Litter size and birth weight data compiled from the farrowing records of 275 litters out of 109 purebred Berkshire sows of the Oregon State University swine herd during the years 1953 to 1960 inclusive were used in this study. Genetic and environmental factors influencing four components of reproductive performance, namely, within litter variance of birth weights, litter size, number born dead and mean birth weight of pigs within a litter were evaluated by the method of stepwise multiple regression analysis.

The estimate of within litter variance of birth weight was greater for larger litters but was decreased as the inbreeding coefficient of the litter increased. Litter size was depressed as inbreeding of dam increased; however, due to the structure of the herd there was an unusual positive relationship between inbreeding of litter and litter size. The latter observation leads to the conclusion that litter size is more strongly influenced by the genotype of the sow than by the genotype of the offspring. The number born dead in a litter increased as litters became larger. A disproportionate number of highly productive sows kept in the herd to advanced ages brought about an unusual age-of-dam effect; there was, however, no basis for establishing that a greater number of dead pigs occurred in litters out of sows of different ages. The average birth weights of pigs within litters was smaller in larger litters. Average birth weight was also decreased as the inbreeding of dam increased. Age-of-dam effects were not found to be important for any of the components of reproductive performance studied nor were consistent environmental effects found.
An analysis of variance of sib groups was used to derive estimates of repeatability and heritability for within litter variance of birth weights, litter size and litter weight. Data for these analyses were taken from the farrowing records of 44 sows which had farrowed two or more litters. The estimates of repeatability of within litter variance of birth weights was 0.02. This indicates that there was no tendency for sows to exhibit permanent differences for this character.

The repeatability estimates of litter size and litter weight were 0.208 and 0.135 respectively. The heritability estimates of litter size as derived from the dam and sire component of the covariance of half sibs were 0.198 and 0.237. The estimate of heritability of litter weight at birth was 0.199. From these estimates it appears that progress from selection for improvement in all of the components of reproductive performance would be slow. An increased rate of progress will require a more accurate identification of superior genotypes which can be accomplished, in part, by stabilizing temporary environmental factors.
GENETIC AND ENVIRONMENTAL INFLUENCES UPON LITTER SIZE AND VARIATION OF BIRTH WEIGHS IN BERKSHIRE SWINE

by

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GENETIC AND ENVIRONMENTAL INFLUENCES
UPON LITTER SIZE AND VARIATION OF BIRTH WEIGHTS
IN BERKSHIRE SWINE

INTRODUCTION

One of the unique features distinguishing swine from other classes of farm animals is the multiparous character of reproduction. Multiple births are an important economic advantage to the producer of swine and make possible a yield of salable product per breeding unit which exceeds the capabilities of other classes of farm animals. The multiparous character of reproduction is also a valuable biological asset to the animal breeder because it allows greater opportunity for evaluation of the genetic merits of breeding stock than is possible in normally monoparous farm animals. The larger number of offspring further allows increased opportunity for segregation and recombination of desired genetic characteristics.

Coupled with the advantages of multiparous reproduction are unique problems not found in monoparous species where fertility is a discrete factor (i.e. a fetus is present or absent). In swine, the producer and breeder is faced with a continuous distribution of number farrowed in a litter; litters vary from one pig to seventeen pigs or more. In addition to differences in litter size (number
of pigs farrowed), the swine producer and breeder also encounters a variation of birth weights both within and between litters. Stillborn pigs and mummified fetuses occur frequently enough to be of concern also.

The above factors of litter size, birth weights and stillborn pigs are the components of the reproductive performance of sows.

Litter size establishes the population size from which profits are realized or parental evaluation and future selections can be made. Litter size seems to be primarily regulated by embryo mortality which occurs during the early stages of embryo development, probably during implantation. Studies of the reproductive performance of sows (14; 20; 41) indicate that an average of 30 to 40 per cent of the ova shed fail to develop to parturition. The cause of this mortality has been indicated by many workers (20; 27; 26; 32) to be largely due to an inability of the sow to provide an adequate uterine environment for all of the embryos.

Birth weights and possibly still-births, while related to the number of pigs born, seem to be determined by the adequacy of the uterine environment during the fetal period. The birth weights of the pigs are important to the breeder and producer of swine because of their relationship with survival and subsequent growth performance.
Data from the records of the Oregon State University swine herd and from other studies (29; 37) show that seventy to eighty per cent of the pigs which weighed less than two pounds at birth failed to survive to weaning, whereas the ability to survive increased sharply in those pigs which were heavier at birth. A similar relationship existed for weaning weights; those surviving pigs of the group weighing less than two pounds at birth were markedly lighter at weaning than the heavier birth-weight pigs.

Many studies have been conducted to determine the influence of various genetic and environmental factors upon litter size and birth weights of swine. Some of the more prominent environmental influences include age of dam, plane of nutrition, and season-year effects. Genetic factors which have been studied extensively include inbreeding and crossbreeding of dam and litters and breed of dam. Heritability estimates indicating the total genetic variation between sows and the additive genetic variation associated with prolificacy have been computed in numerous studies. These studies show heritability estimates for prolificacy averaging 10 to 15 per cent. Repeatability estimates for litter size have been computed by many workers (19; 22; 13). These studies usually show repeatability estimates which average from 10 to 20 per cent. Cummings et al. (9) report a heritability estimate
of 40 per cent for total weight of the litter at birth.

Lush et al. (21) derived estimates indicating that most of the variation in birth weights is due to differences in uterine environment within and between sows and not to individual growth capacity of the pigs themselves.

Factors influencing fetal mortality and stillbirths in swine may be of value in determining factors associated with variation in fetal weight. This may be especially true if the small and/or mummified pigs are caused by inadequate uterine environment rather than by inherent genetic or pathological abnormalities of the fetuses.

Studies of variation in fetal weights (31; 24; 39) indicate possible uterine position effects upon fetal weight. These studies also discuss and present evidence concerning the optimal amounts of uterine space required for fetal growth and development.

Factors influencing embryo survival and litter size have been well elucidated by many studies. Little is known, however, about the ability of a sow to provide a similar uterine environment, as expressed by variance of birth weights within litter, between successive litters. The specific objectives of the present study include an appraisal of factors influencing the within litter variance of birth weights and a determination of the individuality of sows in providing similar uterine
environments between successive litters.

The broad objective of this analysis is an evaluation of the reproductive performance of sows in the Oregon State University swine herd. Included will be litter size, average birth weights and the uniformity of birth weights of the pigs within a litter. The study will be divided into two parts to accomplish this broad objective: (1) an analysis of genetic and environmental factors influencing reproductive performance; and (2) by appropriate grouping of available data estimates will be obtained of environmental, total genetic and additive genetic variation. These variance components will then be utilized to estimate repeatability and heritability of the components of the reproductive performance of sows.
REVIEW OF LITERATURE

Litter size, birth weights, fetal mortality and the uniformity of birth weights within litters may be influenced by many similar factors either by direct or indirect association. To maintain a distinction between the periods of embryonic and fetal development the literature concerning the various components of reproductive performance will be discussed separately.

Lerner et al. (20) worked with 104 strain crossed gilts and concluded that (1) litter size is controlled primarily by embryonic mortality; (2) embryonic mortality and litter size are affected by the number of ova shed and the adequacy of the intra-uterine space; and (3) neither morphological abnormalities of the female tract nor the relative fertility of the boar significantly affect litter size.

Based upon the above conclusion and the findings of other workers (11; 31; 26; 27; 28; 36), it is apparent that litter size is the compound expression of the number of ova shed by the ovaries and the amount of embryonic mortality. The former factor, ovulation rate, establishes the maximum limits of expression, while the latter factor, embryonic mortality, seems to be the primary regulator of litter size.
Studies of ovulation rate, as determined by counting corpora lutea, have examined the correlation of many phenotypic, physiological, and environmental factors with the number of ova shed. Corner (8), has shown that there is an increasing number of ova shed with increasing age of dam. Similar findings are reported by Waldorf et al. (39) who showed that sows ovulated an average of four more ova than gilts. These observations are based upon corpora lutea counts at 102 and 108 days of gestation in 46 gilts and 34 sows.

Increased age of breeding of gilts is found to be associated with the number of ova shed (31, p. 14; 36, p. 8). The size of the gilt at 154 days and at weaning has also been shown to be associated with increased ovulation rate. Rathnasabapathy et al. (31, p. 12) show that each one pound increase in weaning weight results in 0.127 more ova shed and that each pound increase in 154 day weight results in 0.045 more ova shed. The reason for the higher relationship between weaning weight and ovulation is not given but it is probably due to the greater magnitude of differences represented by one pound at weaning as compared with one pound difference at 154 days of age.

Two Missouri studies (31, p. 12; 20, p. 15) have correlated the phenotypic characters of backfat thickness and length of body with ovulation rate. Rathnasabapathy
et al. (31, p. 36) found that an increase of one millimeter of average backfat thickness resulted in 0.128 more ovulated (r = +0.221). These results are similar to the findings of Lerner et al. (20, p. 14) who found a significant correlation of r = +0.28 between backfat thickness and ovulation rate. The relationship between backfat and ovulation rate is in agreement with studies concerning the plane of nutrition. Reviews by Casida (7), Carrol and Krider (6, Chapter 10) and by Robertson et al. (33) show that a high plane of nutrition is associated with increased ovulation.

Lerner et al. (20, p. 15) found a within group correlation of r = +0.24 between length of body and number of corpora lutea. The regression of length of body and number of corpora lutea shows that an increase of one centimeter in body length results in an increase of 0.28 corpora lutea shed by the ovaries. Inasmuch as length of body is associated with body size and possibly increased age this correlation is probably an indirect phenotypic association and not a direct cause and effect phenomenon.

Although ovulation rate is markedly influenced by environmental factors such as feeding regimen and stress and by physiological phenomena such as amount of stored body fat and stage of development there is evidence showing that ovulation rate is controlled in part by genetic mechanisms. In the study by Lerner et al. (20, p. 15)
there were significant differences in ovulation rate between crossbred gilts sired by boars of two separate inbred Poland China lines. Rathnasabapathy et al. (31, p. 17) also found significant differences between sire families of crossbred gilts. Other Missouri investigators, Squiers et al. (36, p. 11) found highly significant differences between breeding groups in the number of ova shed. When crossbred gilts were compared with the performance of parental strains it was found that crossbred gilts shed an average of 1.19 ova more than the mean performance of the parental strains. In this study the advantage is equivalent to .55 ova per ten per cent inbreeding in parental strains. The differences in degree of inbreeding within purebred parental stocks was not sufficient, however, to adequately test the effects of inbreeding upon ovulation rate.

