197.3
Landrace 333	3	206.0
Landrace 149	4	199.2
Poland 92	4	203.8
Poland 93	3	197.7
Poland 175	4	204.8
Poland 295	6	208.7
Poland 296	4	196.0
Poland 305	2	203.5

TABLE 6 -- ANALYSIS OF VARIANCE FOR BREEDING AGE OF LANDRACE X POLAND GILTS

Source of variation	Degrees of freedom	Sum of squares	Mean square	F
Sire groups	11	805.5	73.23	.220*
Breed groups of sires	1	45.6	45.60	.137*
Individuals	29	9665.5	333.29	
Total	41	10516.6		

*Not significant

Ovulation Rate

Information on ovulation rate was provided by 42 gilts which averaged 13.4 ± 2.5 ova, with a range from 10 to 21. The means for the sire groups and service groups are given in Tables 7 and 8. The average of 13.7 for gilts which had two services at 24-hour intervals during the heat period was, however, not significantly different from the single service

TABLE 7 -- MEAN OVULATION RATE IN LANDRACE X POLAND GILTS BY SIRE GROUPS

Sire group	Number of gilts studied	Mean Number of corpora in the ovaries
Landrace 3	3	15.3
Landrace 5	2	12.0
Landrace 8	4	15.0
Landrace 105	3	15.0
Landrace 333	3	11.7
Landrace 149	4	13.5
Poland 92	4	14.8
Poland 93	3	12.3
Poland 175	4	13.5
Poland 295	6	11.5
Poland 296	4	13.8
Poland 305	2	11.5

TABLE 8 -- MEAN OVULATION RATE IN LANDRACE X POLAND GILTS BY SERVICE GROUPS

Number of services	Number of gilts studdied	Mean ovulation rate	T
Single	25	13.1	
Two at an interval of 24 hours	17	13.7	.776*

*Not significant.

TABLE 9 -- ANALYSIS OF VARIANCE FOR OVULATION RATE IN LANDRACE X POLAND GILTS

Source of variation	Degrees of freedom	Sum of squares	Mean square	F
Sire groups	11	81.9	7.44	1.34*
Service groups	1	3.5	3.50	.63*
Individuals	29	160.2	5.52	
Total	41	245.6		

*Not significant.

group mean of 13.1. Analysis of data gave an overall impression that the sires and the number of services were not significant sources of variation (Table 9). But, when the means for ovulation rate were adjusted to a constant breeding age by the covariance technique, the variation due to sires became increasingly significant, nearing the probability level of 0.05 (Table 10).

Factors Related to Ovulation Rate

The association of ovulation rate with weaning weight, 154-day weight, and with breeding age was positive and significant as shown in Figures 4, 5, and 6 ($P < .05$). For every 1 pound increase in weaning weight and in 154-day weight 0.127 and 0.045 more ova were produced, respectively. Every 10 days increase in the breeding age resulted in 0.48 more ova being shed by the gilts. Ovulation rate was also highly corre-

TABLE 10 -- ANALYSIS OF COVARIANCE FOR OVULATION RATE IN LANDRACE X POLAND GILTS AND TEST OF SIGNIFICANCE OF MEANS ADJUSTED FOR AGE

Source of variation	Degrees of freedom	Sum of squares and products			Errors of estimate			
		Sum of x^2	Sum of xy	Sum of y^2	Sum of squares	Degrees of freedom	Mean squares	F
Total	41	10517.0	509.0	245.6				
Sire groups	11	805.9	-119.7	81.9				
Service groups	1	1975.7 *	83.2	3.5				
Error	29	7735.4	545.5	160.2	121.7	28	4.3	
Service error	30	9711.1	628.7	163.7	123.0	29		
Difference for testing adjusted service group means					1.3	1	1.3	.30
Sire group error	40	8541.3	425.8	242.1	220.9	39		
Difference for testing adjusted sire group means.					99.2	11	9.0	2.09*

*Approaches significance at probability level of 0.05.

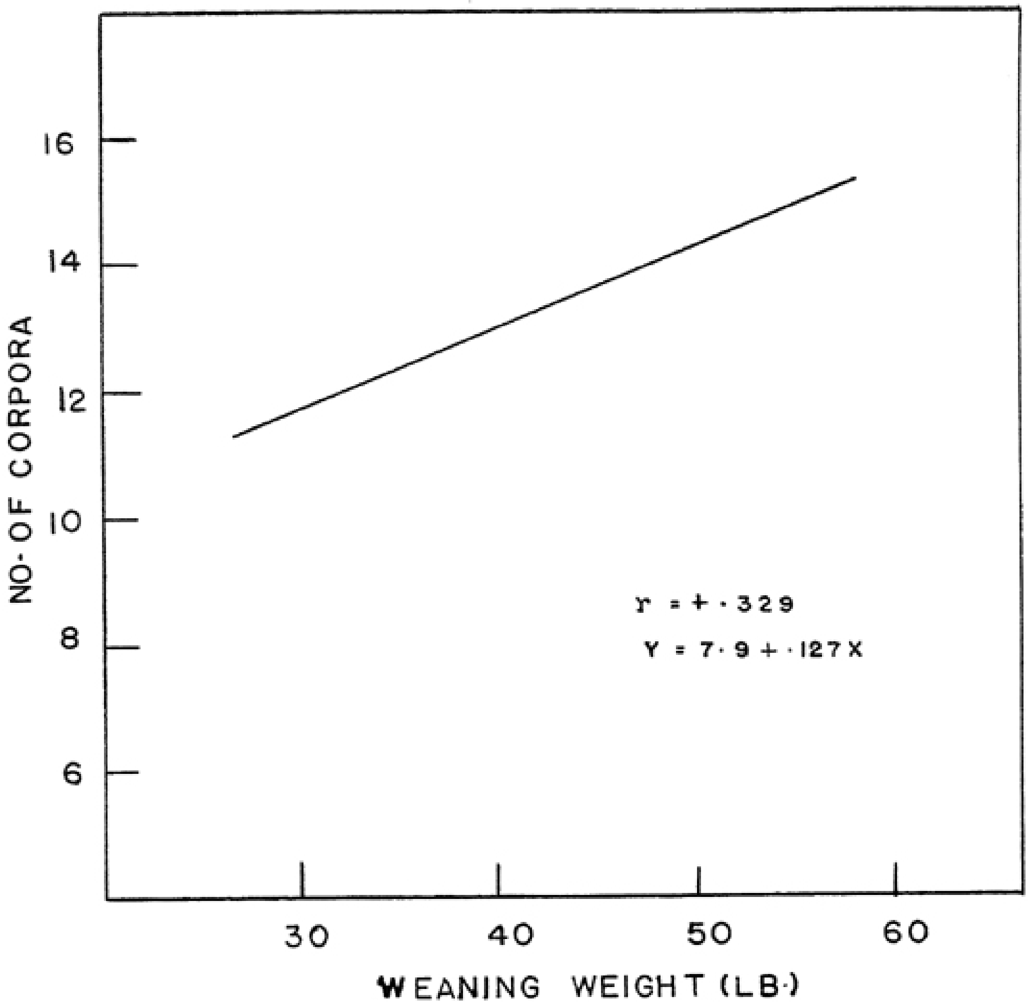


Fig. 4—Regression of number of corpora on weaning weight in Landrace x Poland gilts.

lated in a positive manner with the average backfat thickness, though not significantly (r = .221).

It seems, therefore, that good growth, as conditioned by heavier body weight, older age and fatness, was suggestive of increased reproductive potentialities of the gilts.

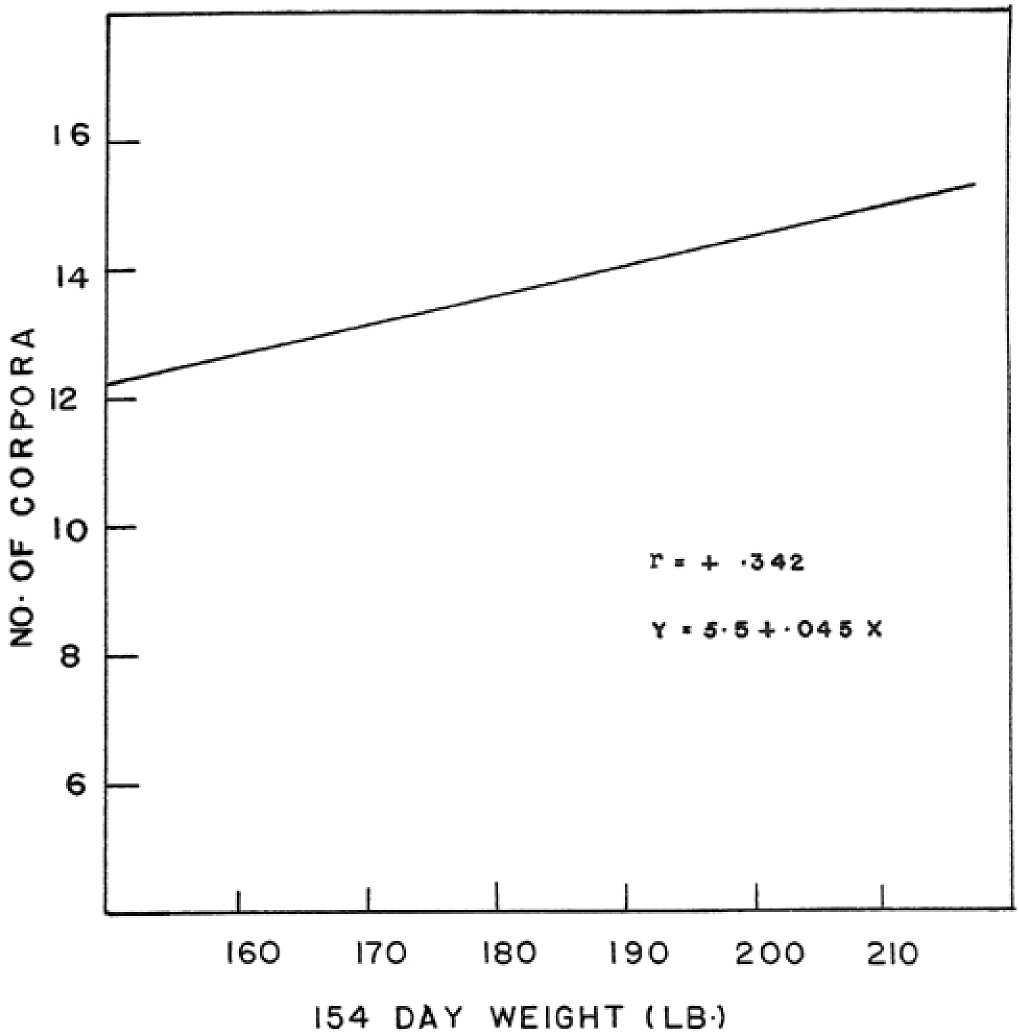


Fig. 5—Regression of number of corpora on 154-day weight in Landrace x Poland gilts.

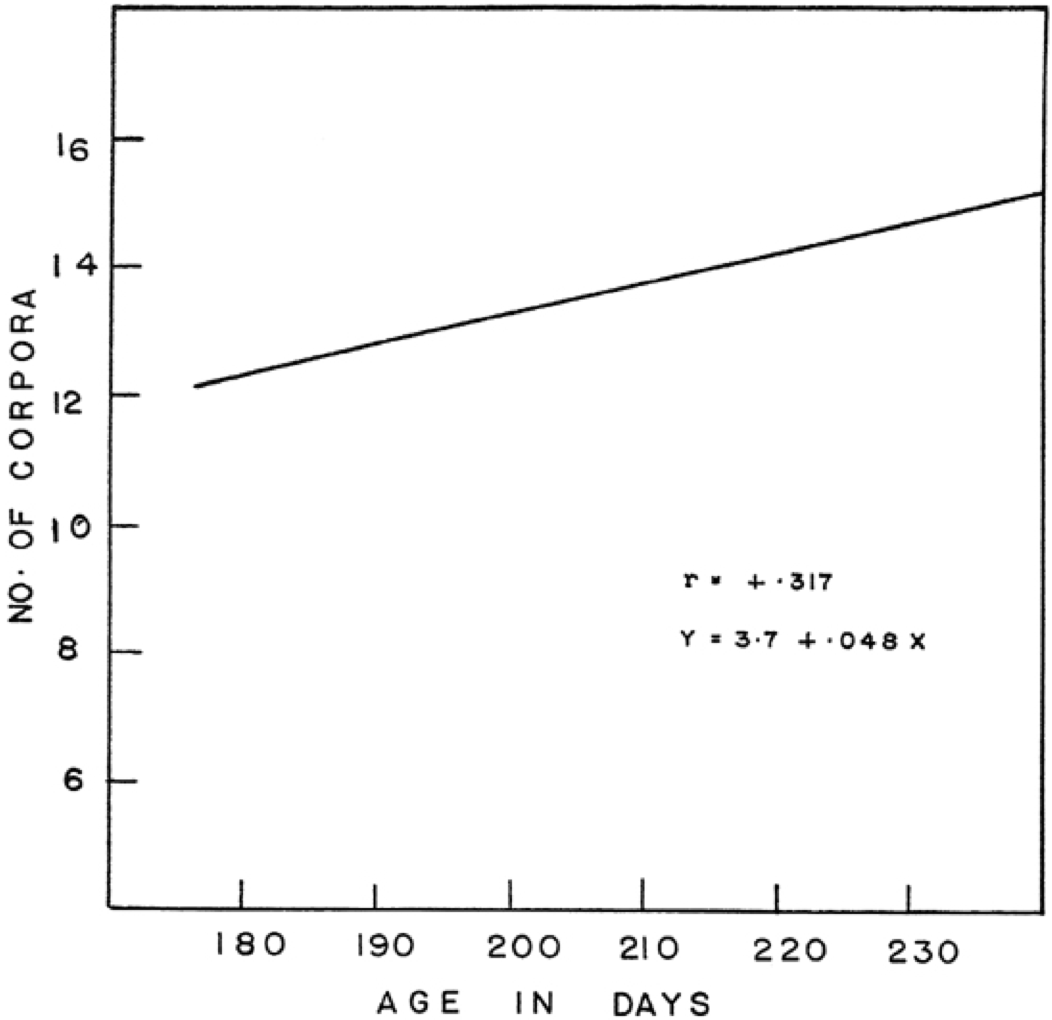


Fig. 6—Regression of number of corpora on breeding age in Landrace x Poland gilts.