It is of interest to note that all three of the Missouri studies cited (20; 31; 36) found differences in rate of ovulation between sire groups of crossbred gilts. This strongly suggests that there are differences between parental stocks in combining ability for ovulation rate.

Many studies have determined the rate of embryo mortality in swine during the early stages of gestation (3; 8; 14; 20; 26; 27; 28; 31; 32; 36). Most of these studies indicate an average incidence of embryo mortality
during the first 25 to 30 days of gestation of 20 to 35 per cent.

Lerner et al. (20, p. 16) compared the differences in per cent mortality of gilts slaughtered on day 17 post-mating and on day 25 post-mating. Assuming 95 per cent fertilization (36, p. 20), it was found that 28.6 per cent of the ova shed failed to survive to the 25th day of gestation and that 20.1 per cent of the ova shed perished by the 17th day of gestation. These data indicate that most of the embryonic deaths occur before the 17th day of gestation.

Corner (8) found that most of the in-utero migration of embryos had stopped by the 13th day of gestation and suggests that the embryo is attaching to the uterine wall at this time. In this study, Corner further observed that the embryos tended to become evenly distributed throughout both of the uterine horns. Other workers (20, p. 22; 41) also found that the migration of embryos occurred during the first two weeks of gestation. All of these workers (20; 41; 8) indicate that the embryos become evenly distributed throughout both uterine horns and that this distribution is accomplished by trans-uterine migration and not by transfer of the ova to the infundibulum of the opposite uterine horn.

Rathnasabapathy et al. (31, p. 22) discuss
intra-uterine space requirements of embryos and suggest that natural spacing mechanisms do not cause embryo mortality but that the lack of receptivity during the time of implantation of the uterine mucosa adjacent to the blastocyst is part of the cause of embryo mortality. An additional suggested cause of embryo mortality is the possibility of sub-optimal uterine environment during the critical period of embryo implantation. Evidence indicating that sub-optimum conditions may be a contributing factor is given by Reddy et al. (32). In a study including 94 crossbred gilts it was found that treatments with exogenous progesterone and estrogen in minute therapeutic doses administered during the first two or three weeks of pregnancy significantly increased the proportion of surviving embryos. The physiological effects of this treatment included (1) increased uterine size and weight and (2) greater accumulation of fluids by the uterus. Histological studies revealed increased progestational proliferation in the uterine lining of treated gilts as compared with non-treated gilts.

Two of the apparent causes of sub-optimum uterine environment are overfeeding and/or overfatness of the dam during the early embryonic period of gestation. Reviews of feeding experiments (6; 7) indicate that a high plane of nutrition, especially a diet high in energy, is
detrimental to embryo survival. Two studies (20, p. 20; 31, p. 29) show that increased backfat thickness in the dam is related to increased embryo mortality. The correlations found in these studies between backfat thickness and embryo mortality are $r = 0.24$ (20, p. 20) and $r = 0.365$ (31, p. 29). These findings suggest that excessive fat deposits or high levels of energy in the system inhibit the formation or action of the hormones responsible for promoting the development of a favorable uterine environment.

Uterine infection has been studied by Rathnasabapathy et al. (31, p. 31) as a factor affecting uterine environment. A review of this topic is also given by Casida (8). These workers conclude that uterine infection is not an important factor in altering embryo survival, especially in animals of good health. Casida points out, however, that while the infection may not persist, the uterine endometrial physiology may be altered sufficiently to upset embryo requirements.

Genetic influences upon embryo survival in swine have been found by Lerner et al. (20), Rathnasabapathy (31) and Perry (26; 27) and in mice by Fekete (11). The genetic influences in swine were observed as differences in families established by sire groups. Two of the studies (20;
were with crossbred gilts; the differences in embryo mortality found are similar to the differences observed in ovulation rate as a result of crossbreeding. Perry (26), working with 36 gilts, counted the corpora lutea early in pregnancy by laparotomy and then counted the number of young at parturition. From these studies Perry found that daughters of different sires tended to experience a characteristic embryonic loss irrespective of their dams or the sire of the pigs and that the observed differences between sire families of dams were significant.

Differences in embryo survival have been reported by Fekete (11) in mice strains DBA and C57 black. These strains ovulated similar numbers of ova but were characteristically different in the number of mice born. From the results of this study Fekete concluded that (a) there were no appreciable differences in the viability of the eggs of DBA and C57 black mice and (b) that the uterine environment of C57 black mice was more favorable for development of the embryo than that of DBA.

One of the classic studies concerning the effects of inbreeding and crossbreeding was conducted on guinea pigs by Wright (44). In this study Wright found a depression in litter size and fertility with inbreeding and when he crossed inbred families there was a marked increased performance of the traits of fertility and reproduction
in the crossbred female.

One of the most consistent and widely observed influences upon number of pigs farrowed is the age of dam. Lush and Molln (22) have made an extensive analysis of data collected from ten herds including 7,415 litters from 2,560 different sows. In this study, litter size increased from an average of eight pigs per litter for sows farrowing their first litters to an average of almost ten pigs per litter when the sow was three years of age. The average litter size remained close to ten pigs per litter until the dams were five years of age and then began to decline as the sow became older. The most significant increases occurred between the first and second litters. Farrowing records from older sows were not sufficient to determine the true effect of increasing age of dam past five years of age. Similar age-of-dam effects have been found by many other workers (5; 16; 35).

Lush and Molln (22, p. 19) further utilized their data to determine the individuality of the sow with regard to litter size, as expressed by the correlation between different litters from the same sow. This estimate is a measure of the degree to which differences between sows within one season are likely to be found between them in future production. The estimate of repeatability found in this study was 0.147 which indicates that those sows
which farrowed one more pig than the average of the herd for first litters will farrow second litters averaging 0.147 pigs more than the average of the herd. Lush and Molln reviewed similar studies conducted by European workers which, for the most part, arrived at similar estimates of repeatability. Most of these workers used a correlation of litter size between different seasons to determine their estimate and found values averaging from 0.13 to 0.20. A study by Keith (19) involving seven breeds and 935 litters farrowed between 1903 and 1925 shows an average repeatability estimate of 0.20. Hallqvist (13) derived an interclass correlation coefficient of 0.20 from the ratio of total variance minus variance between litter from the same sow divided by total variance. Hallqvist tested his estimate by dividing his sows into two groups; one group was comprised of sows with litter sizes less than the herd averages, and the second group consisted of sows above the herd average. The mean difference between these groups was 4.8 pigs. According to the estimate of repeatability a 20 per cent or .9 pig difference should be obtained between these two groups in subsequent farrowings. The actual difference found in this study was 1.0 pig which is very close to the estimated difference.
It should be noted that an estimate of repeatability is much the same as an estimate of heritability in the broad sense (23, Chapter 8) which is derived by the ratio of the total genetic variance to phenotypic or total variance. The estimate of repeatability differs from the broad sense heritability in that permanent differences between sows may be caused not only by differences in genetic make-up but also by differential effects of development or by permanent environmental effects upon the reproductive capacity and performance of the sow. The total genetic differences between sows are due to the effects of dominance, epistasis and genetic mechanisms acting in an additive fashion. Heritability in the narrow sense estimates the effects of the mechanisms acting in an additive manner. Narrow sense heritability estimates for prolificacy which have been computed range from 0.03 to 0.44 (4; 9; 22; 34; 42). In the study by Lush and Molln (22, p. 37) the heritability estimate for prolificacy was calculated to be 0.17. European studies cited by Lush and Molln give estimates of 0.13 to 0.17.

Minnesota workers (4; 9; 34) have extensively studied the inheritance of litter size in their herds. In the earlier studies (9; 34) estimates of 0.15 ± .23, based upon intra-sire regression of the records of 475 daughter-dam pairs, and 0.19 ± .14, using the records of
532 daughter-dam comparisons, were obtained for heritability of prolificacy in swine. Later work (4) found the heritability to be 0.03 ± .07. This later estimate is based upon a larger sample size than the previous studies and the decreased estimate may be a reflection of the high degree of inbreeding and selection carried on within the Minnesota lines.

Factors Influencing Birth Weights

In general, the factors controlling and influencing fetal growth and development, and possibly fetal mortality, are different from those factors which control ovulation rate and embryo survival. The nutrient requirements are likely to be more critical, especially quantitatively, during the fetal period as compared with the initial stages of pregnancy. The ability of the uterine tissue to transfer large amounts of nutrients and remove waste materials becomes increasingly important as fetal growth and development advances. It is possible that this ability to transfer nutrients is not related to the ability of the endometrial mucosa to respond to hormones and provide a suitable environment for the nurturing of the blastocyst and the implantation of the embryo.

There are some associations between factors influencing embryo survival, as expressed by litter size, and fetal
growth and development, as expressed by birth weight. Whether these associations are direct or indirect as a result of the marked relationship of birth weight and litter size may not be directly discernable.

One of the most important factors influencing birth weight is total litter size and the number of fetuses per uterine horn. Two Wisconsin studies (2; 32) found that litter size had a direct positive effect upon fetus weight at 25 days postmating. In the later stages of gestation the effect of litter size was reversed with increasing numbers of pigs depressing fetus weights. The change in relationship is explained by these workers on the basis that uterine conditions favoring embryo survival also produced heavier embryos in the initial stages of gestation while at the later stages of gestation, fetal development was impaired by a decreased amount of uterine space available per fetus.

Casida (7, p. 20) found that the effect of number of fetuses per uterine horn rather than total litter size was an important factor regulating fetus weight. He found an increasing negative correlation between number of fetuses per horn and fetus weight as gestation advanced and concluded that crowding within a uterine horn is one of the major factors affecting fetal weight.