Embryo and Fetal Survival up to 55 Days of Gestation

As described earlier, litter size at 55 days of gestation was determined by counting the number of normal fetuses recovered from the uterus. The difference between the number of normal fetuses and the number of corpora lutea was considered to represent total ovum mortality, on the presumably valid assumption that one ovum was shed for each functional corpus present at 55 days. Fetal survival in these studies varied from 3 to 14 with an average of 9.2 ± 2.6 for the 41 Landrace x Poland gilts. Family differences in the Landrace x Poland gilts contributed a significant portion of the total variation in litter size, indicating that the variation in litter size was at least partly genetic (Tables 11 and 12). The mean weights of fetuses by sire groups appearing in Table 13 and the analysis of vari-

TABLE 11 -- MEAN LITTER SIZE IN LANDRACE X POLAND GILTS AT 55 DAYS OF GESTATION BY SIRE GROUPS

Sire group	Number of gilts studied	Litter size at 55 days of gestation
Landrace 3	3	12.7
Landrace 5	2	11.0
Landrace 8	4	11.5
Landrace 105	3	7.3
Landrace 333	3	9.0
Landrace 149	4	8.0
Poland 92	4	8.5
Poland 93	3	10.0
Poland 175	3	5.3
Poland 295	6	9.3
Poland 296	4	9.8
Poland 305	2	7.5

TABLE 12 -- ANALYSIS OF VARIANCE FOR LITTER SIZE IN LANDRACE X POLAND GILTS

Source of variation	Degrees of freedom	Sum of squares	Mean square	F
Sire groups	11	135.7	12.3	2.86*
Service groups	1	17.8	17.8	4.14
Individuals	28	120.9	4.3	
Total	40	274.4		

*Significant.

TABLE 13 -- MEAN WEIGHTS OF 55 DAY OLD FETUSES OF LANDRACE X POLAND GILTS BY SIRE GROUPS

Sire group	Number of fetuses studied	Mean weight G.
Landrace 3	38	76.66
Landrace 5	22	82.50
Landrace 8	36	77.21
Landrace 105	22	92.54
Landrace 149	32	81.46
Landrace 333	27	99.18
Poland 92	21	100.49
Poland 93	31	82.73
Poland 175	17	79.50
Poland 295	42	84.17
Poland 296	39	76.86
Poland 305	15	80.59

TABLE 14 -- ANALYSIS OF VARIANCE FOR WEIGHT OF FETUSES OF LANDRACE X POLAND GILTS

Source of variation	Degrees of freedom	Sum of squares	Mean square	F
Sex	1	1647.18	1647.18	9.685*
Sire groups	11	19882.90	1807.54	10.628*
Individuals	329	55958.15	170.08	
Total	341	77488.23		

*Highly significant.

ance for the weight of fetuses appearing in Table 14, show that families established by sires were highly significant sources of variation ($P < .01$). If the body weight is indicative of the general health and survival ability, which is undoubtedly true within limits, then this phenomena of litter size must be, at least partly, genetic in nature.

Effect of Two Services

The gilts were bred once each day as long as they remained in heat. As a result, some received two services and others one. Litter size did not vary significantly between these two groups. Twenty-four gilts which had a single service during the heat period had an average litter size of 9.8, compared with 8.4 for the gilts which received two services (Table 15).

TABLE 15 -- EFFECT OF NUMBER OF SERVICES ON LITTER SIZE AT 55 DAYS OF GESTATION IN LANDRACE X POLAND GILTS

Number of services*	Number of gilts studied	Mean litter size at 55 days of gestation	T
Single	24	9.8	
Two services at interval of 24 hours	17	8.4	.172**

*Dependent on number of days gilts were in heat.
**Not significant.

The "two-service" group, in spite of its larger ovulation rate (13.7 vs. 13.1), had a smaller litter size than the "single-service" group, which had a smaller ovulation rate but a larger litter size. These observations plus the results of analysis of variance suggest that the number of services was not a significant source of variation in litter size (Table 12) and indicate the existence of other stronger influences, in addition to fertilization rate, which affect the litter size.

Length of the Uterus

Figure 7 illustrates the association of litter size with the length of the uterus at this time, which was positive and highly significant ($P < .01$; $r = .406$). There were 0.135 more live fetuses for each 10 cm. increase in length of the uterus. The mean length of the uterus by sire groups (Table 16) and the analysis of variance of these data (Table 17) seem to indicate that the length of the uterus, which is an important factor in the determination of the litter size, was by itself strongly influenced by other environmental conditions, probably the internal secretions, and had very little hereditary basis, at least as far as the sires were concerned. It has been shown by Hammond (1935) that the growth of the uterus during pregnancy in rabbits is partly due to the contact effect of the embryos. Hence, in determining the sire effect, the variation due to the difference

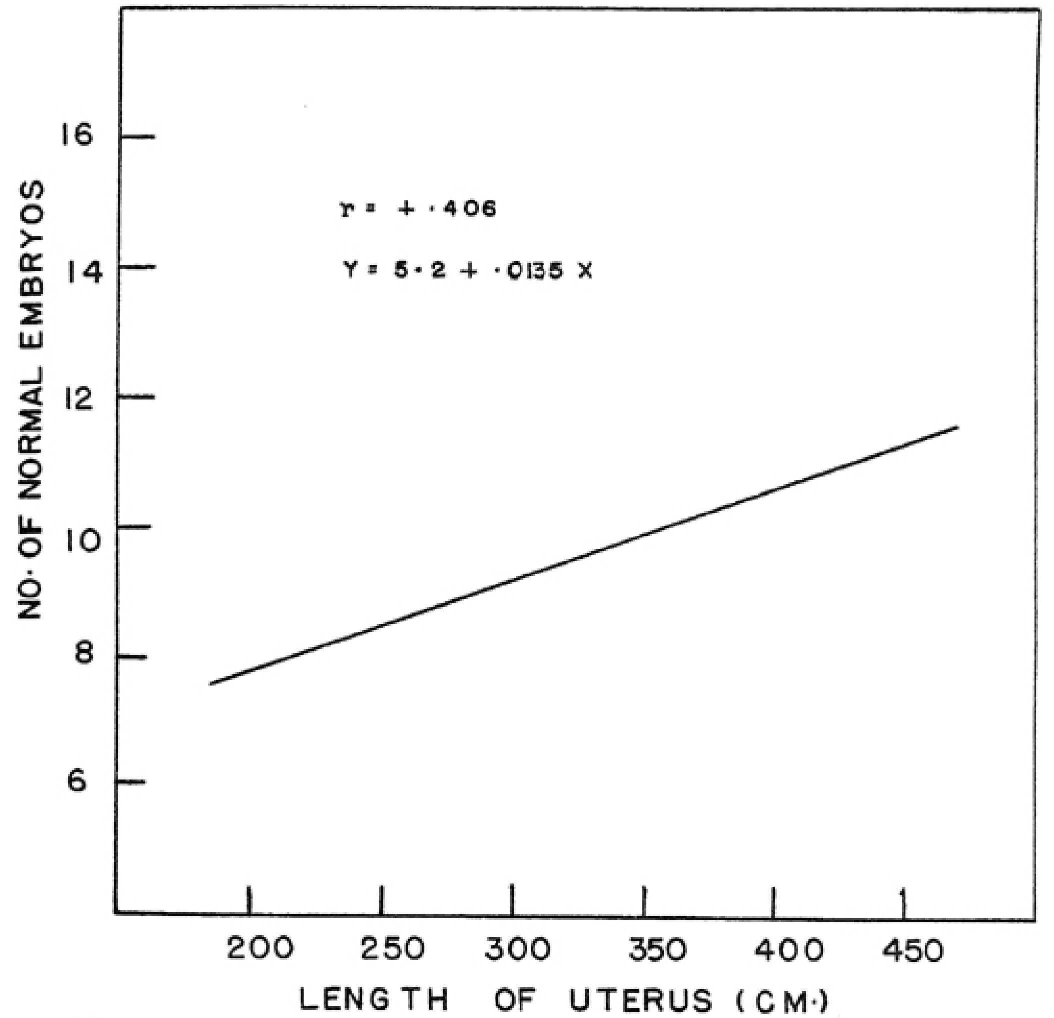


Fig. 7—Regression of litter size on length of uterus in Landrace x Poland gilts at 55 days of gestation.

TABLE 16 -- MEAN LENGTH OF UTERUS AT 55 DAYS OF PREGNANCY BY SIRE GROUPS IN LANDRACE X POLAND GILTS

Sire group	Number of gilts studied	Mean length of uterus mm.
Landrace 3	3	3141
Landrace 5	2	2966
Landrace 8	3	3055
Landrace 105	3	3123
Landrace 149	4	2502
Landrace 333	3	3227
Poland 92	3	2594
Poland 93	3	2498
Poland 175	3	2385
Poland 295	4	3521
Poland 296	4	2980
Poland 305	2	2732

TABLE 17 -- ANALYSIS OF VARIANCE FOR LENGTH OF UTERUS IN LANDRACE X POLAND GILTS AT 55 DAYS OF GESTATION

Source of variation	Degrees of freedom	Sum of squares	Mean squares	F
Sire groups	11	4538681	412607.4	.831*
Individuals	25	12418131	496725.2	
Total	36	16956812		

*Not significant.

in the number of fetuses was removed by the covariance technique. Even then, the sires were not an important source of variation in length of the uterus at mid-pregnancy (Table 18).

The significance of the length of the uterus as a factor associated with litter size is further exemplified by the highly significant and posi-

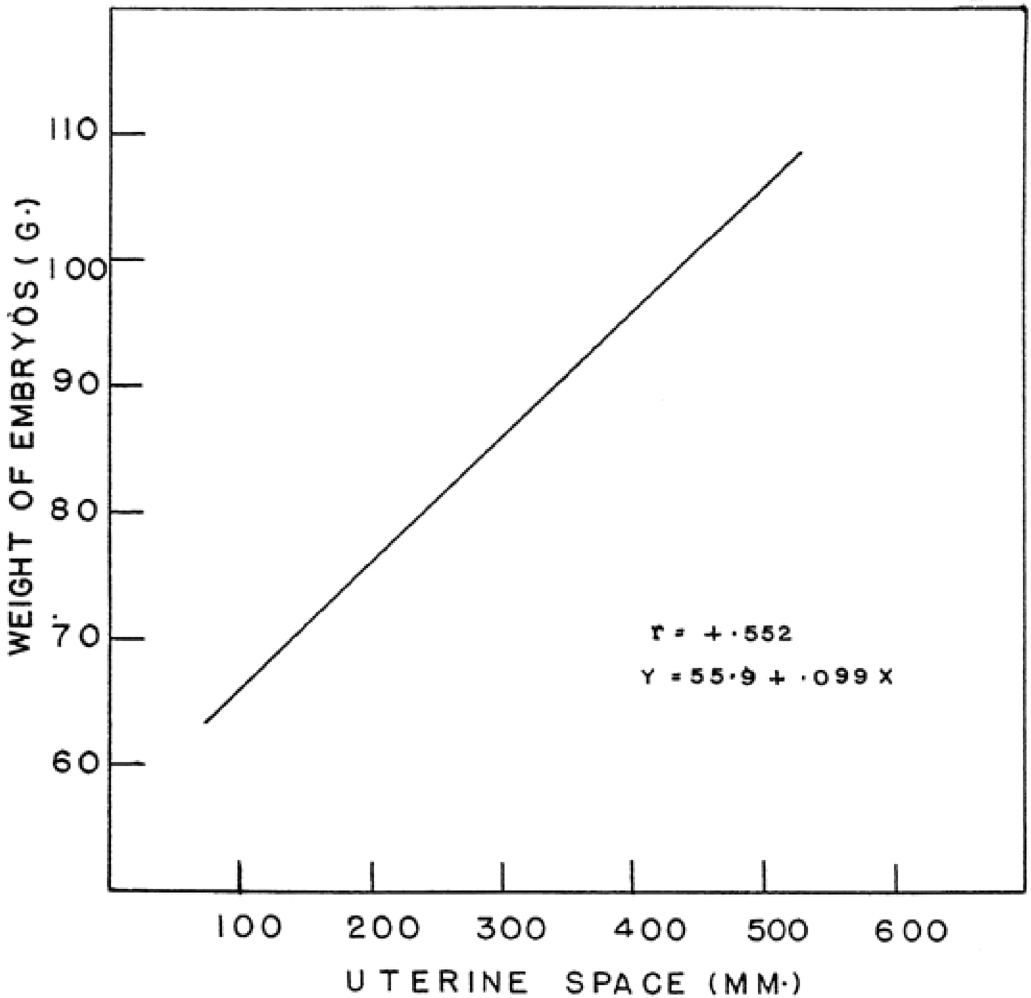


Fig. 8—Regression of weight of fetuses on uterine spacing in Landrace x Poland gilts at 55 days of gestation.

TABLE 18 -- ANALYSIS OF COVARIANCE FOR LENGTH OF UTERUS OF LANDRACE X POLAND GILTS AND TEST OF SIGNIFICANCE OF MEANS ADJUSTED FOR NUMBER OF EMBRYOS

Source of variation	Degrees of freedom	Sum of squares and 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	36	241.7	29996.1	16956812	13234155.8	35		
Sire groups	11	157.3	15507.3	4538681				
Error	25	84.7	14488.8	12418131	9930864.1	24	413786.0	
Difference for testing adjusted sire group means.					3303291.7	11	300299.2	.798*

*Not significant.

tive correlation of the weight of the fetuses with the uterine space occupied by them, as shown in Figure 8 ($P < .01$; $r = .552$). This points out the need for adequate space in the uterus if all the fertilized ova are to grow in a normal manner to the time of parturition.

Intra-Uterine Migration

Intra-uterine migration, nature's mechanism for distributing the fertilized ova equally in the available uterine space, was encountered in 15 out of the 42 gilts studied. This amounts to 35.7 percent of the total number of cases. Of the 15 cases cited, only in nine instances did one ova migrate to the opposite side, while in four cases two ova migrated and in the other two a total of three ova migrated. Transference always occurred from the side carrying the larger number of corpora lutea to the side carrying the lesser number.

Body and Growth Characteristics

None of the body characteristics studied had any significant association with litter size. The 154-day weight, age at breeding, and average back fat thickness, all of which had significantly positive correlations with ovulation rate, were negatively associated with litter size even though insignificantly.

Ovulation rate was not definitely indicative of the litter size because of an insignificant correlation ($r = .170$). Mortality appeared to be the decisive factor, as illustrated in Figure 9, because of its highly significant and negative relationship with litter size ($P < .01$; $r = -.669$).

Fetal Mortality to 55 Days of Gestation

Of the total of 548 ova shed by the 41 Landrace x Poland gilts, 177 could not be accounted for on the 55th day of pregnancy. This amounted

TABLE 19 -- MEAN MORTALITY RATE IN LANDRACE X POLAND GILTS AT 55 DAYS OF GESTATION BY SIRE GROUPS.

Sire group	Number of gilts studied	Mean mortality rate
Landrace 3	3	2.7
Landrace 5	2	1.0
Landrace 8	4	3.5
Landrace 105	3	7.7
Landrace 149	4	5.5
Landrace 333	3	2.7
Poland 92	4	6.2
Poland 93	3	2.3
Poland 175	3	8.3
Poland 295	6	2.2
Poland 296	4	4.0
Poland 305	2	4.0

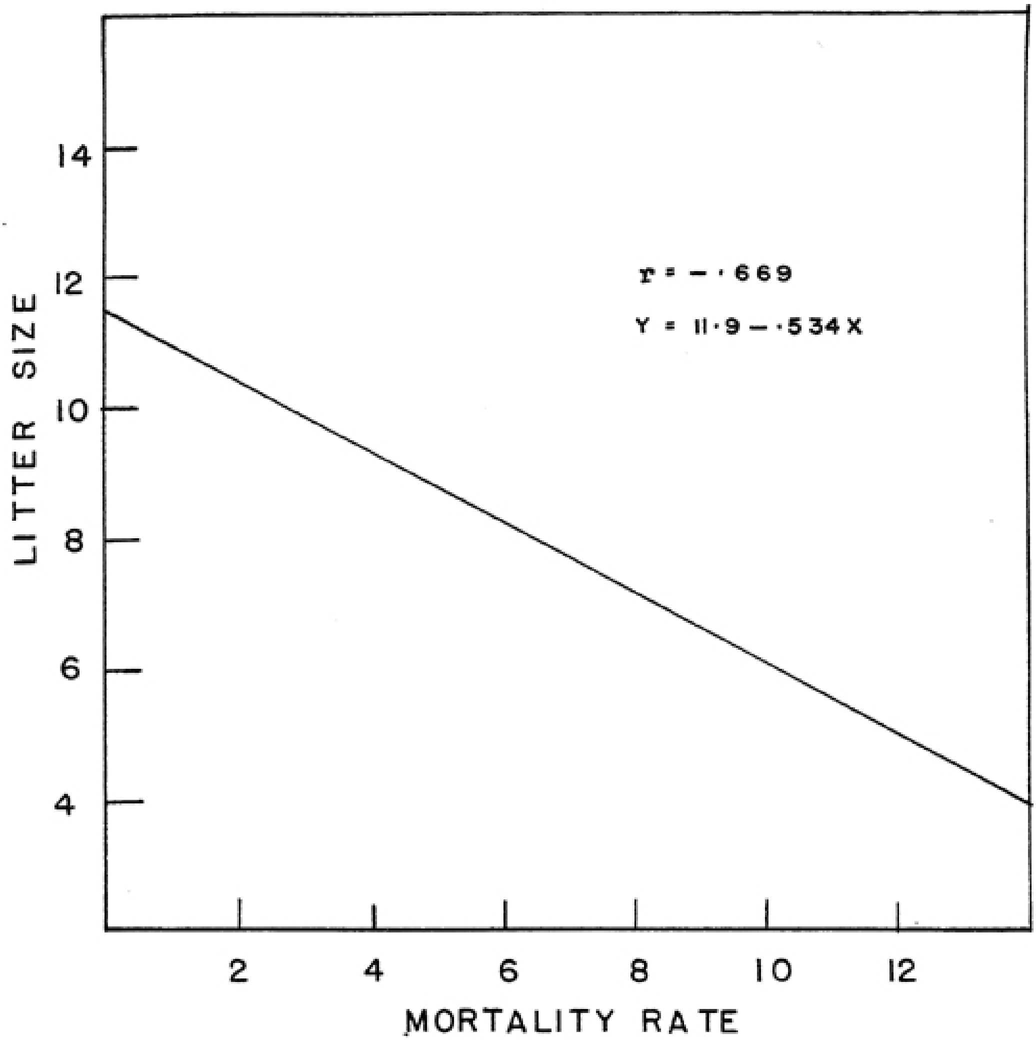


Fig. 9—Regression of litter size on mortality rate in Landrace x Poland gilts at 55 days of gestation.

to a fetal mortality of 31.3 percent at this stage of pregnancy. Family differences within the gilts were significant ($P < .01$; Tables 19 and 20). A highly significant ($P < .01$) sire influence on the variation in mortal-

TABLE 20 -- ANALYSIS OF VARIANCE FOR MORTALITY RATE IN LANDRACE X POLAND GILTS

Source of variation	Degrees of freedom	Sum of squares	Mean square	F
Sire groups	11	202.9	18.44	2.69*
Service groups	1	36.7	36.70	5.35*
Individuals	28	192.2	6.86	
Totals	40	431.8		

*Significant ($P < .05$).

TABLE 21 -- ANALYSIS OF COVARIANCE FOR MORTALITY RATE IN LANDRACE X POLAND GILTS AND TEST OF SIGNIFICANCE OF MEANS ADJUSTED FOR AGE

		Sum of squares and products			Errors of estimate			
Source of variation	Degrees of freedom	Sum of x^2	Sum of xy	Sum of y^2	Sum of squares	Degrees of freedom	Mean square	F
Total	40	10446.0	684.0	431.8				
Sire groups	11	892.0	-48.4	202.9				
Service groups	1	1913.9	264.9	36.7				
Error	28	7640.1	467.5	192.2	163.6	27	6.06	
Service + error	29	9554.0	732.4	228.9	172.8			
Difference for testing adjusted service group means.					9.2	1	9.20	1.34
Sire group + error	39	8532.1	419.1	395.1	374.5			
Difference for testing adjusted sire group means.					210.9	11	19.17	3.16*

*Highly significant.

TABLE 22 -- ANALYSIS OF COVARIANCE FOR MORTALITY RATE IN LANDRACE X POLAND GILTS AND TEST OF SIGNIFICANCE OF MEANS ADJUSTED FOR NUMBER OF OVA SHED.

		Sum of squares and products			Errors of estimate			
Source of variation	Degrees of freedom	Sum of x^2	Sum of xy	Sum of y^2	Sum of squares	Degrees of freedom	Mean square	F
Total	40	245.5	201.5	431.8				
Sire groups	11	82.1	64.7	202.9				
Service groups	1	3.4	11.0	36.7				
Error	28	160.0	125.7	192.2	93.4	27	3.46	
Service + error	29	163.4	136.7	228.9	114.5			
Difference for testing adjusted service group means					21.1	1	21.10	6.098*
Sire group + error	39	242.1	190.4	395.1	245.4			
Difference for testing adjusted sire group means.					152.0	11	13.82	3.994**

*Significant. **Highly significant.

ity rate was observed when the means were adjusted for a constant breeding age and ovulation rate, thus tending toward a genetic explanation of this phenomenon (Tables 21 and 22).

Effect of Two Services

The means of mortality rates for the single and two-service groups (length of heat period) were 3.4 and 5.3 embryos, respectively (Table 23).

TABLE 23 -- EFFECT OF SINGLE AND TWO SERVICES DURING THE HEAT PERIOD ON MORTALITY RATE OF FETUSES IN LANDRACE X POLAND GILTS

Number of services*	Number of gilts studied	Mean mortality rate at 55 days of gestation	T
Single	24	3.4	
Two Services at interval of 24 hours	17	5.3	1.88**

*Number of services dependent on length of time gilts remained in heat.
**Not significant.

The number of services was a significant source of variation, even when the number of ova was kept constant (Table 20 and 22); but when the age influence was removed it lost its significance (Table 21). The reason for the greater mortality in the two-service group could not be determined. It is, however, surmised that the greater ovulation rate in this group might have been partly responsible for the increased loss. Other possibilities will be discussed later.