Two of the papers reviewed (29; 39) discussed the
possible effects of litter size upon variation in fetal weight within litters. In a study of fetal growth in 80 litters out of outbred sows, Pomeroy (29, p. 37) found an increase in variation of fetal weights with increasing litter size. Waldorf et al. (39, p. 7) found that litter size per se, independent of its association with number of fetuses per horn, had little effect on variation in fetal weight. On the basis of the latter study it is probable that the observed association of litter size and variation in birth weights in the study by Pomeroy is largely due to an indirect association through number of fetuses per horn.

Two studies present evidence indicating that position in the uterine horn influences fetal weight. In a study of mice (24) two hypothetical mechanisms influencing variations in fetal weight are discussed. One of the mechanisms discussed is the haemodynamic theory proposed by Eckstein et al. According to this theory the primary cause of differential fetal weights is a difference in blood pressure to the different parts of the uterine horn. The effect of this difference in blood pressure is expressed by lower weights for fetuses in the center of the uterine horn and a tendency for larger pigs to be found at the ends of the uterine horn. Waldorf et al. (39) found that a quadratic regression equation of fetal weight
upon uterine position best described this relationship. While no evidence indicated that the quadratic regression coefficients were heterogeneous over various numbers of fetuses per horn, it was apparent that fetuses at the ends of the uterine horns were larger than those towards the middle. These findings are also in agreement with observed position effects in guinea pigs found by Ibsen (17). Similar position effects were not as apparent in the Missouri study with swine by Rathnasabapathy et al. (31, p. 25). By separating the uterine horn into four quarters and determining the mean fetal weight at 55 days gestation for each section, they concluded that position effects were not significant. It is quite probable that the method of measurement and the early stage of development of the fetuses did not allow an adequate expression of the true variation normally present in fetuses at parturition.

The weight of the fetal membrane is frequently mentioned as a factor influencing fetal weight. It may well be that factors influencing fetal weight do so as a result of differential membrane size. Wisconsin workers found that Chester White sows in their herd had a tendency to promote fetal membrane growth earlier in gestation than Poland China sows and concluded that this factor accounted for heavier fetal weights in litters from Chester White
sows. Casida (7) reports a correlation of $r = 0.54$
between membrane weight and fetal weight.

Many workers report that the age of dam has a marked
effect upon fetus weight (39; 5; 12). These results
indicate that uterine environment improves with succeeding
litters. Data presented by Waldorf et al. (39) show an
increase of three pigs in litters farrowed by sows compared
to gilt litters and an average increase in birth weight of
80 to 100 grams per pig. The increase in average fetal
weight in the sow litters was accompanied by an increase
in the standard deviation of fetus weight. This increased
standard deviation is based upon the within breeding group
mean square which includes differences between dams as
well as within litter variation. It is probable that the
increased standard deviation associated with increased
age of dam is due to the increased size of litter.

The sex of the fetus has been shown (21; 12) to
influence birth weights. The estimates of these effects
range from zero to five or six per cent of the variation
of fetal weights. It is probable that differences in
birth weight due to the capacity of the individual pig are
partly due to sex dimorphism.

The concept that embryo or fetal mortality may be due
in part to genetic abnormalities of the fetus has been
advanced by Berliner (3). In a study of 115 gravid uteri
he found that 9.9 per cent of the fetuses were abnormal. The causes of the abnormalities cannot be directly determined since 112 of the uteri examined were of unknown background. Berliner postulates that abnormal fetuses are largely of genetic origin and that the genetic cause of these abnormalities may be due in part to chromosome aberration or deletions; however, the evidence presented is not conclusive enough to support this hypothesis. The possible action of genetically lethal factors upon pre-natal mortality cannot be entirely overlooked or ignored but at this time the evidence is insufficient to support or refute its importance.

In the discussion of the effects of inbreeding and breed effects upon litter size it was shown that these factors have a direct effect upon the uterine environment. Inbreeding effects similar to those noted on litter size have been observed on birth weight in swine (12) and in guinea pigs (44). Breed effects influencing birth weights have also been observed by many workers (21; 5; 12; 39).

It has been shown that the weight of the pig at birth is largely controlled by maternal influences. Studies of fetal mortality in swine indicate that this phenomenon is also largely controlled by maternal influences similar in nature to those associated with fetal weights. Based upon the relationship of common maternal influences upon birth
weight and fetal mortality it can be reasoned that those factors which contribute to fetal mortality may also cause decreased weight of fetuses.

Berliner (3, p. 26) studied the possible relationship between uterine position and mortality and concluded from his data that no apparent relationship exists. Berliner further found no association between litter size and mortality indicating that uterine crowding effects are not an important influence on pre-natal mortality. These conclusions are subject to critical review, however, in that they are based upon a highly heterogeneous sampling of sows of unknown breeding and management history and in varying stages of pregnancy.

Studies by Pond et al. (30) and Asdell and Willman (1) report that stillbirths tend to increase with increasing litter size. These workers suggest that crowding and insufficient nutrient supply have a direct effect upon fetal survival.

Godbey and Godley (12, p. 12) report an increasing number of stillbirths as inbreeding increases. Breed differences in percentage of mummified fetuses, average number of mummified fetuses per litter, average number of stillborn pigs per litter, and percentage of stillborn pigs per litter are reported (30). These findings show that maternal environment and thus stillbirths are
directly influenced by the genotype of the dam.

Possible genetic mechanisms influencing birth weight and stillbirths have been discussed but none of the literature reviewed discussed these factors as characteristics of individual sows. Lush and Molln (22, p. 37) report repeatability for litter weight at weaning to be 0.18 in their study and similar figures for litter weight at four weeks of age in European studies. Cummings et al. (9) report an estimate of 0.44 for heritability of litter weight at birth. The studies by Waldorf et al. (39) and McLaren and Michie (24) have discussed and presented data showing that birth weights are largely controlled by individual uterine positions, but there are no indications of the constancy of differences in capacities of sows to provide a more adequate or uniform uterine condition. An evaluation of the repeatability and heritability of these factors should indicate possible methods for obtaining larger and more uniform litters of swine.
MATERIALS AND METHODS

The data used for this study are compiled from the farrowing records of the Oregon State University swine herd during the years 1953 to 1960 inclusive. Included in this study are litter size and birth weight data on 275 litters out of 109 purebred Berkshire sows. Farrowing was divided into two seasons per year, spring and fall, and distributed over periods of three to four months duration within each season. Litter size and birth weight data were recorded by the herdsman shortly after the completion of farrowing.

Breeding History of the Oregon State University Swine Herd

In the spring of 1954, a program to eliminate atrophic rhinitis (18) was conducted which required the disposal of all of the older breeding herd. To establish a non-infected herd, pigs were caught during farrowing and removed to uncontaminated quarters. During the first days the pigs were hand carried to the previously washed and disinfected sow for nursing so that the pigs could receive the necessary colostrum milk.

To prevent any new introduction of disease problems, the herd was closed to the introduction of outside stock after the non-infected herd had been established. This
policy remained in effect throughout the duration of the time covered by this study so that all of the breeding herd from 1954 to 1960 is descended from the initial non-infected herd of nine sows and 2 boars.

All of the nine sows and two boars from which the total population was established were sired by Miami Elation II, which had been introduced into the herd just prior to the program to eliminate atrophic rhinitis. These nine sows are from three litter groups, two of which are full sibs out of sow 49-137. The third litter group of two sows and one boar, 54-9, are out of sow 50-63 which is a half-sib to 49-137. The remaining boar, 53-149, is out of a sow which is not closely related to the other foundation stock. As a result of this initial population structure, the 69 sows included in this study are highly related to the boar Miami Elation II. The coefficients of relationship to Miami Elation II are 0.50 for the sows in the early years of the study and decrease very slightly as inbreeding increased in the succeeding generations. The degree of relationship of many sows to sow 49-137 is also quite high with coefficients of relationship ranging from 0.25 to 0.50.
Method of Analysis

1. Analysis of Factors Influencing Reproductive Performance

To determine the influence of recorded genetic and environmental factors upon the components of reproductive performance under consideration in this study, four multiple linear regression models were designed.

The effects of total number of pigs farrowed (litter size), mean birth weight, weight of litter, inbreeding of dam, inbreeding of litter, interaction of inbreeding of dam and inbreeding of litter, season, and age of dam upon the dependent variable of variance of birth weights within litters were determined by the following model:

\[ Y_{ijklmn} = B_0 + N_i X_i + W_j X_j + W_k X_k + I_d X_d + I_l X_l + I_d X_l + S_m + A_n X_n + A_n^2 X_n + \varepsilon_{ijklmn} \]

where the dependent variable \( Y_{ijklmn} \) is the variance of birth weights within a given litter and:

- \( B_0 \) = the general mean effect common to all litters.
- \( N_i \) = a constant proportional to the linear relationship of total number of pigs farrowed per litter to the dependent variable \( Y_{ijklmn} \).
- \( W_j \) = a constant proportional to the linear relationship of the mean weight of the pigs within a litter to the dependent variable \( Y_{ijklmn} \).
$W_k = \text{a constant proportional to the linear relationship of the weight of the litter at birth to the dependent variable } Y_{ijklmn}.$

$I_d = \text{a constant proportional to the linear relationship of the inbreeding of the litter and the dependent variable.}$

$I_L = \text{a constant proportional to the linear relationship of the inbreeding of the litter and the dependent variable.}$

$I_d \times I_L = \text{interaction of inbreeding of dam and inbreeding of litter upon the dependent variable.}$

$S_m = \text{the added effect of the } m^{th} \text{ season and where } m = \text{ months (1-6) and (7-12)}.$

$A_n' = \text{a constant proportional to the linear relationship of the age of dam to the dependent variable.}$

$A_n'' = \text{a constant proportional to the curvilinear relationship of the age of dam to the dependent variable.}$

$e_{ijklmnd} = \text{random error which is normally and independently distributed with a mean equal to zero and variance equal to } \sigma^2.$

The effects of age of dam, inbreeding of dam, inbreeding of litter, season, interaction of inbreeding of dam and inbreeding of litter, age of dam and inbreeding of dam, and the interaction of inbreeding of dam and
season upon litter size were analyzed by the following model:

\[ Y_{dLmm} = B_0 + A_1X_1 + A_1^2X_1^2 + S_m + I_dX_d + I_LX_L + I_d \times I_L \]

\[ + I_d \times A_n + I_d \times A_n^2 + I_d \times S_m + e_{dLmn} \]

where the dependent variable \( Y_{dLmm} \) is the total number of pigs born in a given litter.

The factors of \( B_0, A_n, S_m, I_d, I_L, \) and \( e \) are the same as the factors defined in the previous model.

The effects of litter size, age of dam, inbreeding of dam, inbreeding of litter, season, interaction of inbreeding of dam and age of dam, and the interaction of inbreeding of dam and season upon each of the two remaining components, namely, number born dead and mean birth weight, was accomplished by the same following model:

\[ Y_{idLmm} = B_0 + N_1X_1 + I_dX_d + I_LX_L + A_nX_n + A_n^2X_n^2 + S_m \]

\[ + I_d \times I_L + I_d \times S_m + I_d \times A_n + (I_d \times A_n^2) \]

\[ + e_{iLmn} \]

where the dependent variable \( Y \) is either the number of pigs born dead in a given litter or the mean birth weight of that litter. The factors \( B_0, N_1, I_d, I_L, S_m, A_n, \) and \( e_{iLmn} \) are the same as those factors described in the first model.

The effects of season have been obtained by grouping month of farrowing into two discrete groups of months 1-6
and 7-12. The effect of season is then calculated as deviations from the mean so that the effect of season 1-6 plus the effect of season 7-12 is equal to zero.

Many studies (22, p. 4; 7; 14; 16; 19; 21; 22; 25; 39) show that reproductive performance increases to a plateau at about the third litter and then declines after eight or nine litters. In the present study, age of dam is included as a continuous variable and it is assumed that the dependent variables are linear or curvilinear functions of this variable. The respective dependent variables are assumed to be linear in the variables of litter size, mean birth weight of pigs within a given litter, total litter weight at birth, inbreeding of dam and inbreeding of litter.

Simple correlations between all variables were computed (Table 1). A stepwise multiple linear regression analysis was used which omitted those independent variables from the regression equation which had multiple regression coefficients with F values, which were less than one. This type of analysis also deleted the independent variables for which the multiple regression coefficient dropped below the F value of one when an additional variable was added to the equation. Each of the remaining variables in each model was tested by "Student's" t test to determine whether the regression due to an individual
variable was significantly greater than zero.

The coefficient of determination, which estimates the total amount of variation accounted for by the regression model, was calculated for each of the regression models.

Method of Analysis

2. **Repeatability and Heritability of Components of Reproductive Performance**

The differences in the phenotypic expression of traits between individuals includes variation due to temporary environmental effects, variation due to total genetic differences, and differences due to environmental effects which have permanently influenced the expression of a trait. The differences due to variation in total genetic effects and permanent environmental effects constitute repeatability. An estimate of the repeatability of a trait is expressed by the following ratio (10, p. 142-149)

\[
r = \frac{V_G + V_{Eg}}{V_P}
\]

where \( r \) is the estimate of repeatability, \( V_G \) is the total genetic variation between sows, \( V_{Eg} \) is the variation due to permanent environmental effects, and \( V_P \) is the total phenotypic variation.

In the present study four sire groups composed of
45 progeny (Table 7) were used for deriving the components of variance used for estimating repeatability of litter size, litter weight at birth, and the uniformity of birth weights within litters. These were derived by the following analysis of variance model:

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>Degrees of freedom</th>
<th>Component</th>
</tr>
</thead>
<tbody>
<tr>
<td>Between sires</td>
<td>3</td>
<td>$V_e + n_o V_p + \bar{n}_o k_o V_d$</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$+ n_o k_o b_o V_s$</td>
</tr>
<tr>
<td>Between dams within sires</td>
<td>14</td>
<td>$V_e + n_o V_p + n_o k_o V_d$</td>
</tr>
<tr>
<td>Between progeny within dams</td>
<td>26</td>
<td>$V_e + n_o V_p$</td>
</tr>
<tr>
<td>Between litters within progeny</td>
<td>147</td>
<td>$V_e$</td>
</tr>
<tr>
<td>Total</td>
<td>190</td>
<td></td>
</tr>
</tbody>
</table>

In this model the weights of progeny, dam and sire variance components — $n_o$, $k_o$ and $b_o$ respectively — are the adjusted average numbers of observations per component where:

- $n_o$ = the adjusted average number of litters per progeny.
- $k_o$ = the adjusted average number of progeny per dam.
- $b_o$ = the adjusted average number of dams per sire.

These adjustments are necessary since the number of observations within each group and between groups are disproportional. This adjustment was accomplished by the formula (22, p. 12) $\bar{n} - \frac{V_{\bar{n}}}{\sum n}$, where $\bar{n}$ is the mean number
of observations per group, \( V_n \) is the variance of the number of observations per group and \( \Sigma n \) is the total number of observations. In this study the values of \( n_0, k_0, \) and \( b_0 \) were 4.20, 2.28 and 4.35 respectively.

An analysis of covariance model was used to correct for influences of inbreeding of dam upon reproductive performance of the sows in this study. The factors corrected for inbreeding of dam were litter size and birth weight of litter.

Estimates of heritability of the components of reproductive performance were obtained by the method of half-sib analysis outlined by Falconer (10, p. 174). This method employs the sire component as an estimate of the covariance of half-sibs which is shown to be equivalent to one-fourth of the additive genetic variance. The estimate of heritability was obtained from the ratio

\[
h^2 = \frac{V_A}{V_P}
\]

where \( h^2 \) is the estimate of heritability, \( V_A \) is the additive portion of the genetic variance and \( V_P \) is the phenotypic or total variance.
RESULTS

Within Litter Variation of Birth Weights

Mean birth weight, litter weight, and inbreeding of litter were the three variables used in the regression analysis (Table 2). Litter size, inbreeding of dam, interaction of inbreeding of dam and inbreeding of litter, season effects, and age of dam were deleted from the regression analysis because the F test for the significance for each of these variables was less than one. The coefficient of determination for the regression analysis ($R^2 = .061$) indicated that 6.1 per cent of the total variation was accounted for by the variation associated with the three retained variables. The regression coefficients, coefficients of determination and constants for the step-wise equations are shown in Table 2.

Litter Weight

There was a highly significant positive effect ($P < .01$) of litter weight at birth upon the within litter variation of birth weights. The regression coefficient became larger and showed increased significance as each of the three variables was added to the regression equation. The regression coefficient with all three variables included is 0.0058. Thus, there was an increase of 0.0058 pounds squared in the estimate of within litter variance.
Table 1. Simple correlations between genetic and environmental factors and the components of reproductive performance studied in the outlined analyses.

<table>
<thead>
<tr>
<th></th>
<th>Variance of birth weight</th>
<th>Litter size</th>
<th>Mean birth weight</th>
<th>Litter weight</th>
<th>Fx dam</th>
<th>Fx litter</th>
<th>Fx dam X Fx litter</th>
<th>Season</th>
<th>Age of dam</th>
<th>Age of dam X Fx dam</th>
<th>Season X Fx dam</th>
<th>Number dead</th>
</tr>
</thead>
<tbody>
<tr>
<td>Variance of birth weight</td>
<td>1.000</td>
<td>0.220</td>
<td>0.004</td>
<td>0.223</td>
<td>-0.121</td>
<td>-0.070</td>
<td>-0.103</td>
<td>0.061</td>
<td>-0.020</td>
<td>-0.51</td>
<td>-0.069</td>
<td>0.102</td>
</tr>
<tr>
<td>Litter size</td>
<td>1.000</td>
<td>-0.174</td>
<td>0.924</td>
<td>-0.257</td>
<td>0.315</td>
<td>0.020</td>
<td>0.214</td>
<td>0.047</td>
<td>-0.231</td>
<td>0.047</td>
<td>0.332</td>
<td></td>
</tr>
<tr>
<td>Mean birth weight</td>
<td>1.000</td>
<td>0.189</td>
<td>-0.181</td>
<td>-0.195</td>
<td>-0.217</td>
<td>0.001</td>
<td>0.145</td>
<td>-0.013</td>
<td>-0.089</td>
<td>-0.127</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Litter weight</td>
<td>1.000</td>
<td>-0.328</td>
<td>0.245</td>
<td>-0.068</td>
<td>0.209</td>
<td>0.112</td>
<td>-0.237</td>
<td>0.000</td>
<td></td>
<td>0.315</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fx dam</td>
<td>1.000</td>
<td>0.321</td>
<td>0.751</td>
<td>-0.080</td>
<td>-0.044</td>
<td>0.305</td>
<td>0.571</td>
<td>-0.324</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fx litter</td>
<td>1.000</td>
<td>0.726</td>
<td>-0.018</td>
<td>0.150</td>
<td>0.150</td>
<td>0.292</td>
<td>-0.050</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fx dam X Fx litter</td>
<td>1.000</td>
<td>-0.154</td>
<td>0.494</td>
<td>0.541</td>
<td>-0.216</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Season</td>
<td>1.000</td>
<td>-0.092</td>
<td>-0.139</td>
<td>-0.590</td>
<td>0.160</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Age of dam</td>
<td>1.000</td>
<td>0.245</td>
<td>-0.086</td>
<td>0.147</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Age of dam X Fx dam</td>
<td>1.000</td>
<td>0.373</td>
<td>-0.266</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Season X Fx dam</td>
<td>1.000</td>
<td>-0.123</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Number dead</td>
<td>1.000</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 2. Multiple regression coefficients, coefficients of determination and constants in regression from successive stepwise multiple linear regression analysis of factors influencing the within litter variance of birth weights.

<table>
<thead>
<tr>
<th>Independent variables</th>
<th>Equation Number</th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>I</td>
<td>II</td>
<td>III</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Regression coefficients</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Litter weight at birth</td>
<td>.0047**</td>
<td>.0054**</td>
<td>.0058**</td>
<td></td>
</tr>
<tr>
<td>Inbreeding of litter</td>
<td></td>
<td>-.2427**</td>
<td>-.2792**</td>
<td></td>
</tr>
<tr>
<td>Mean birth weight of litter</td>
<td></td>
<td></td>
<td>-.0341</td>
<td></td>
</tr>
<tr>
<td>( R^2 )</td>
<td>.0461</td>
<td>.0593</td>
<td>.0613</td>
<td></td>
</tr>
<tr>
<td>Constant in regression</td>
<td>.1586</td>
<td>.1807</td>
<td>.2750</td>
<td></td>
</tr>
</tbody>
</table>

Variables deleted from analysis
- Litter size
- Inbreeding of dam
- Season effect
- Interaction - Inbreeding of dam X inbreeding of litter
- Age of dam

* Significant at \( P < .05 \)
** Significant at \( P < .01 \)

Mean = .1926
Standard deviation = .2674
for each increased pound in litter weight at birth. The coefficient of determination for the regression of litter weight upon within litter variance of birth weight is 0.046.