Uterine Environment

The uterus was subjected to a critical study in an attempt to define its role in the process of fetal atrophy. The possible existence of sites of predilection for embryos was ruled out, when all the four quarters of the uterine horns were found to contain almost equal numbers of fetuses (Table 24). There was no indication of any greater mortality in one horn than in the other. Of the total number of ova produced, 45.6 percent and

TABLE 24 -- NUMBER OF LIVE FETUSES PRESENT IN THE FOUR QUARTERS OF THE RIGHT AND LEFT HORNS OF THE UTERI OF 37 LANDRACE X POLAND GILTS AT 55 DAYS OF GESTATION

Location	RIGHT HORN Total Length mm.	RIGHT HORN Number of fetuses present	Mean weight of fetuses G.	LEFT HORN Total Length mm.	LEFT HORN Number of fetuses present	Mean weight of fetuses G.
Quarter I	352	39	85.08	374	48	81.07
Quarter II	352	43	83.63	374	46	84.08
Quarter III	352	46	81.93	374	43	84.18
Quarter IV	352	38	84.32	374	37	86.62
Total	1408	166	83.66	1497	174	84.01

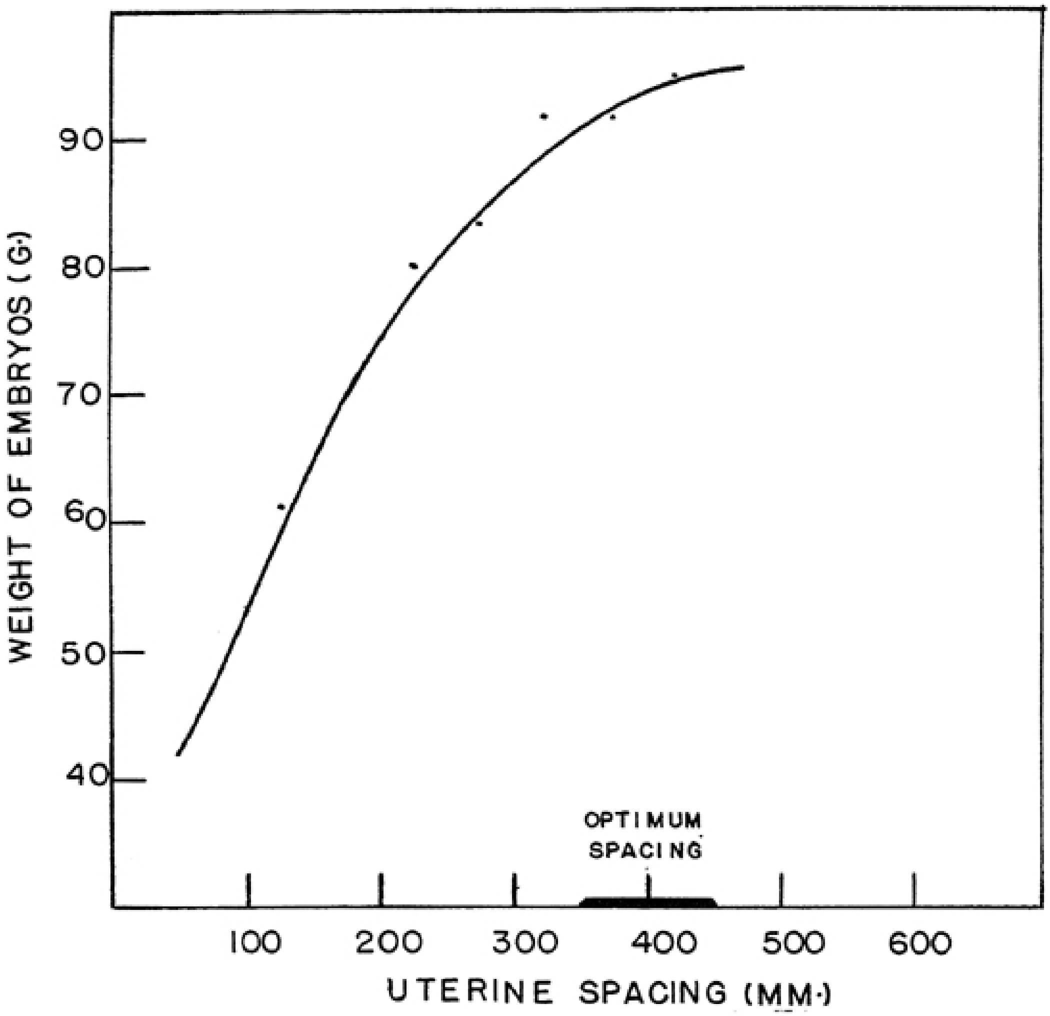


Fig. 10—Relationship of weight of fetuses and uterine spacing at 55 days of gestation in Landrace x Poland gilts.

54.4 percent were shed by the right and left ovaries and 48.5 percent and 51.5 percent of the embryos were found in the right and left horns, respectively.

It is quite obvious from Figure 10, which illustrates the relationship of the weight of the fetuses and the uterine space occupied by them, that over-crowding was an important cause of fetal mortality in these animals. The association was curvilinear in nature and the weights of the fetuses were not directly proportional to the space but obeyed the law of diminishing returns up to a stage when further growth was found impossible. When the space was 50 to 100 mm. the average weight of the fetus was 41.88 gm. An addition of 50 mm. space resulted in a weight increase of

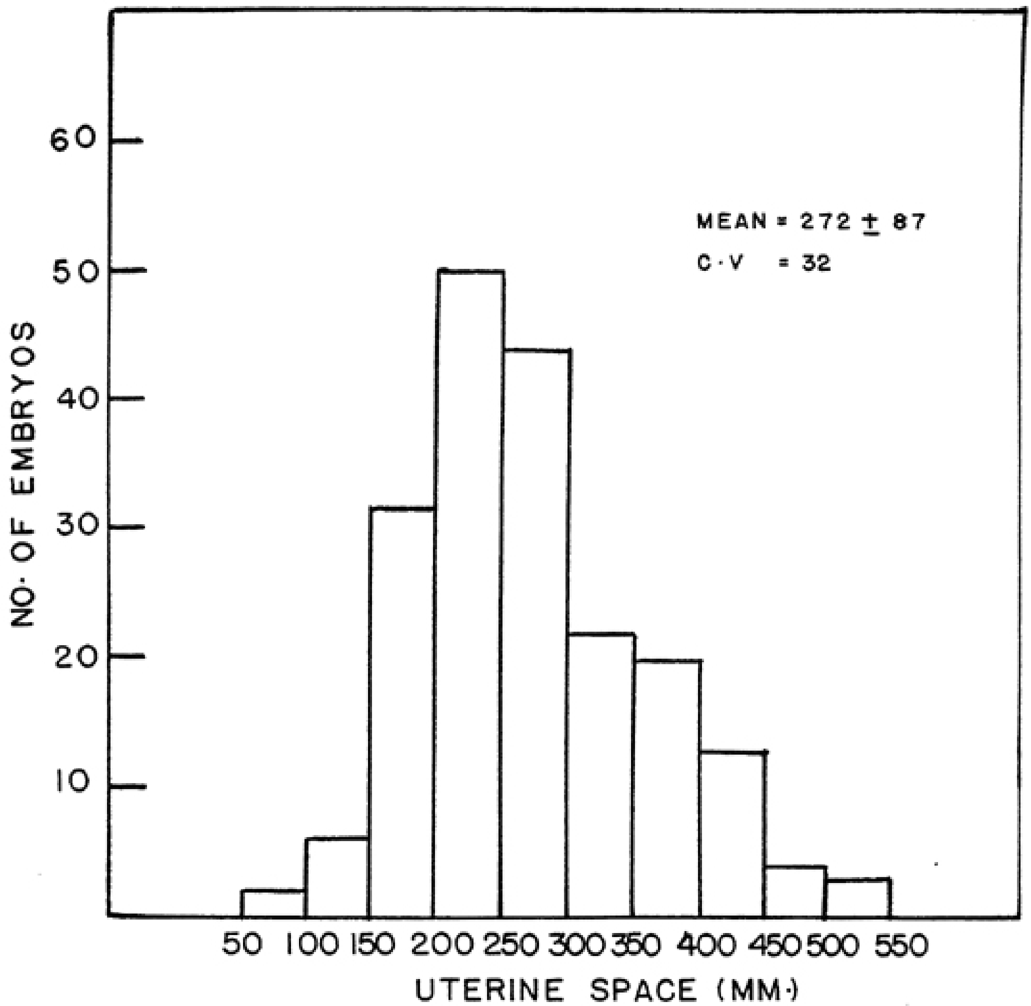


Fig. 11—Histogram showing the distribution of 195 fetuses according to the uterine space occupied by them at 55 days of gestation in Landrace x Poland gilts.

18.74 gm. Every subsequent addition of one unit space up to 200 mm. was then associated with only 10 gm. of increased fetal weight. Further addition in length up to 400 mm. brought less than a 10 gm. weight increase in the fetuses. Beyond 400 mm., additional space resulted in no further increase in the weight of the fetuses. It was estimated from these findings that an optimum space of 350 to 450 mm. was necessary for every fetus for maximum growth at this stage of pregnancy. Inadequate space is bound to cause fetal atrophy and more space is not likely to give additional returns, unless other determinants are operating effectively.

The column diagram in Figure 11 describes the distribution of 195 fetuses over the scale of spacing. Note that 125 (64 percent) had space between 150 and 300 mm., 8 (4 percent) had less than 150 mm. and 62 (32 percent) more than 300 mm. of uterine space available. There is, apparently, a natural tendency for the fetuses to distribute themselves equally in the uterus. The existence of a few fetuses with inadequate space can only be explained by the limited nature of the total uterine space; and the existence of the few with over 400 mm. space may be explained by the death of the neighbors due to various causes and not by a special preference to them for spacing in the uterus.

Other Factors Related to Mortality

Factors which were positively associated with ovulation rate were, in general, associated in a similar manner with mortality rate. The correla-

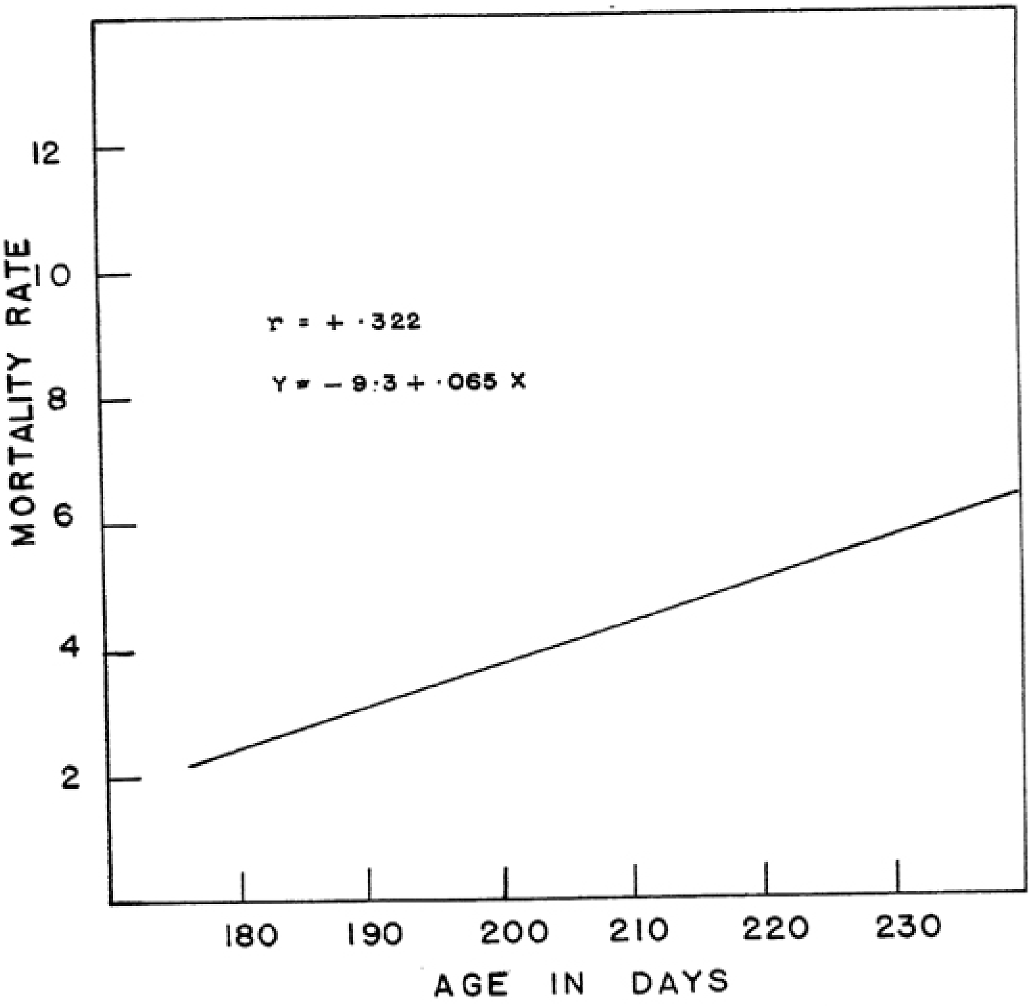


Fig. 12—Regression of mortality rate on breeding age in Landrace x Poland gilts.

tion coefficients of mortality with breeding age and average backfat thickness were 0.322 and 0.365 and the regression coefficients 0.065 and 0.281, respectively ($P < .05$; Figures 12 and 13). The hip fat and chest measurement in millimeters also had significant and positive correlations ($P < .05$; $r = .367$ and $.335$) with mortality; their regression coefficients being 0.226 and 0.049, respectively.

The highly significant association of mortality with ovulation rate, as seen in Figure 14 ($P < .01$; $r = .618$) suggests that the excess of ova produced only resulted in an increased mortality rate due to conditions that did not favor their development.