**Inbreeding of Litter**

Inbreeding of litter showed a significant negative relationship ($P < .05$) with within litter variance of birth weights. The regression coefficient for the analysis including all three variables was $-.279$. This shows that with each increase of 10 per cent in the inbreeding of litters there was a corresponding decrease of $0.0279$ pounds squared in the estimate of within litter variance. The coefficient of determination increased from 0.046 to 0.059 with the addition of this variable to the regression equation.

**Mean Birth Weight**

The variable mean birth weight was retained in the regression equation but the effect, as shown by the "Student's t", was not significant.

**Factor Deleted From the Regression Equation**

Litter size shows a positive simple correlation with within litter variance of birth weights ($r = 0.22$) but it was not included in the regression equation. This factor
was omitted from the analysis because of its high relationship with litter weight ($r = +.924$). Inbreeding of dam, interaction of inbreeding of dam and inbreeding of litter, season, and age of dam showed low non-significant simple correlations (Table 1) with within litter variance of birth weight.

**Litter Size**

Six of the variables of the outlined multiple regression model were included in the final analysis of litter size. These six variables were the quadratic component of age of dam, inbreeding of dam, inbreeding of litter, season, interaction of age of dam and inbreeding of dam, and interaction of season and inbreeding of dam. The two variables deleted from the regression equation because the F value of the test of significance was less than one were interaction of inbreeding of dam and inbreeding of litter and the linear component of age of dam. The coefficient of determination is .273 for the final analysis containing the six variables. Table 3 contains the regression coefficients, coefficients of determination and constants in regression for each equation of the step-wise regression analysis.
Table 3. Multiple regression coefficients, coefficients of determination and constants in regression from successive stepwise multiple linear regression analysis of factors influencing litter size.

<table>
<thead>
<tr>
<th>Independent variables</th>
<th>Equation Number</th>
<th>Regression coefficients</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>I</td>
<td>II</td>
</tr>
<tr>
<td>Season X Fx dam</td>
<td>7.4643**</td>
<td>7.5475**</td>
</tr>
<tr>
<td>Age of dam X Fx dam</td>
<td></td>
<td>0.1541</td>
</tr>
<tr>
<td>Age of dam²</td>
<td></td>
<td>0.1541</td>
</tr>
<tr>
<td>Season</td>
<td></td>
<td>0.1541</td>
</tr>
<tr>
<td>R²</td>
<td>.0968</td>
<td>.2376</td>
</tr>
<tr>
<td>Constant in regression</td>
<td>6.5969</td>
<td>7.4965</td>
</tr>
</tbody>
</table>

Variable deleted from analysis

- Age of dam
- Inbreeding of dam X inbreeding of litter

* Significant at P ≤ .05
** Significant at P ≤ .01

Mean = 8.07
Standard deviation = 3.12
**Inbreeding of Dam**

Inbreeding of dam showed a highly significant \((P < .01)\) negative effect upon litter size. The regression coefficient \((b = -22.5)\) indicates that there is an average decrease of 2.25 pigs farrowed for each 10 per cent increase in the inbreeding of dam. The coefficient of determination increased from 0.0967 to 0.1375 when the variable inbreeding of dam was added to the regression equation.

**Inbreeding of Litter**

Contrary to most findings concerning the effects of inbreeding, there was a highly significant \((P < .01)\) positive relationship between inbreeding of litter and the number of pigs farrowed. The most feasible explanation of this phenomenon is the fact that about one-fourth of the litters in this study were farrowed by outbred dams mated to related boars. Secondly, many inbred sows were mated to non-related boars in 1960. These two factors brought about inbred pigs farrowed by outbred dams and outbred pigs farrowed by inbred dams. The regression coefficient for this variable \((b = 13.1)\) indicates that there is an average increase of 1.31 pigs farrowed for each increased 10 per cent in inbreeding of litter. The coefficient of determination for this factor alone is 0.096.
Season and Age of Dam Effects

Both of these effects were retained in the equation but neither of these variables had a significant effect upon litter size. The coefficients of determination for steps five and six (Table 3) show that these two factors contribute about 0.3 per cent to the variation described by the multiple regression model.

Interaction

The interaction of age of dam and inbreeding of dam approached significance at the five per cent level (t = 1.86). This relationship suggests that the age of dam effects became more important with increased inbreeding of dam.

In the regression analyses which omit the effect of season (steps III, IV, and V, Table 3) the interaction of inbreeding of dam and season is highly significant (P < .01). When the season effect is included in the regression equation (step VI), however, the effect of this interaction becomes non-significant. The physical meaning of this interaction implies that inbred dams are more variable in performance than outbred sows. The data presented in Table 6 shows that there were consistent differences in litter size between seasons. Because this interaction becomes non-significant when season effects
are held constant it does not seem likely that inbred dams are more variable in their performance between seasons than outbred dams.

Variables Deleted From the Analysis

The linear component of age of dam was eliminated from the analysis because the quadratic component of age of dam accounted for most of the variation due to this variable. The simple correlation of age of dam and litter size \( r = 0.112 \) indicates slight age-of-dam effect.

The deletion of the interaction between inbreeding of dam and inbreeding of litter was probably due to the character of the data which caused the unusual expression of the effects of inbreeding of litter.

Factors Influencing the Number of Pigs Born Dead

Six of the nine variables of the constructed model were retained in the regression analysis. These variables included: age of dam - quadratic component, inbreeding of litter, season effects, litter size, interaction of age of dam and inbreeding of dam, and interaction of inbreeding of dam and season. The F test for significance of age-of-dam (linear component), inbreeding of dam, and interaction of inbreeding of dam and inbreeding of litter were less than the minimum F level set for retaining
variables in the analysis. The coefficient of determination for the regression equation containing the six variables was 0.197. The stepwise regression analyses are shown in Table 4 which includes regression coefficients, constants in regression and coefficients of determination for each analysis.

Age of Dam

The effect of the quadratic component of age of dam was highly significant ($P < .01$) in a positive manner. The data in Table 7 show that the sire group ME II contained outbred sows kept in the herd for a longer period of time than sows of other groups. It is further shown that the sows of this sire group tended to have a higher incidence of stillborn pigs. The positive curvilinear effect of age of dam is the result of the mean incidence of mortality increasing to the level of the outbred group as age of dam increases to the point that outbred sows make up the population.

Season Effect

The effect of season upon number of pigs born dead is significant ($P < .05$) in a positive direction. This indicates that there tended to be more stillbirths in the spring farrowed litters. This effect may be due in part to the larger litter sizes of spring litters.
Litter Size

The effect of litter size upon number born dead was highly significant \((P < .001)\). For each increase in litter size of one pig there was an average increase of .09 pigs born dead in that litter. The coefficient of determination for this variable as a simple linear regression against number born dead was 0.107.

Interactions

The interaction of age of dam and inbreeding of dam shows a negative association with number of pigs born dead which approaches significance \((P < .10)\). This interaction confirms the age-of-dam effects discussed previously and shows that at the younger ages the outbred sows tended to have more dead pigs per litter while at the older ages the inbred dams tended to have fewer dead pigs per litter than the population average.

Inbreeding of Litter and Interaction of Season and Inbreeding of Dam

The coefficients of determination in steps VI, VII, and VIII in Table 4 show that these factors, inbreeding of litter and interaction of season and inbreeding of dam, add very little to the variation described by the regression equation.
Table 4. Multiple regression coefficients, coefficients of determination and constants in regression from successive stepwise multiple linear regression analysis of factors influencing the number of pigs born dead.

<table>
<thead>
<tr>
<th>Independent variables</th>
<th>I</th>
<th>II</th>
<th>III</th>
<th>IV</th>
<th>V</th>
<th>VI</th>
<th>VII</th>
<th>VIII</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Regression Coefficients</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Litter size</td>
<td>.1065</td>
<td>.0854**</td>
<td>.0861**</td>
<td>.0793**</td>
<td>.0837**</td>
<td>.0935**</td>
<td>.0969**</td>
<td>.0945**</td>
</tr>
<tr>
<td>Fx dam</td>
<td>-2.6335**</td>
<td>-2.3015</td>
<td>-2.2644**</td>
<td>-1.2504</td>
<td>-1.0092</td>
<td>.5667</td>
<td>deleted</td>
<td></td>
</tr>
<tr>
<td>Age of dam²</td>
<td></td>
<td>.00014*</td>
<td>.00014*</td>
<td>.00014*</td>
<td>.00015*</td>
<td>.00018**</td>
<td>.00018**</td>
<td></td>
</tr>
<tr>
<td>Season</td>
<td></td>
<td>.1910</td>
<td>.3849*</td>
<td>.3614*</td>
<td>.3614*</td>
<td>.3554*</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Season X Fx dam</td>
<td></td>
<td>-1.6723</td>
<td>-1.5162</td>
<td>-1.6895</td>
<td>-1.6895</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fx litter</td>
<td></td>
<td>-.6931</td>
<td>-.9270</td>
<td>-.2432</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Age of dam X Fx dam</td>
<td></td>
<td>-.0612</td>
<td>-.0487</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>R²</td>
<td></td>
<td>.1069</td>
<td>.1651</td>
<td>.1814</td>
<td>.1870</td>
<td>.1903</td>
<td>.1911</td>
<td>.1845</td>
</tr>
<tr>
<td>Constant in regression</td>
<td>-.2774</td>
<td>.1997</td>
<td>.0506</td>
<td>-.0135</td>
<td>-.1675</td>
<td>-.1668</td>
<td>-.2056</td>
<td>-.1580</td>
</tr>
</tbody>
</table>

* Significant at $P < .05$
** Significant at $P < .01$

Mean = .581
Standard deviation = 1.00
Variables Deleted From the Analysis

The linear component of age-of-dam was not included in the analysis because, as in litter size, the quadratic component accounted for most of the age of dam effects. The simple correlation between number born dead and age-of-dam ($r = 0.147$) indicates a tendency for older dams to have greater numbers of dead pigs. This was explained on the basis of the increasing importance of the outbred dams on the population mean at the older ages.