Undue growth of the dam during conception and afterward was found to be unfavorable for survival of embryos, as indicated by the signi-

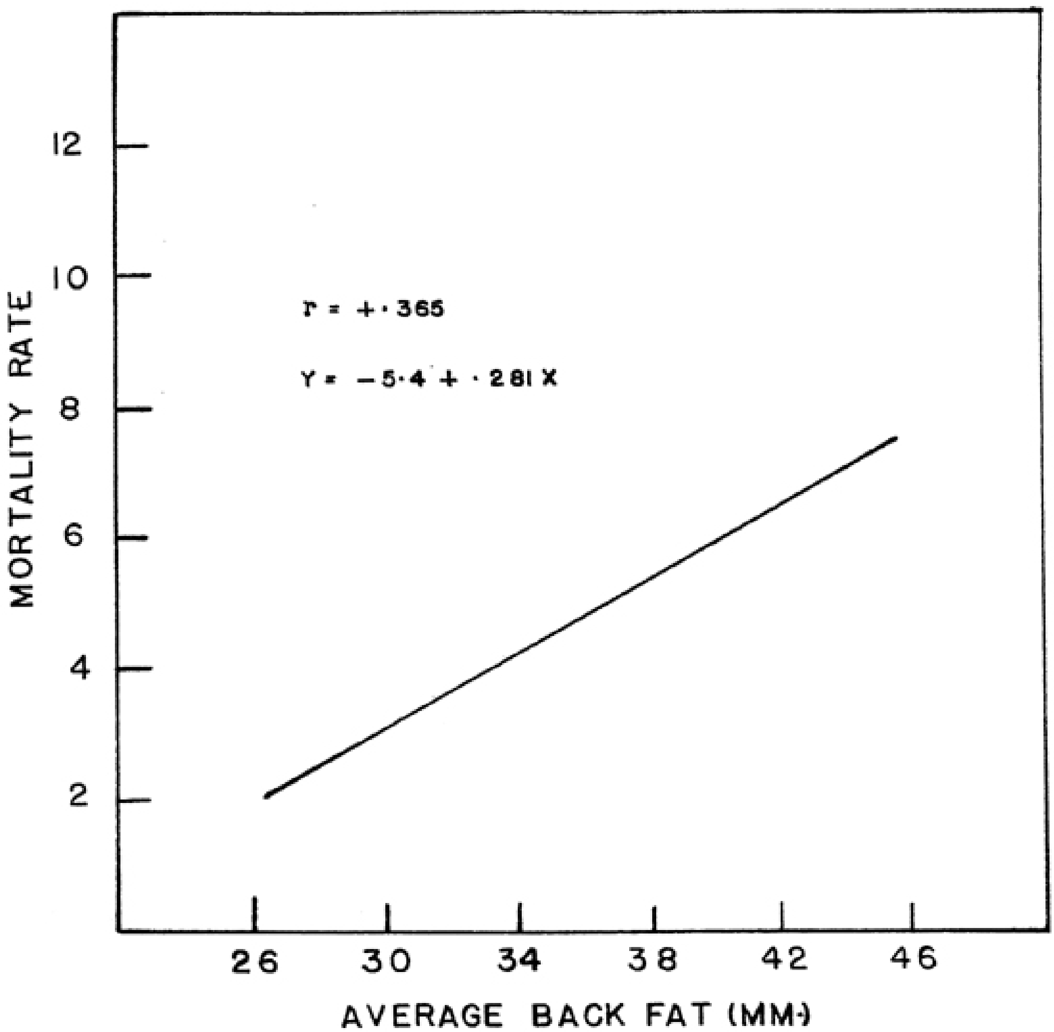


Fig. 13—Regression of mortality rate on average back fat thickness in Landrace x Poland gilts at 55 days of gestation.

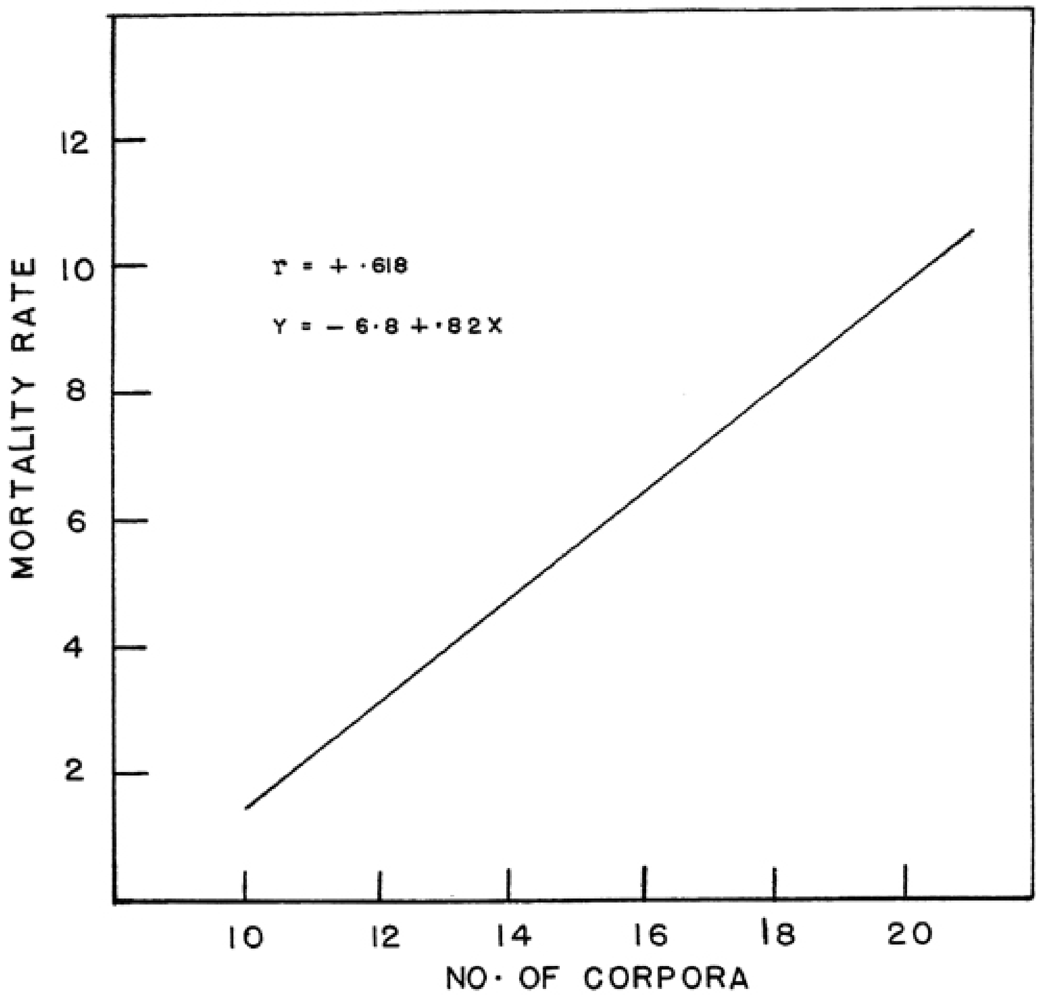


Fig. 14—Regression of mortality rate on ovulation rate in Landrace x Poland gilts at 55 days of gestation.

ficant and positive correlation of embryonic mortality with gains made from 200 pounds to the 55th day of pregnancy and with the weight of dam at mid-pregnancy ($P < .05$; $r = .351$ and $.358$).

Attempts to measure the hormonal relationships with the reproductive processes, by correlating the weight of the ovaries and the weight of corpora lutea with litter size and fetal mortality, did not give encouraging results. The high positive correlation of mortality rate with the weight of corpora lutea suggests that the weight of the corpora lutea may not be indicative of their secretory activity. Gawienowski (1956) did find, however, a significant correlation between the progesterone content and the weight of the corpora.

Bacterial Infection

Bacterial infection was not an important cause of fetal mortality. Thirty-eight pregnant gilts whose uteri and vaginae were examined for the presence of bacteria revealed only five cases of infections. The different kinds of bacteria isolated from the cultures and their locations are given in Table 25. It would be premature to assess the extent of pathogenicity of these organisms before carrying out inoculation experiments and pathological studies; but the possibility of these organisms having a destructive role under conditions when the body vitality is lowered cannot be ruled out.

The means, standard deviations, and simple correlations of the numerous factors studied in relation to ovulation, embryonic mortality and litter size at 55 days of gestation in Landrace x Poland gilts are given in Table 26, Appendix, with the object of making the information available for future studies.

TABLE 25 -- BACTERIAL FLORA OF THE VAGINA AND UTERUS OF 38 LANDRACE X POLAND GILTS AT 55 DAYS OF FESTATION

Organisms isolated	No. of cases	
	Vagina	Uterus
Aerobacter aerogenes	--	3
Pasteurella suiseptica	1	--
Micrococcus aureus	--	1
No organisms	37	34

Note: The authors are indebted to Dr. Harry H. Berrier of the Veterinary Pathology Department for these observations.

Fetal Mortality from 55 Days of Gestation to Parturition

It has already been shown that only about 68.7 percent of the ova produced were represented by apparently normal fetuses at the 55th day of gestation in the Landrace x Poland gilts. In order to learn the extent of fetal mortality after 55 days, one group of 27 gilts was allowed to farrow litters in the spring of 1955. The gilts retained to farrow were bred when about 47.3 days older than those slaughtered at 55 days of gestation. Analysis of data indicated the regression of litter size on age in days was 0.00845 pigs and this was used to adjust the mean litter size at parturition of this group of gilts to the same mean age at breeding as that of the gilts slaughtered at 55 days.

The results indicate that mortality of fetuses from 55 days to birth amounted to 0.2 of a pig. This raises the fetal mortality from 31.3 percent at 55 days to 32.8 percent at parturition.

Gross Abnormalities

Very few gross reproductive abnormalities were found in the population of 74 females studied. There were three cases of completely blocked cervices. The ovaries and uteri were functioning normally in these females as evidenced by the presence of corpora lutea and endometrial changes (Figure 15). Failure of conception, therefore, was due to the inability of the spermatozoa to get into the uterus. In another repeat breed-

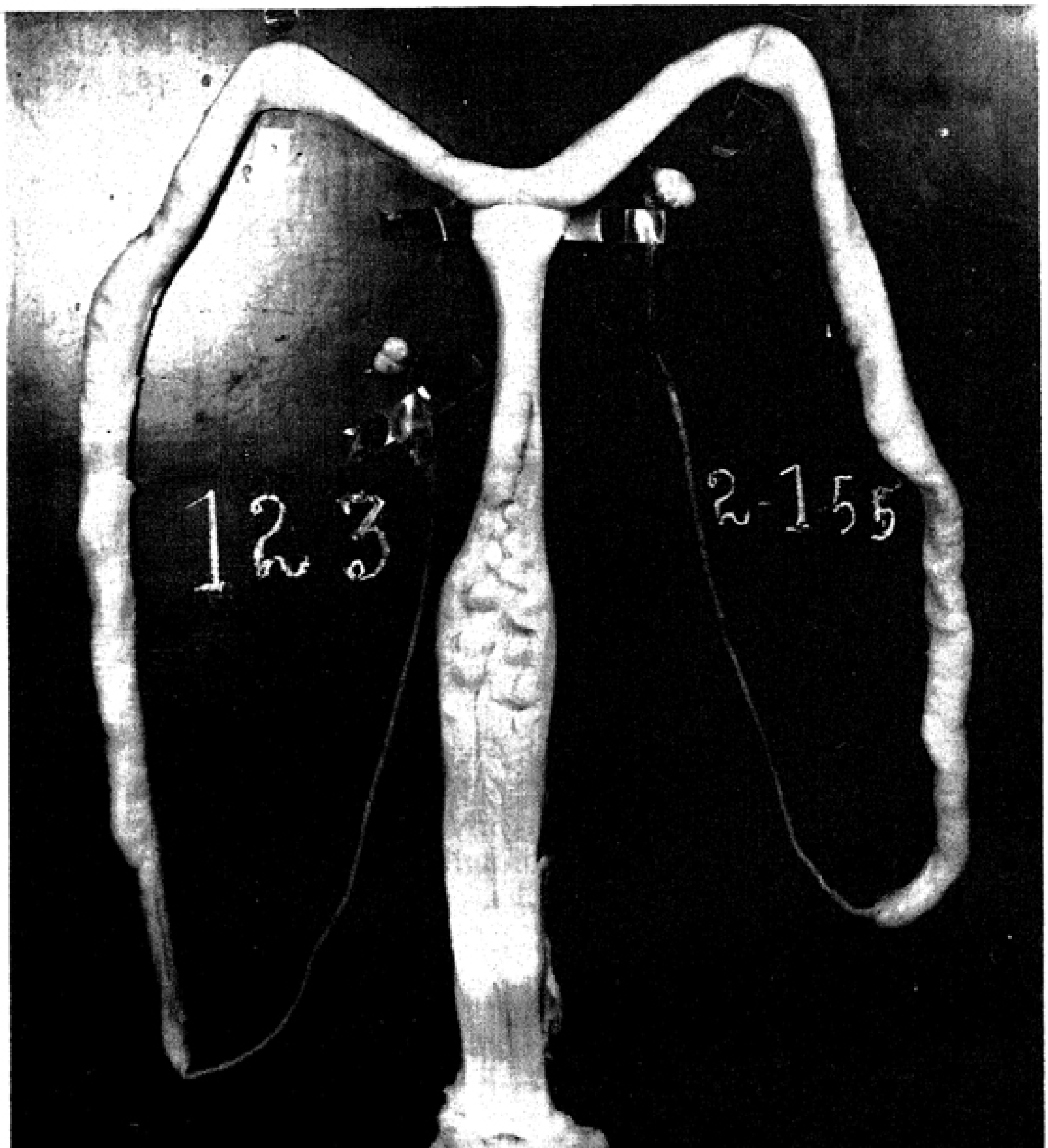


Fig. 15—Blocked Cervix in a Landrace x Poland gilt.