The lack of association of inbreeding of dam and number of pigs born dead is at first surprising considering the high simple correlation between these factors shown in Table 1 ($r = -0.325$). The reason for deleting this variable becomes more clear, however, upon examination of the analysis. It can be seen from Table 4 that the effect of inbreeding of dam was highly significant when entered into the regression equation (steps II, III and IV). This effect of inbreeding of dam was decreased markedly, however, by adding to the regression equation the interaction terms inbreeding of dam and season (step V) and inbreeding of dam and age of dam (step VII). These latter terms account for the major portion of the association for inbreeding of dams shown by the simple correlation.
Factors Influencing Mean Birth Weight

The six variables, litter size, age-of-dam (both linear and quadratic), inbreeding of dam, interaction of age-of-dam and inbreeding of dam, and season and inbreeding of dam were included in the regression analysis of factors influencing mean birth weights. The remaining three variables included in the original model namely, inbreeding of litter, season, and interaction of inbreeding of litter and inbreeding of dam, were not included in the final analysis because the F value in the test of significance of these variables did not exceed the minimum value of one. The coefficient of determination for the analysis containing the six variables was 0.134. Table 5 shows the stepwise regression analysis of the factors influencing number of pigs born dead.

Litter Size

Litter size had a highly significant (P < .01) negative effect upon mean birth weight. For each one pig increase in litter size there was an average decrease of 0.034 pounds in the estimate of mean birth weight of the pigs within a litter. The coefficient of determination increased from 0.044 to 0.069 when this variable was added to the regression equation.
Table 5. Multiple regression coefficients, coefficients of determination and constants in regression from successive stepwise multiple linear regression analysis of factors influencing the mean birth weight of pigs within a litter.

<table>
<thead>
<tr>
<th>Independent variables</th>
<th>Equation Number</th>
<th>Regression Coefficients</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>I</td>
<td>II</td>
</tr>
<tr>
<td>Fx dam X Fx Litter</td>
<td>-4.0634**</td>
<td>-4.0002**</td>
</tr>
<tr>
<td>Litter size</td>
<td>-0.0238**</td>
<td>-0.0249**</td>
</tr>
<tr>
<td>Age of dam(^2)</td>
<td>0.00007**</td>
<td>0.00007(^*)</td>
</tr>
<tr>
<td>Fx dam</td>
<td>0.00007**</td>
<td>0.00007(^*)</td>
</tr>
<tr>
<td>Age of dam X Fx dam</td>
<td>0.9747</td>
<td>-0.9383**</td>
</tr>
<tr>
<td>Season X Fx dam</td>
<td>0.0533**</td>
<td>0.0595**</td>
</tr>
<tr>
<td>Age of dam</td>
<td>0.6912**</td>
<td>0.6639**</td>
</tr>
<tr>
<td>(R^2)</td>
<td>.0438</td>
<td>.0691</td>
</tr>
<tr>
<td>Constant in regression</td>
<td>2.9588</td>
<td>3.1595</td>
</tr>
</tbody>
</table>

Variables deleted from analysis:
- Inbreeding of dam X Inbreeding of litter
- Inbreeding of litter
- Season

* Significant at \(P < .05\)
** Significant at \(P < .01\)

Mean = 2.88
Standard deviation = .44
Inbreeding of Dam

Inbreeding of dam showed a highly significant \( P < .01 \) negative effect upon mean birth weight. The regression coefficient \( b = -2.60 \) estimates a decrease of .26 pounds in mean birth weight for each 10 per cent increase in the inbreeding of dam.

Interactions

The interactions of inbreeding of dam and age of dam was highly significant \( P < .01 \). This effect is positive and indicates that the estimate of mean birth weight increases with increasing age of dam in inbred dams.

The interaction of inbreeding of dam and season approaches significance at the five per cent level in the final analysis containing six variables. In the analysis containing five variables (step VII - Table 5) this interaction is significant \( P < .05 \). This interaction indicates that inbred dams tend to be more variable in their performance between successive seasons than outbred dams.

Age of Dam

Both the linear and the quadratic components of age-of-dam were retained in the analysis but neither of these effects were significant. The "t" value was larger for the quadratic component which indicates a possible curvilinear trend in the relationship between age of dam and
Variables Deleted From the Analysis

In the analysis which included the variables litter size, age-of-dam (quadratic component), and interaction of inbreeding of dam and inbreeding of litter (step III) the interaction of inbreeding of dam and inbreeding of litter has a negative and significant effect upon mean birth weight of the litter. The effect becomes non-significant, however, when the variable inbreeding of dam (step IV) is added to the regression equation. Because of this apparent confounding this interaction term was removed from the regression equation (step V).

The simple correlation between inbreeding of litter and mean birth weight \( r = -0.195 \) was similar to the correlation between inbreeding of dam and mean birth weight \( r = -0.181 \). The exclusion of this variable from the regression equation is probably due to a confounding between inbreeding of dam and inbreeding of litter.

Repeatability and Heritability

Within Litter Variance of Birth Weight

The estimate of repeatability of within litter variance of birth weight is derived from the analysis of variance shown in Table 8. The estimate derived from the
Table 6. Seasonal and yearly means of the components of reproductive performance.

<table>
<thead>
<tr>
<th>Year</th>
<th>No. of litters</th>
<th>Litter size</th>
<th>Mean b.w.</th>
<th>Ave. s2*</th>
<th>Litter weight</th>
<th>Season 0 (mo. 7-12)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>No. of litters</td>
</tr>
<tr>
<td>1953</td>
<td>16</td>
<td>7.4</td>
<td>3.28</td>
<td>.3069</td>
<td>24.43</td>
<td>12</td>
</tr>
<tr>
<td>1954</td>
<td>15</td>
<td>8.8</td>
<td>2.66</td>
<td>.2830</td>
<td>23.42</td>
<td>3</td>
</tr>
<tr>
<td>1955</td>
<td>8</td>
<td>10.3</td>
<td>2.76</td>
<td>.2535</td>
<td>28.27</td>
<td>11</td>
</tr>
<tr>
<td>1956</td>
<td>16</td>
<td>9.9</td>
<td>2.83</td>
<td>.3321</td>
<td>28.13</td>
<td>24</td>
</tr>
<tr>
<td>1957</td>
<td>17</td>
<td>8.2</td>
<td>2.87</td>
<td>.2511</td>
<td>23.56</td>
<td>23</td>
</tr>
<tr>
<td>1958</td>
<td>26</td>
<td>8.8</td>
<td>2.95</td>
<td>.3275</td>
<td>25.99</td>
<td>24</td>
</tr>
<tr>
<td>1959</td>
<td>26</td>
<td>9.1</td>
<td>2.73</td>
<td>.2414</td>
<td>24.52</td>
<td>18</td>
</tr>
<tr>
<td>1960</td>
<td>23</td>
<td>8.3</td>
<td>2.93</td>
<td>.2338</td>
<td>24.63</td>
<td>12</td>
</tr>
<tr>
<td></td>
<td>147</td>
<td>8.76</td>
<td>2.89</td>
<td>.2785</td>
<td>25.31</td>
<td>126</td>
</tr>
</tbody>
</table>

* Average of within litter variance of birth weight
Table 7. Reproductive performance of sire groups used for deriving estimates of repeatability and heritability.

<table>
<thead>
<tr>
<th>Sire</th>
<th>No.</th>
<th>Sows</th>
<th>Litters</th>
<th>Pigs</th>
<th>Dead</th>
<th>Dead</th>
<th>Ave. of Fx of b.w.</th>
<th>Ave. litters of b.w.</th>
<th>Ave. of litters: per sow</th>
<th>Ave. of dams: litter</th>
</tr>
</thead>
<tbody>
<tr>
<td>ME II</td>
<td>8</td>
<td>64</td>
<td>645</td>
<td>68</td>
<td>10.5</td>
<td>.0000</td>
<td>10.1 23.82 .2799 2.86</td>
<td>6.6 2 .1685</td>
<td></td>
<td></td>
</tr>
<tr>
<td>53-149</td>
<td>6</td>
<td>24</td>
<td>201</td>
<td>5</td>
<td>2.5</td>
<td>.1250</td>
<td>8.4  24.39 .2503 2.91</td>
<td>4.0 3 .1800</td>
<td></td>
<td></td>
</tr>
<tr>
<td>54-9</td>
<td>18</td>
<td>62</td>
<td>503</td>
<td>23</td>
<td>5.6</td>
<td>.1622</td>
<td>8.1  23.33 .2606 2.88</td>
<td>5.4 8 .2160</td>
<td></td>
<td></td>
</tr>
<tr>
<td>55-39</td>
<td>12</td>
<td>41</td>
<td>332</td>
<td>11</td>
<td>3.3</td>
<td>.1914</td>
<td>8.1  20.68 .2006 2.55</td>
<td>5.4 6 .1939</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>44</td>
<td>191</td>
<td>1685</td>
<td>112</td>
<td></td>
<td></td>
<td>11.2 47.3 421.2 28</td>
<td>6.6 .1094 8.82 24.74</td>
<td>.2529 2.80 4.34 4.75</td>
<td></td>
</tr>
</tbody>
</table>

*Ave. $s^2$ = Average within litter variance of birth weights*
Table 8. Analysis of variance of within litter variation of birth weights.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>D.F.</th>
<th>M.S.</th>
<th>Component estimated</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total</td>
<td>100</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Between sows</td>
<td>43</td>
<td>.0335546</td>
<td>$V_E + n_0V_p$*</td>
</tr>
<tr>
<td>Within sows</td>
<td>147</td>
<td>.0310846</td>
<td>$V_E$</td>
</tr>
</tbody>
</table>

Repeatability

$$V_p = \frac{.0335546 - .0310846}{4.2} = .000588$$

$$r = \frac{.000588}{.0310846 + .000588} = .02$$

* $V_p = \text{See page 32.}$
data used in this study is .02 which indicates that there was essentially no tendency for sows to exhibit permanent differences for this character.

Because of the low estimate of repeatability no attempt was made to further partition the between sow variance to obtain estimates of heritability. Table 7 shows the average performance of sows by sire groups. It can be seen from these data that little differences exist between the sire groups for within litter variance of birth weights.

**Litter Size**

The estimate of repeatability of litter size in this study determined from the variance between all progeny was 0.295 (Table 9); however, when the differences between sires and dams were removed the repeatability of litter size was 0.208.

To derive estimates of the covariance of sibs the data were corrected for the effects of inbreeding by an analysis of covariance. These corrected values were then used to estimate heritability. To compensate for inbreeding and the increased relationship between half-sibs in excess of the usual 25 per cent, the degree of relationship within each sire group was estimated from the formula

\[
25 \left( 1 + \frac{5F + F'}{1 + F} \right) \]

(23, p. 322) where \( F \) is the inbreeding
of the progeny and $F'$ is the inbreeding of the parents. The weighted mean of the average relationship within sire groups was then determined and the reciprocal (3.1) used in place of the normal multiplier (4) in estimating the additive variance in the heritability equation. As shown in Table 9 the heritability estimates derived from the dam and sire component of the covariance of half sibs were 0.198 and 0.237 respectively.

**Litter Weight**

The estimates of repeatability and heritability were determined from the analysis shown in Table 10. The repeatability of litter weight among all progeny was 0.367; when the effects of sire and dam were removed the estimate became 0.135.

When the variation between sire groups was corrected by covariance for the effects of inbreeding most of the variance between sire groups was removed so that it was not possible to derive a half-sib covariance estimate from the sire component. The heritability determined from the dam component is 0.189.
Table 9. Analysis of variance and covariance of litter size and sib analysis for estimating repeatability and heritability.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>D.F.</th>
<th>M.S.</th>
<th>Adjusted M.S.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total</td>
<td>190</td>
<td>8.7698***</td>
<td>23.2901</td>
</tr>
<tr>
<td>Among Progeny</td>
<td>43</td>
<td>8.7698***</td>
<td></td>
</tr>
<tr>
<td>Sires</td>
<td>3</td>
<td>29.2979</td>
<td>23.2901</td>
</tr>
<tr>
<td>Dams in sires</td>
<td>15</td>
<td>8.1318</td>
<td>8.6905</td>
</tr>
<tr>
<td>Progeny in sires</td>
<td>25</td>
<td>6.6893*</td>
<td></td>
</tr>
<tr>
<td>Within progeny</td>
<td>147</td>
<td>3.1758</td>
<td></td>
</tr>
</tbody>
</table>

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

Repeatability

1. Among all progeny  \[ \frac{8.7698 - 3.1758}{4.2} = 1.3319 \]
\[ r = \frac{1.3319}{3.1758 + 1.3319} = 0.295 \]

2. Progeny within dams \[ \frac{6.6893 - 3.1758}{4.2} = 0.8365 \]
\[ r' = \frac{.8365}{3.1758 + .8365} = 0.208 \]

Heritability

1. Covariance of half sibs \( (\text{dam}) \) \[ \frac{8.6905 - 6.6893}{9.578} = 0.209 \]
\[ h^2 = \frac{3.1(.2090)}{4.2213} = .153 \]

2. Covariance of half sibs \( (\text{sire}) \) \[ \frac{23.2901 - 8.6905}{41.66} = 0.3504 \]
\[ h^2 = \frac{3.1(.3504)}{4.8717} = 0.237 \]
Table 10. Analysis of variance and covariance of litter weight and sib analysis for estimating repeatability and heritability.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>D.F.</th>
<th>M.S.</th>
<th>Adjusted M.S.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total</td>
<td>190</td>
<td>93.35***</td>
<td></td>
</tr>
<tr>
<td>Among progeny</td>
<td>43</td>
<td>93.35***</td>
<td></td>
</tr>
<tr>
<td>Sires</td>
<td>3</td>
<td>623.25***</td>
<td>20.25</td>
</tr>
<tr>
<td>Dams in sires</td>
<td>15</td>
<td>67.79</td>
<td>64.52</td>
</tr>
<tr>
<td>Progeny in dams</td>
<td>25</td>
<td>45.09</td>
<td></td>
</tr>
<tr>
<td>Within progeny</td>
<td>147</td>
<td>27.***</td>
<td></td>
</tr>
</tbody>
</table>

*** = P < .005

Repeatability

1. Among all progeny

\[ r = \frac{15.71}{27.35 + 15.75} = .365 \]

2. Progeny within dams

\[ r' = \frac{4.22}{27.35 + 4.26} = .134 \]

Heritability

1. Covariance of half sibs (dam)

\[ h^2 = \frac{3.1(2.03)}{27.35 + 4.26} = .199 \]
DISCUSSION

The relationship between increased variance of birth weights within litters and increased weight of litter is in general agreement with other studies. Waldorf et al. (39) found that there was an increased standard deviation of birth weights in heavier and larger sow litters as compared with the standard deviation of birth weights of litters farrowed by gilts whose litters were smaller and lighter. Through use of a bivariate regression analysis to relate the logarithm of within litter variance to stage of pregnancy and litter size, Pomeroy (29, p. 37) found that the stage of pregnancy was the most important variable but that litter size also showed a positive effect. Although the absolute ranges of birth weights were not considered in any of the work reviewed nor in this present study, it seems apparent that the increase in variance with increase in litter size, which was highly correlated ($r = 0.924$) with litter weight, is due to an increase in the range of weights within a litter.

An explanation of the physiological causes of greater variation within larger litters cannot be made within the framework of the data available in this study but some inference can be made from studies more specifically related to the physiological mechanisms. One of the more
feasible explanations is the compound effect of intra-uterine crowding and the position of the fetus within the uterus.

Intra-uterine position effects upon fetus weight have been reported by Waldorf et al. (39), Ibsen (17) and by Healy et al. (15) and postulated by McLaren and Michie (24). The haemodynamic theory of Eckstein as employed in the model outlined by McLaren and Michie (24) and Healy et al. (15) proposes that the differences in fetus weight within litters are due to differences in blood supply to fetuses in different intra-uterine positions. McLaren and Michie further proposed that differences in blood pressure occur between the ends and the middle of the uterine horn. These differences in blood pressure are then expressed by heavier fetuses at the ends of the uterine horns and lighter fetuses at the center of the uterine horn.

An exception to the above model is the decreased weight of fetuses occupying the end position of the uterine horn adjacent to the ovary. Healy et al. (15, p. 378) support the haemodynamic theory of fetal growth by showing that, in crowded uterine horns, the end fetus tends to be smaller than the adjacent fetus. These workers show that the end uterine positions share their arterial blood supply with the ovaries so that the fetus is provided with a decreased blood supply. Further evidence given in support of this theory is the tendency for fetuses with fused placentas to be smaller.
Data from studies with pregnant mice cited by Healy et al. (15, p. 378) shows that pairs of fetuses with fused placentas were 17 per cent lighter than their litter-mates but when one of the fetuses of such a pair had died there was no decrease in weight of the remaining fetus.

Work with swine also lends support to the model outlined by McLaren and Michie (24). Waldorf et al. (39) found that a curvilinear regression best described the relationship between fetus weight and uterine position at 105 to 110 days of gestation. The curvilinear effect indicates that fetuses at the two ends of the uterine horn tended to be heavier than fetuses occupying the center positions of the uterine horns.

Under the conditions of the proposed model, the intra-uterine crowding which may occur with large litters should tend to accentuate the indicated position effects. This is deduced from the relationship of increased variation of fetal weight within larger litters. It was pointed out earlier that this relationship must be the result of an increased range of fetal weights within litters. Inasmuch as increased litter size brings about a general decrease in the weights of all the fetuses within a litter one would expect to find the frequency of smaller pigs increased.

Under the conditions of the proposed model of position
effects it is therefore logical to expect the greatest impairment of growth in the less favorable center positions. The result of the combined effects of crowding and intra-uterine position should be a more marked decrease in the weight of fetuses in the center of the uterine horn as compared with those fetuses at more favorable end positions. The above effects are based upon the assumption that an equal distribution of fetuses throughout both uterine horns occurs. Many workers (31, p. 25; 14; 8) show that a fairly even distribution does occur. Furthermore, when one considers that the uterine space requirements of a fetus may be as high as 350 to 400 mm (31, p. 27) it is hard to visualize how large deviations from an even distribution can occur with large litters within the available uterine space.

In considering the increased variance of birth weights within larger litters the factor of crowding alone does not offer a suitable explanation of this phenomena. Crowding alone would be expected to result in a uniform decrease in weights of all of the fetuses rather than an increase in the variation of fetal weight.

The observed negative effect of inbreeding of litter upon within litter variance will be considered as a direct association rather than an indirect association through litter size. The possibility of an indirect association
through litter size is discounted because of the positive relationship between litter size and inbreeding of litter (Table 3). Under these circumstances, any direct effect of inbreeding of litter through the direct effect of litter size should be in a positive rather than the observed negative direction.

The decrease in variation of birth weights with increased inbreeding of litter can be accounted for on the basis of a decreased fetal growth capacity with increased inbreeding. This was observed in the study by Godbey and Godley (12, p. 8) who found decreased birth weights as inbreeding increased. Similar findings are obscured in this study by the positive association between litter size and inbreeding of litter. England (9a, p. 19) found decreased birth weights in single lambs as inbreeding increased. England also found that when twins occurred the depression of birth weights due to inbreeding was not significant. England postulates that under the relatively optimum in-uterus conditions of single lambs, the environmental conditions are such that the outbred or lowly inbred fetus can more adequately express its greater capacity for growth over the inbred fetus; in the relatively sub-optimum in-uterus conditions of twins, however, the uterine environment for the individual fetus was below the genetic capacity for growth of both inbred and outbred
fetuses. This resulted in essentially no differences in birth weights between inbred and non-inbred twins.

In applying the observed negative inbreeding of litter effects to the proposed intra-uterine position and crowding effects, it is postulated that the center positions of the uterine horns provide a sub-optimum environment which is below the genetic growth capacity of fetuses at any level of inbreeding. Thus, the decrease in variance of birth weights with increasing inbreeding would result from the greater opportunity for the outbred or lowly inbred fetus to grow more rapidly in the more favorable uterine positions without a corresponding depressing effect on inbred fetuses in the center positions.