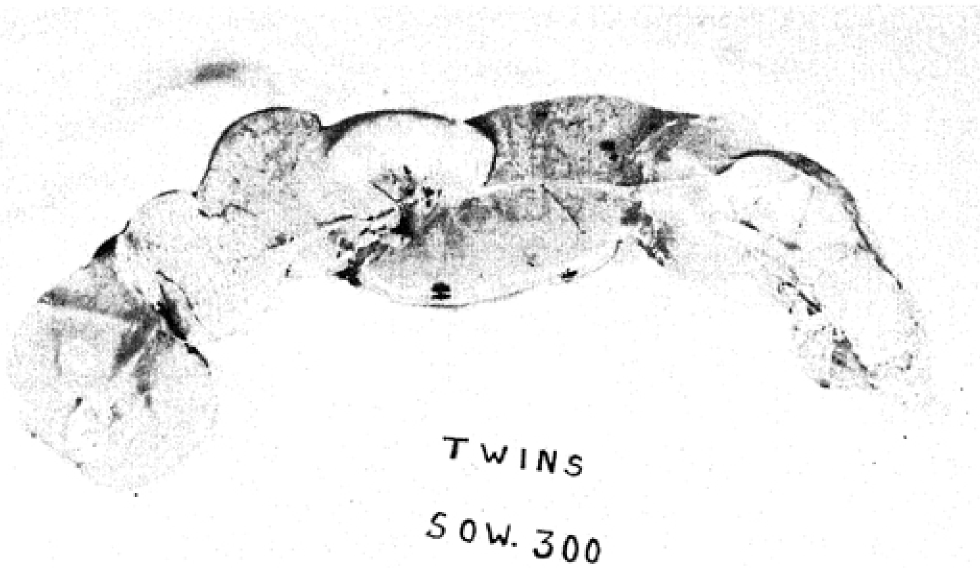


Fig. 16—Fusion of chorion of adjacent embryos originally thought to be identical twins, before dissection.

er, the reproductive tract was normal. No visible signs of reproductive failure could be detected. Figure 16 illustrates the fusion of the chorion of adjacent embryos. This was first thought to be identical twins; but on dissection, the two individuals were found to belong to the opposite sex, the male weighing 81.08 gm. and the female 50.27 gm. There was a single incidence of female identical twins (Figure 17) in gilt no. 471. The

Fig. 17—Identical twins in a Landrace x Poland gilt.

individuals, however, were quite unequal in size, one weighing 83.15 gm. and the other 54.14 gm.

DISCUSSION

Chief purposes of this investigation were (1) to determine some of the genetic and environmental factors that influence ovulation, embryonic mortality, and litter size in swine; (2) to see how these components of fertility are reflected in the phenotypic characteristics in the life of the individual, and (3) to devise ways and means, genetic or otherwise, for improvement of litter size in swine.

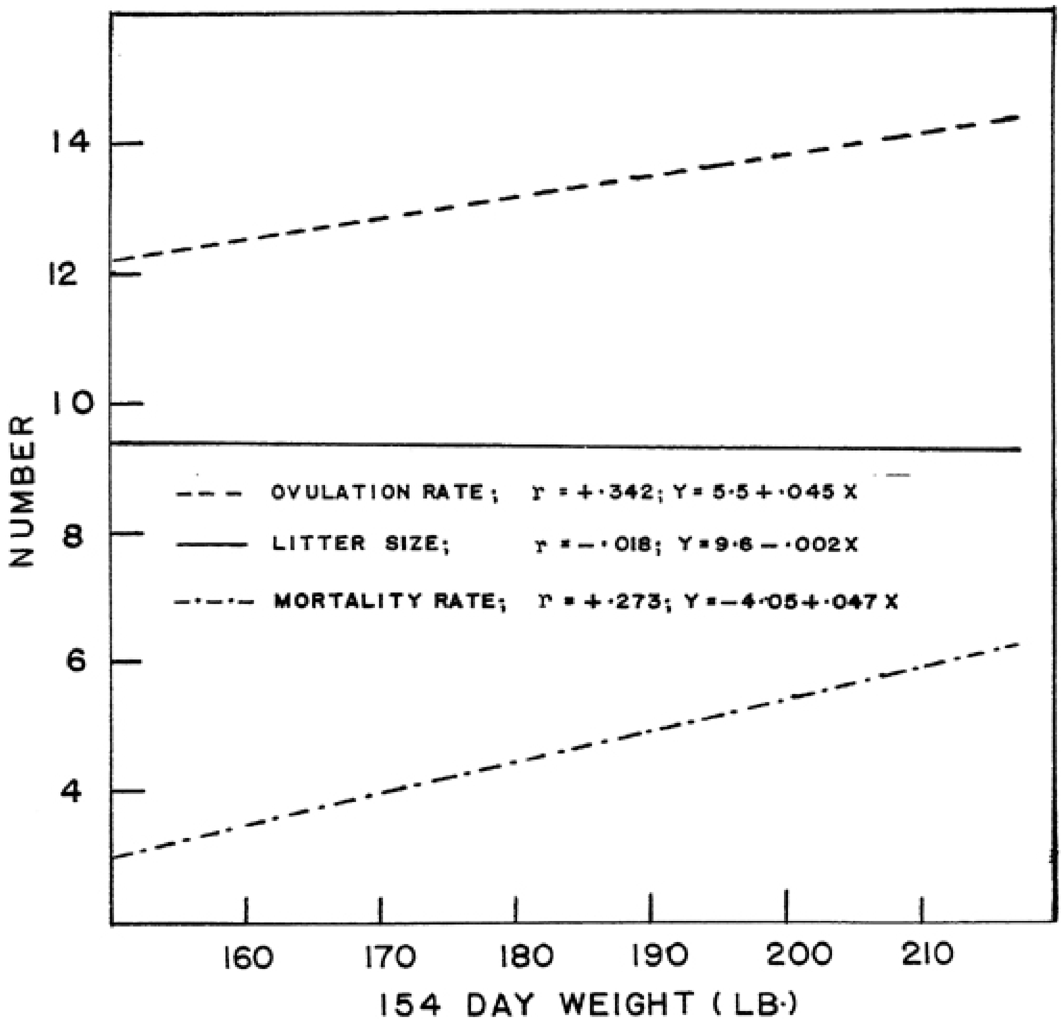


Fig. 18—Regression of ovulation rate, litter size and mortality rate on 154-day weight in Landrace x Poland gilts at 55 days of gestation.

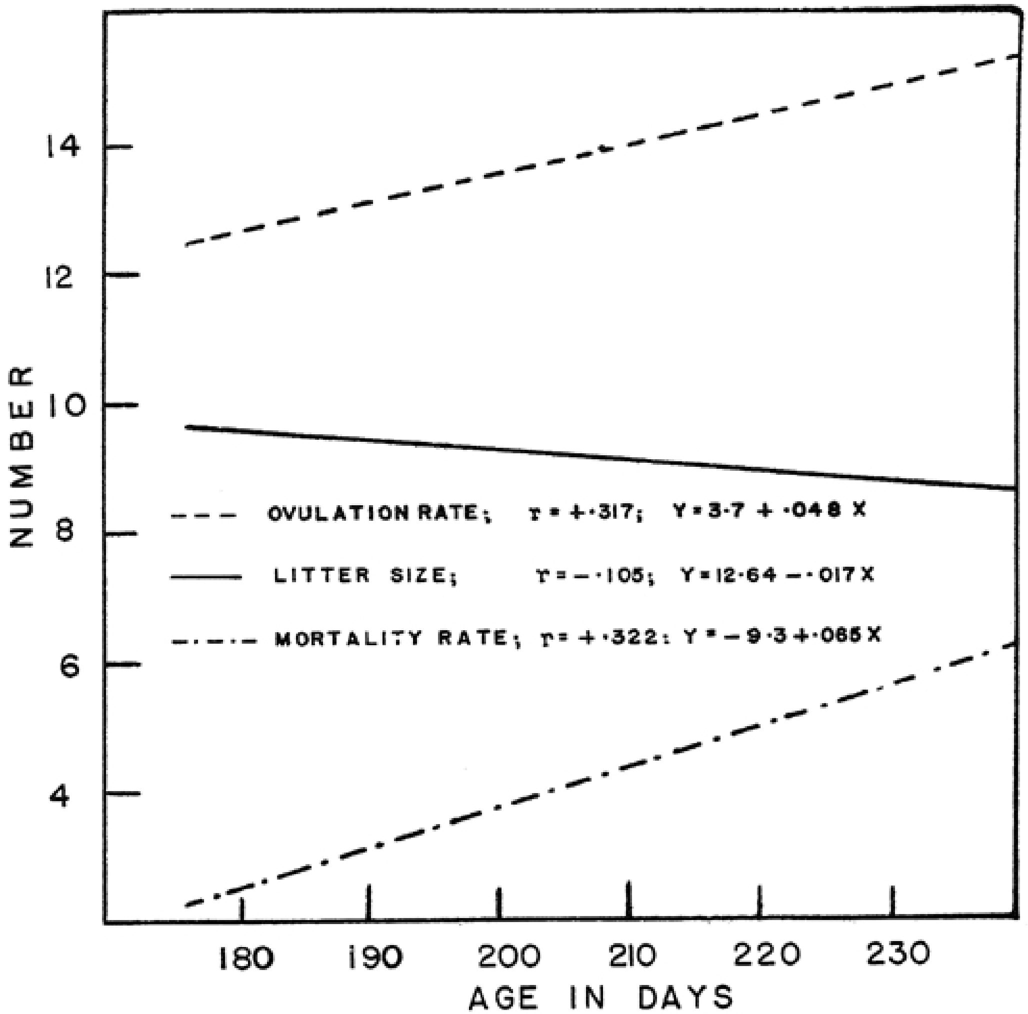


Fig. 19—Regression of ovulation rate, litter size and mortality rate on breeding age in Landrace x Poland gilts at 55 days of gestation.

Relative Importance of Ovulation, Fertility and Mortality

Fertility in mammals, especially of the polytocous species, is dependent on the number of ova shed and the number that are capable of development into viable offspring. The potential reproductive capacity of an individual resides in the ovaries; for it is the functional ova produced by the ovaries upon which the future individuals depend. However, other factors, which hamper the development of ova, play a decisive role in the determination of litter size at birth. This fact has been amply proved by the results of these experiments. An insignificant correlation of ovulation rate with litter size ($r = .170$) and its highly significant association with mortality rate ($P < .01$; $r = -.669$) indicates that mortality was more important than ovulation rate in determining the variation in litter size at 55 days of gestation.

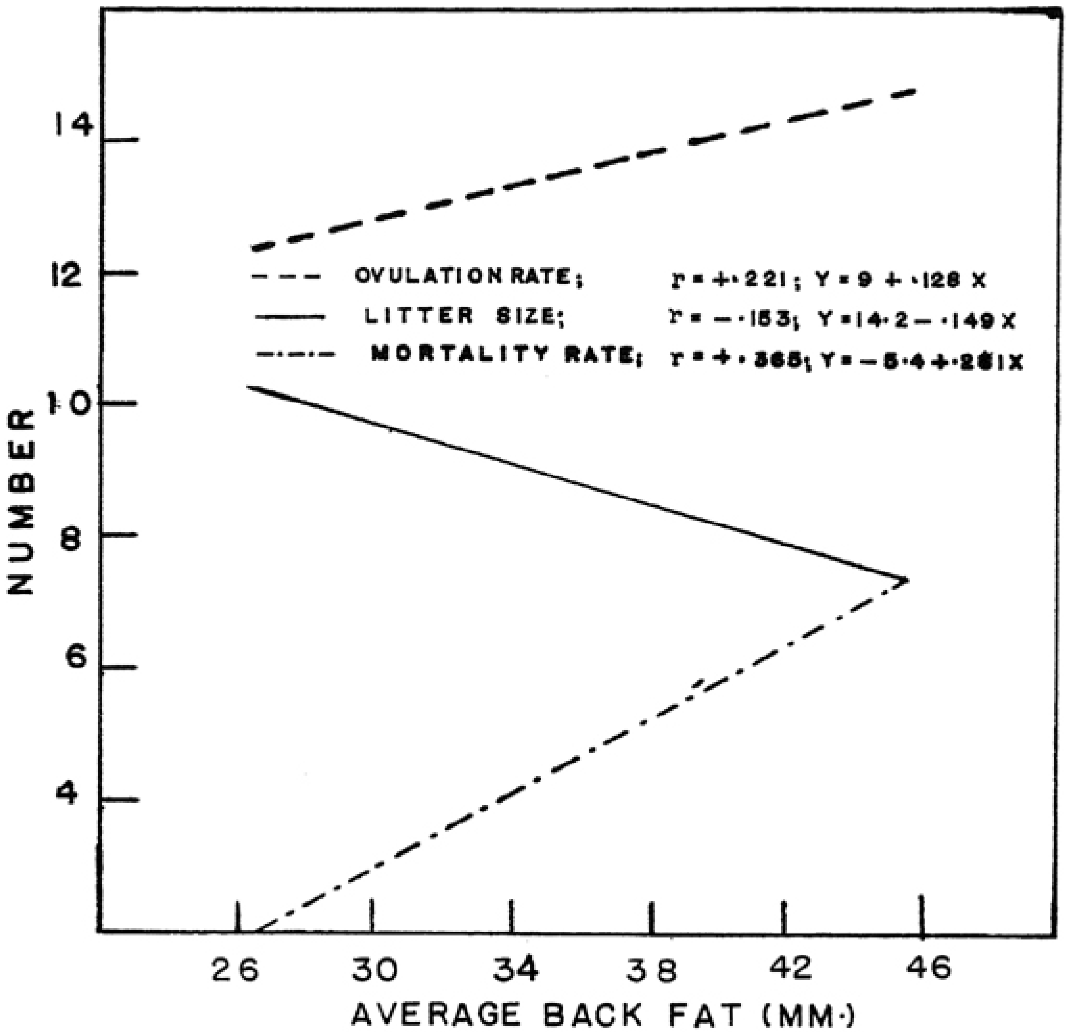


Fig. 20—Regression of ovulation rate, litter size and mortality rate on back fat thickness in Landrace x Poland gilts at 55 days of gestation.

Figures 18, 19 and 20 illustrate the inter-relationships of the three physiological components of fertility under different conditions. Each one-pound increase in the 154-day weight and each one-day increase in the breeding age were associated with the production of 0.045 and 0.048 more ova respectively ($P < .05$). In addition, each increase of one millimeter in back fat at 200 pounds live weight resulted in 0.128 more ova but this was not significant. At the same time, these three factors were associated with mortality rate in a similar manner, the curve of mortality running more or less parallel to the curve of ovulation rate.

The regression line representing the litter size seems to be least affected by the changed conditions. It is quite obvious, therefore, that the excess number of ova produced have gone into fetal mortality under those conditions in which the number of ova shed exceeded optimum litter size.

Therefore, ovulation rate need not necessarily be indicative of litter size, except probably under circumstances which offer unlimited opportunities for the complete development of every ovum produced.

Causes of Fetal Mortality

In the population of 71 Landrace x Poland gilts, an average of 13.4 ova were shed by each gilt. Only 9.2 were represented by viable fetuses at 55 days of gestation and 9 by live pigs at parturition. This represents a total fetal mortality of 32.8 percent with the major portion, 31.3 percent, occurring before the middle of pregnancy. The figures for the total mortality agree in general with those of previous workers in this field (Hammond 1914, 40 percent; Corner 1923, 20-30 percent; Squiers, *et al.* 1952, 46 percent). Moreover, the observation of Pomeroy (1952) that virtually all of the fetal mortality occurs during the first half of pregnancy is well substantiated by the findings with the Landrace x Poland gilts in this investigation. Lerner's (1951) mortality figures of 25.07 percent at 17 days and 33.63 percent at 25 days and Squiers' (1952) figure of 35 percent at 25 days further narrow down the peak of embryonic mortality to the period of implantation and immediately thereafter.

Though several factors were closely associated with embryonic mortality, only a few could possibly be assigned the role of being the immediate cause or causes. The highly significant positive correlation of the number of normal fetuses at 55 days of gestation with the length of the uterus ($P < .01$; $r = .552$) prove rather conclusively that overcrowding, or a primary or secondary uterine deficiency, was the most important and immediate cause of fetal mortality. It was further shown that an optimum uterine space of 350 to 450 mm. per individual fetus was necessary if the fetuses were to survive and develop normally. A smaller uterine space than this was bound to enhance fetal atrophy and more space alone is not likely to give additional survival, (Figure 8).

This view bears additional support from the experiments of Parkes and Hammond (1940) and Casida, *et al.* (1943), who found considerable embryonic mortality in sheep and cattle in spite of multiple pregnancies following gonadotropic treatment. It is also supported by investigations by Warwick, *et al.* (1943), who demonstrated a higher percentage survival of artificially matured ova in host females and females treated with progesterone and estrogen than in the untreated ones and proved that uterine deficiency rather than defects induced in the ova by artificial maturation was the important cause of fetal atrophy.

The high incidence of mortality during and subsequent to implantation, irrespective of the effective natural mechanism of spacing observed by the intra-uterine migration in 33.7 percent of the cases, can be explained in part by the absence of receptivity in the region of the mucosa adjacent to an attached blastocyst, as described by Mossman (1937) and Fawcett, *et al.* (1947). Part can also be attributed to the inability of the uterus to provide an optimal environment by adjusting to the growing needs of the embryos after implantation.

Other causes observed, such as nutritional, bacterial, fusion of chorions, and innate deficiencies in embryos, were negligible in magnitude as compared to the preceding one. Losses due to non-fertilization, which is described to be only about 5 percent by Robertson, *et al.* (1951 a and b), Hauser, *et al.* (1952), Squiers, *et al.* (1952) and several others, were not important.

The significant correlation of mortality rate with back fat thickness ($P < .05$; $r = .365$) seems to be a mere association and not a cause and effect phenomenon. It is, nevertheless, possible that fatness is genetically correlated with increased ovulation rate and a smaller litter size.

The significant relationship of mortality rate with weight gain from 200 pounds to mid-gestation and weight at 55 days of pregnancy appears to agree with the observations of Self, *et al.* (1955) that a full feeding period prior to breeding and then limited feeding thereafter is the most conducive to high ovulation rate and litter size.

Family Variation

Families established by sires were significant sources of variation ($P < .05$) in ovulation rate, litter size, and fetal mortality. They were, also, a highly significant source of variation in mortality rate adjusted for constant breeding age, and number of ova shed. This gives a genetic explanation, at least in part, to the whole reproductive process. It is surmised that environmental conditions in the uterus which are immediately responsible for the development of embryos are controlled genetically. Analysis of variance in length of uterus at 55 days of gestation, however, did not prove that sires were an important source of variation. It is possible that the genetic control over the uterine environment and thus ultimately on the litter size is indirect through internal secretions and other factors. Other means of genetic control of litter size are not ruled out and should be investigated.

Aids in Selection for Litter Size

Results of the present investigation indicate genetic control, direct or indirect, of the physiological components of fertility. Constancy of litter size in different breeds and strains was observed by Winters, *et al.* (1935), Lush and Molln (1942), and Bradford, *et al.* (1953). These findings suggest that a substantial gain in litter size is possible only by genetic improvement, supplemented by favorable environmental conditions.

The weaning weight and 154-day weight were indicative of the potential reproductive capacities of the individual. Each 1 pound increase in weaning weight was significantly associated with 0.127 more ova being produced at the normal breeding age (around 200 days). The corresponding association with 154-day weight was 0.045 more ova.

But if these excess ova are to develop to parturition, the animal should possess, in addition, the necessary uterine capacity. It has been found that 350 to 450 mm. of uterine space per fetus is the optimum for the fullest growth of the fetus at 55 days of gestation in the Landrace x Poland gilts. The comparative study of the size of reproductive organs at different stages indicated that an increase of 292 percent in the length of the uterus had taken place from 169 days of age (about 200 pounds body weight) to the middle of pregnancy, or at about 257 days of age. This optimum space then would be represented by 120 to 154 mm. of uterine length per ovum at about 169 days of age.

There are no phenotypic characteristics which indicate the potential capacity of the uterus in the live animal.

It is certain, however, from the findings reported here that the final length of the gravid uterus is proportional to its initial length before maturity. For instance, the left horn of the uterus in Landrace x Poland gilts, which was longer than the right (373.5 mm. vs. 368.0 mm.) before maturity, had maintained its superiority after maturity and even at 55 days of gestation (1497.3 mm. vs. 1407.5 mm.; Table 4). This initial superiority reflected its capacity to hold more fetuses. Of all the normal fetuses at 55 days of gestation 51.5 percent were found in the left horn and 48.5 percent in the right.

Two possible ways of selecting animals for a better uterine capacity are suggested. One is by exploring new phenotypic correlations which indicate the uterine length, and the other by selection of breeding stock from families or lines which have a longer uterus at about 200 pounds body weight. The length of the uterus in a few sacrificed animals is likely to be representative of the family character.

The significant correlation of the back fat with mortality rate suggests that fatness is a characteristic to be avoided in breeding stock.

Since none of the body measurements such as body length and chest or flank circumference at 200 pounds were significantly correlated with litter size, selection on the basis of type is not likely to give favorable results.

Optimum Breeding Age

Cole and Miller (1933) and Bell, *et al.* (1941), working with anestrous ewes found that invariably all the ewes failed to exhibit signs of heat during the first ovulation period that was induced artificially. They did manifest estrous symptoms, after a lapse of one estrous cycle, during the second ovulation period. In order to avoid this, the gilts in this study were slaughtered instead of being tested with boars for signs of ovulation and determination of pubescent age. The average number of ova produced by the gilts during the first ovulation period at a mean age of 183 days was 8.6 which was found to be slightly less than the normal litter size of 9.2 for the Landrace x Poland gilts. At an average age of 202 days, i.e., during the second ovulation period, they produced an average of 13.4 ova which was in excess of the normal litter size of 9.2.

By breeding gilts at the third heat period, a still further increase in the number of ova may be expected, as indicated by the significant and positive correlation of ovulation rate with breeding age. However, this is not likely to increase the litter size because age at breeding also was significantly associated with mortality rate, but not with litter size. This delayed breeding is certain to increase the feed cost and probably is not practical.

Hence, the optimum age for breeding these gilts seems to be the second ovulation period, when the number of ova produced (13.4) still allows sufficient margin for any unavoidable embryonic losses. If 12 of the ova would develop to fetuses this would be a substantial addition to the existing litter size.

Since breeds differ significantly in the age at puberty, the optimum breeding age will vary from breed to breed and even among different families.

Number of Services

The unfavorable results obtained with the gilts with two services during the heat period might possibly be due to the abnormally long heat period they were in, as a result of some disturbance in the hormonal mechanism, rather than directly due to the number of services. Other possible causes may be the greater ovulation rate in this group and consequent high mortality or polyspermy. Since the differences between these two groups were not significant on statistical treatment, the results could have been due to mere chance. The observations of Squiers, *et al.* (1952) indicate very little hope of a second service increasing the litter size. However, it can increase the conception rate, which may lead to an increased survival rate of embryos when other factors are quite favorable for the development of all the zygotes.

Nutrition

The significant positive correlation of ovulation rate with 154-day weight, of mortality rate with gains made from 200 pounds to mid-pregnancy and also with the weight of dam at 55 days of gestation agrees in principle with the findings of Self, *et al.* (1955), that a full feeding period before conception and limited feeding thereafter are the most conducive for a higher ovulation rate and a larger litter size.

Hygiene

There were 5 cases of bacterial infection of reproductive tracts out of 38 examined; but in none of these could fetal atrophy be attributed to bacterial infection. This must have been due to the good health of the animals and the good hygienic conditions under which they were kept.

Gross Abnormalities

The incidence of gross abnormalities in the population was small, amounting to less than 6 percent of all females studied. This is in agreement with the results of Wilson, *et al.* (1949), Warnick, *et al.* (1949) and Squiers, *et al.* (1952). Of special interest, were the blocked cervices observed in three out of the total four abnormalities.

CONCLUSIONS

As stressed previously, the study of embryonic mortality and improvement of litter size is a long-term project involving investigations in several branches of science concerned with reproduction. The relative importance of ovulation, embryonic mortality, and litter size and the genetic and environmental factors associated with litter size, especially the need of a better uterine environment, have been thoroughly substantiated by this study.

The positive correlation between mortality rate and weight of corpora at 55 days of gestation seems most confusing, and calls for a chemical investigation of the hormone content of the corpora lutea at various stages of pregnancy. The role of bacteria in the reproductive tract under farm conditions, where not much attention is paid to hygiene should be explored. Whether the congenital abnormalities observed, such as a blocked cervix, have any hereditary basis needs further study.

BIBLIOGRAPHY

Bradford, G. E., A. B. Chapman and R. H. Grummer. 1953. Performance of hogs of different breeds and from straight bred and cross-bred dams on Wisconsin farms. J. Animal Sci. 12:582

Burger, J. F. 1952. Sex physiology of pigs. The Ondersteepoort J. of Vet. Res. Supplement No. 2.

Casida, L. E., R. K. Meyer, W. H. McShawan and W. Wisnicky. 1943. Effects of pituitary gonadotropins on the ovaries and the induction of superfecundity in cattle. Amer. Jour. Vet. Res. 4:76.

Cole, H. H., and R. E. Miller. 1933. Artificial induction of ovulation and oestrum in the ewe during anoestrum. Amer. Jour. Physiol. 104:165.

Corner, G. W. 1921. Cyclic changes in the ovaries and uterus of swine and their relation to mechanism of implantation. Contribution to Embryology, Carnegie Inst., Washington. 13:117.

Corner, G. W. 1923. The problem of embryonic pathology in mammals with observations upon intra-uterine mortality in the pig. Amer. Jour. Anat. 31:523.

Craft, W. A. 1953. Results of swine breeding research. U.S.D.A. Circuar 916.

Donald Bell, T., L. E. Casida, G. Bohstedt, and A. E. Darlow. 1941. Production of heat and ovulation in the anestrous ewe. Jour. Agr. Res. 62:619.

Fawcett, D. W., G. B. Wislocki, and C. M. Waldo. 1947. The development of mouse ova in the anterior chamber of the eye and in the abdominal cavity. Amer. Jour. Anat. 81:413.

Gawienowski, Anthony Michael. 1956. The determination of progesterone in ovarian and adrenal tissues by a chemical and chromatographic procedure, Ph.D. dissertation, Graduate School, University of Missouri.

Hammond, J. 1914. On some factors controlling fertility in domestic animals. Jour. Agr. Sci. 6:263.

Hammond, J. 1921. Further observations on the factors controlling fertility and fetal atrophy. Jour. Agr. Sci. 11:37.

Hammond, J. 1935. The changes in the reproductive organs of the rabbit during pregnancy. Trans. Dynamics of Development.

Hauser, E. R., G. E. Dickerson and D. T. Mayer. 1952. Reproductive development and performance of inbred and Cross-bred boars. Mo. Agr. Exp. Sta. Res. Bul. 503

Hughes, J. S., C. E. Aubel and H. F. Lienhardt. 1928. The importance of vitamin A and vitamin C in swine rations. Kansas Agr. Exp. Sta. Tech. Bul. 23.

Lerner, E. H. 1951. Early embryonic mortality in gilts as found in several strain crosses. M.S. Thesis, University of Missouri.

Lush, J. L. and A. E. Molln. 1942. Litter size and weight as permanent characteristics of sows. U.S.D.A. Tech. Bul. 836.

Machens, A. 1915. Fruchtbarkeit und Geslechtsverhaltnis beim Veredelten Landschwein. Berl. Turartzl. Wchschr. 31:559.

McKenzie, F. F. 1928. Growth and reproduction in swine. Mo. Agr. Exp. Sta. Res. Bul. 118.

Mossman, H W. 1937. Comparative morphogenesis of the fetal membranes and accessory uterine structures. Contr. Embryol. Carneg. Inst. 26:129.

Parks, A. S. and J. Hammond. 1940. Induction of fertility by the injection of gonadotropic preparations. The Vet. Rec., Issue No. 2716:540.

Pomeroy, R. W. 1952. Prenatal mortality in an inbred strain of large white pigs. The second international congress of physiology and pathology of animal production and of artificial insemination. Cambridge, England. p. 5.

Robertson, G. L., R. H. Grummer, L. E. Casida and A. B. Chapman. 1951 a. Age at puberty and related phenomena in out-bred Chester White and Poland China pigs. Jour. Animal Sci. 10:647.

Robertson, G. L., R. H. Grummer, L. E. Casida and A. B. Chapman. 1951 b. Some feeding and management factors affecting age at puberty and related phenomena in Chester White and Poland China gilts. Jour. Animal Sci. 10:841.

Self, H. L., R. H. Grummer and L. E. Casida. 1955. The effects of various sequences of full and limited feeding on the reproductive phenomena in Chester White and Poland China gilts. Jour. Animal Sci. 14:573.

Sinclair and Syrotuck. 1928. Age as a factor in swine reproduction. Scientific Agr. 8:492. Quoted by Burger. 1952.

Snedecor, G. W. 1950. Statistical Methods. Fourth Edition. The Iowa State College Press, Ames, Iowa.

Squiers, C. D., G. E. Dickerson and D. T. Mayer. 1952. Influence of inbreeding, age and growth rate of sows on sexual maturity, rate of ovulation, fertilization and embryonic survival. Mo. Agr. Exp. Sta. Res. Bul. 494.

Stewart, H. A. 1945. An appraisal of factors affecting prolificacy in swine. Jour. Animal Sci. 4:250.

Warwick, E. J., R. L. Murphee, L. E. Casida and R. K. Meyer. 1943. Maintenance of pregnancy induced in the female rabbit following treatment with pituitary gonadotropin. Anat. Rec. 87:279.

Weaver, L. A. and Ralph Bogart. 1943. Some factors influencing efficient production of sows. Mo. Agr. Exp. Sta. Res. Bul. 461.

Wiggins, E. L., L. E. Casida and R. H. Grummer. 1950. The incidence of female genital abnormalities in swine. Jour. Animal Sci. 9:269.

Winters, L. M., O. M. Kiser, P. S. Jordan and W. H. Peters. 1935. A six year study of cross-breeding swine. Minn. Agr. Exp. Sta. Bul. 320.

APPENDIX

TABLE 26 -- MEANS, STANDARD DEVIATIONS AND SIMPLE CORRELATIONS FOR OVULATION, LITTER SIZE AND EMBRYONIC MORTALITY AND RELATED VARIABLES IN LANDRACE X POLAND GILTS, AT 55 DAYS OF GESTATION.

Independent variables X (1)	Dependent variables Y (2)	Number of obser- vations (3)	Corre- lation r. XY (4)	Regres- sion b. XY (5)	Means of X (6)	Means of Y (7)
Birth weight (lb.)	Ovulation rate	42	+.122	+.447	3.2 ± .7	13.4 ± 2.5
	Litter size	41	+.237	+.926	3.2 ± .7	9.2 ± 2.6
	Mortality	41	-.099	-.485	3.2 ± .7	4.2 ± 3.3
Weaning weight (lb.)	Ovulation rate	42	+.329*	+.127	43.4 ± 7.4	13.4 ± 2.5
	Litter size	41	+.153	+.053	43.4 ± 7.4	9.2 ± 2.6
	Mortality	41	+.169	+.074	43.4 ± 7.4	4.2 ± 3.3
154 day weight (lb.)	Ovulation rate	42	+.342*	+.045	175.7 ± 18.7	13.4 ± 2.5
	Litter size	41	-.018	-.002	175.7 ± 18.7	9.2 ± 2.6
	Mortality	41	+.273	+.047	175.7 ± 18.7	4.2 ± 3.3
Average daily gain wean to 200 pounds. (lb.)	Ovulation rate	40	+.223	+3.41	1.46 ± .16	13.4 ± 2.5
	Litter size	39	-.085	-2.19	1.46 ± .16	9.1 ± 2.6
	Mortality	39	+.286	+5.82	1.46 ± .16	4.3 ± 3.3
Shoulder fat (mm.)	Ovulation rate	40	+.215	+.110	42.0 ± 4.9	13.4 ± 2.5
	Litter size	39	-.089	-.077	42.0 ± 4.9	9.1 ± 2.6
	Mortality	39	+.284	+.196	42.0 ± 4.9	4.3 ± 3.3
Hip fat (mm.)	Ovulation rate	40	+.224	+.105	30.4 ± 5.3	13.4 ± 2.5
	Litter size	39	-.155	-.121	30.4 ± 5.3	9.1 ± 2.6
	Mortality	39	+.367*	+.226	30.4 ± 5.3	4.3 ± 3.3
Ham (mm.)	Ovulation rate	40	+.134	+.074	31.2 ± 4.5	13.4 ± 2.5
	Litter size	39	-.157	-.144	31.1 ± 4.5	9.1 ± 2.6
	Mortality	39	+.301	+.221	31.1 ± 4.5	4.3 ± 3.3
Average back fat (mm.)	Ovulation rate	40	+.221	+.128	34.6 ± 4.3	13.4 ± 2.5
	Litter size	39	-.153	-.149	34.5 ± 4.3	9.1 ± 2.6
	Mortality	39	+.365*	+.281	34.5 ± 4.3	4.3 ± 3.3
Length of body (mm.)	Ovulation rate	40	-.020	-.001	1060 ± 36	13.4 ± 2.5
	Litter size	39	-.167	-.019	1059 ± 36	9.1 ± 2.6
	Mortality	39	+.197	+.018	1059 ± 36	4.3 ± 3.3
Chest (mm.)	Ovulation rate	40	+.302	+.034	1005 ± 22	13.4 ± 2.5
	Litter size	39	-.084	-.016	1005 ± 22	9.1 ± 2.6
	Mortality	39	+.335*	+.049	1005 ± 22	4.3 ± 3.3

TABLE 26 -- CONTINUED

Independent variables X (1)	Dependent variables Y (2)	Number of obser-vations (3)	Corre-lation r. XY (4)	Regres-sion b. XY (5)	Means of X (6)	Means of Y (7)
Frank (mm.)	Ovulation rate	40	+.072	+.004	1001 ± 38	13.4 ± 2.5
	Litter size	39	-.170	-.018	1000 ± 38	9.1 ± 2.6
	Mortality	39	+.272	+.024	1000 ± 38	4.3 ± 3.3
Total gain from 200 lb. to slaughter (lb.)	Ovulation rate	40	+.275	+.014	115.9 ± 47.3	13.4 ± 2.5
	Litter size	39	-.089	-.009	116.9 ± 47.3	9.1 ± 2.6
	Mortality	39	+.351*	+.028	116.9 ± 47.3	4.3 ± 3.3
Age at breeding (days)	Ovulation rate	42	+.317*	+.048	202.1 ± 16	13.4 ± 2.5
	Litter size	41	-.105	-.017	202.3 ± 16	9.2 ± 2.6
	Mortality	41	+.322*	+.065	202.3 ± 16	4.2 ± 3.3
Ovulation rate	Litter size	41	+.170	+.180	13.4 ± 2.5	9.2 ± 2.6
	Mortality	41	+.618**	+.820	13.4 ± 2.5	4.2 ± 3.3
Mortality	Litter size	41	-.669**	-.534	4.2 ± 3.3	9.2 ± 2.6
Weight at slaughter (lb.)	Litter size	41	-.138	-.008	318.6 ± 45.6	9.2 ± 2.6
	Mortality	41	+.358*	+.026	318.6 ± 45.6	4.2 ± 3.3
Weight of ovaries with out Corpora (G.)	Litter size	41	+.185	+.248	9.22 ± 1.97	9.2 ± 2.6
	Mortality	41	+.223	+.374	9.22 ± 1.97	4.2 ± 3.3
Weight of corpora (G.)	Litter size	41	+.038	+.088	7.81 ± 1.12	9.2 ± 2.6
	Mortality	41	+.492**	+1.45	7.81 ± 1.12	4.2 ± 3.3
Length of uterus (mm.)	Litter size	41	+.406**	+.0014	3028 ± 786	9.2 ± 2.6
	Mortality	41	-.299	-.0012	3028 ± 786	4.2 ± 3.3
Wt. of ovaries without corpora (G.)	Wt. of embryos (G)	37	+.003	+.423	8.93 ± 1.5	774.7 ± 214.5
Wt. of corpora (G.)	Wt. of embryos (G.)	37	-.182	-40.9	7.80 ± .96	774.7 ± 214.5
Uterine space occupied (mm.)	Length of embryo	195	+.158*	+.014	272 ± 87	124 ± 8
	Weight of embryo	195	+.552**	+.099	272 ± 87	82.20 ± 15.59
Length of fetus (mm.)	Weight of fetus (G.)	195	+.903**	+1.79	124 ± 8	82.20 ± 15.59
No. of corpora in Rt. Ovary	No. of corpora in Lt. Ovary	42	-.526**	-.566	6.1 ± 2.4	7.2 ± 2.6
No. of corpora in Lt. Ovary	No. of corpora in Rt. Ovary	42	-.526**	-.491	7.2 ± 2.6	6.1 ± 2.4

* = Significant. ** = Highly significant.