Another means of explaining variation of birth weights is the possibility of differences in time of ovulation and/or fertilization. Studies of ovum transfers in rabbits by Noyes et al. (25) show large differences in fetal weights late in gestation between fetuses of different ages within the same pregnant female. Differences in fetal age was accomplished by transferring four-day-old embryos to females in the third day of gestation. Inasmuch as some workers (6, p. 155) have found increased litter sizes in sows bred on two successive days it may be possible that part of the variation in birth weight is due to a difference in physiological age which resulted from
differences in time of ovulation and fertilization. Unfortunately, no mating records are available to further investigate this possibility.

At the present time the model proposed by McLaren and Michie (24) and the effects of crowding seem to be founded on rather strong evidence jointly and are the most attractive hypothesis of the causes of within litter variation of birth weights.

The estimate of repeatability \( r = 0.02 \) was derived from the analysis of variance shown in Table 3. It is possible that a higher repeatability could have been derived by correcting the data for litter weight or size but in considering the low coefficient of determination \( (0.061) \) it is doubtful whether such a correction would have been beneficial. It is apparent that the magnitude of within litter variation of birth weights was not a permanent characteristic of sows in the Oregon State Berkshire herd. The results in this study suggest that the variation in birth weights within litters is influenced by temporary environmental conditions occurring during gestation. It may be that an analysis of litters which have more than eight or nine pigs will more readily reveal characteristic variation of birth weights within litters.

The negative effect of inbreeding of dam upon litter size (Table 3) is similar to results reported by other
workers (12, p. 3; 36, p. 34; 44). The relationship
between average inbreeding of dam within sire groups and
the corresponding average litter size (Table 7) also indi-
cate that the effects of inbreeding upon reproduction may
not be linear. The apparent leveling off of inbreeding
effects upon litter size might be accounted for by two
factors. The first of these is the possibility of a
critical level of inbreeding for a particular trait within
a population. This concept was advanced by England (9a,
p. 21) in describing certain non-linear inbreeding effects
in sheep. England proposed that a trait is depressed pro-
portionally to increasing inbreeding to a particular level
where it remains constant regardless of further inbreeding.
This concept suggests that the population becomes essen-
tially homozygous for a trait and that no further segre-
gation can occur.

A second factor which can account for the litter size
expression of the sire group 55-39 (Table 7) is chance
segregation or genetic drift. Under conditions of small
population size such occurrences are not infrequent (10,
p. 50-57) and with the sampling conditions used in this
herd such a phenomenon is probable.

The repeatability of litter size (Table 9) of 0.295
is somewhat larger than the estimates of 0.146 and 0.20
found by Lush and Molln (22, p. 37), Hallqvist (13) and Kieth (19) respectively. When differences between sows are corrected for sire and dam groups differences there is a decrease in the repeatability of litter size to 0.208. While the corrected figure more clearly reflects the capacity of the sows within this herd to repeat litter size in successive litters, it must be recognized that by definition the larger figure is repeatability. In considering the nature of the data used in this study the estimate of 0.295 is probably the best estimate of total genetic variability or broad sense heritability.

The narrow sense estimate of heritability of litter size vary between 0.198 and 0.237 for the dam and sire component. These estimates are within the range 0.03 to 0.44 of estimates reported by other workers. Lush and Molln (22, p. 37) derived an estimate of 0.17. Minnesota workers (4; 9; 34) report estimates of 0.16, 0.19 and 0.03 respectively. The latter estimate is based upon a larger population size than the former two studies and may be a reflection of the high degree of inbreeding and selection which occurred within the Minnesota lines.

Falconer (10, p. 181) discussed the efficiency of the various methods of determining heritability estimates and suggests that an optimum size half-sib family would be 20 to 30 individuals. Table 7 shows that the average family
size in this study is 11.2; there is, however, an average of 4.34 litters per individual which provides an average of 47.8 observations per family which should make up for the fewer number of progeny per sire family.

The unusual positive association between inbreeding of litter and litter size (Table 3) is explained by the female composition of the herd. The small nucleus of foundation females kept after the herd clean-up program of 1953 were kept for a longer period of time than other sows in the herd; these eight outbred sows with high performance were kept for an average of 6.6 litters (Table 7). These high producing non-inbreds were mated to related males in each case with resultant litters that were inbred 12.5 to 25.0 per cent. The inbreeding of litter effect was further accentuated by mating inbred sows to non-related boars in 1960.

The observed inbreeding of dam and inbreeding of litter effects strongly suggest that litter size, in this study, is more markedly influenced by maternal characteristics than by the genotype of the offspring. This is especially evident where inbred dams farrowed outbred litters (sire group 55-39, Table 7). This conclusion is in agreement with findings of other studies which show a marked influence of the dam upon litter size either through
ovulation rate (20; 31; 36) or embryo survival (11; 20; 31; 36; 26; 27).

The high negative relationship between litter size and mean birth weight (Table 5) is in general agreement with results reported by other workers (7; 2; 23). This relationship supports the concept that increased numbers of fetuses within a uterine horn restrict fetal membrane size and fetal growth.

The overall reproductive capacity of the sow is probably best expressed by the weight of the litter at birth inasmuch as this factor is the compound expression of ovulation rate, embryo mortality and fetal growth. The estimates of repeatability and heritability of litter weight (Table 10) were derived from the data shown in Table 7.

The repeatability estimate derived from the variation among all progeny is 0.367. When the differences between progeny were corrected for sire group and dam group differences the estimate of repeatability decreased to 0.135. The former estimate (0.367) is a good reflection of the total genetic variability within the population but the latter estimate (0.135) is probably a better estimate of the repeatability of this trait among contemporary sows. The latter estimate is in closer agreement with the estimate of 0.18 reported by Lush and Molln (22, p. 37).
The heritability estimate for litter weight (0.153) was determined from the adjusted dam component of the half-sib analysis (Table 10). The covariance adjustment for inbreeding of dam effects removed most of the variance between sire groups and thus made it impossible to obtain an adjusted sire component for the half-sib analysis. Only one estimate of heritability of 0.44 (9) for litter weight was noted in the literature reviewed.

Litter weight did not level off as did litter size as shown in Table 7. These data further show that average birth weights tended to remain constant as inbreeding increased with each successive sire group up to sire 55-39. Average birth weight declined rather markedly in the 55-39 sire group, even though litter size did not continue to decrease. Maintenance of birth weights at a rather constant level with decreasing litter size and decreased birth weights without decrease in litter size indicates that the uterine environment and fetal growth capacity were decreasing at a rate proportional to the rate of inbreeding. It is probable that mean birth weights were not altered in the first three groups because decreased litter size was compensating for the decreased adequacy of the uterine environment.

The small differences in average inbreeding-of-litter between sire groups might lead to the conclusion that
since inbreeding of litter remained fairly constant, differences in fetal growth capacity, as measured by birth weight, are largely due to maternal effects. Similar conclusions were derived by Lush et al. (23, p. 341) who showed that only eight per cent of the variance in birth weights was due to differences in fetal growth capacity. The averages of inbreeding for sire groups are somewhat misleading in this study and are in need of some clarification. Four of the litters in sire group 54-9 and seven litters in sire group 55-39 were outbred so that the average rate of inbreeding for inbred pigs in these groups was between 23 to 24 per cent.

The positive relationship between litter size and number born dead (Table 4) is similar to the results of other studies (1; 5; 30). These findings indicate that crowding limits the growth and viability of the fetus. Position effects upon fetal death were discussed by Berliner (3, p. 26) who concluded that no relationship existed between uterine position and mortality. Under the conditions of the proposed model of McLaren and Michie (24) one would expect to find a greater amount of fetal mortality in the center positions of the uterine horns. These position effects would be applicable only in cases where fetal death was caused by an inadequate nutrient supply to the fetus. Berliner's evidence does not favor the
model postulated by McLaren and Michie but it does not seem sufficient to refute the postulated position effects upon fetal growth.

The positive curvilinear age-of-dam effect found in the study is somewhat unusual and implies that the number of dead pigs farrowed increases markedly as sows become older. Essentially, this is true in that this relationship is a description of the population and not of individual sows. This effect is a result of the high incidence of pigs born dead in the sire group ME II. At the younger ages the performance of these sows does not markedly influence the population mean of number of pigs born dead; however, as age of dam increases the number of sows in the older age groups decreases to the point that the population is made up of the sows in the sire group ME II.

The negative interaction of age of dam and inbreeding of dam upon number born dead (Table 6) further illustrates the curvilinear age of dam effects in this study. As age of dam increased the performance of the outbred dams of the ME II sire group essentially pulled the mean of the population away from the level of performance of the inbred dams of the other groups and thereby created an interaction effect. The disparity between the outbred sows and the mean of the population at younger ages would further contribute to the interaction effect.
The character of the population from which these data were taken offers some interesting observations and results which have been useful in illuminating certain concepts regarding the effects of inbreeding upon reproductive performance of sows. Furthermore, these data and the results of the statistical analysis performed on them very pointedly show that a literal interpretation of statistical results is misleading and may not be a true reflection of the biological character of the population under study. This is especially illustrated by the positive inbreeding of litter effects upon litter size and the age of dam effects upon number of pigs born dead found in these analyses.

The lack of significant age-of-dam effects upon other traits studied is surprising inasmuch as many of the studies reviewed (7; 14; 16; 19; 21; 22; 25; 39) found such effects. This lack of agreement with other studies may be due to a confounding of factors in the statistical analysis or it may be that the population studied was not markedly influenced by age-of-dam effects.

The validity of correcting the sib-analyses for inbreeding of dam effects is questionable inasmuch as inbreeding effects are genetic; it was felt, however, that this was necessary to bring the various sow groups to a uniform level with respect to a variable that has a marked
effect upon performance for the traits studied. This procedure is justified on the basis that selections are usually made from contemporary groups of sows and if estimates of repeatability or heritability are to be of value, they must reflect the predictive values useful for selection.

The low estimates of repeatability for litter size, litter weight and within litter variance of birth weights indicates that it may not be sound to cull a sow on the basis of a single record of performance for these traits. The relatively low estimates of heritability for litter size (Table 9) and litter weight (Table 10) further suggest that improvement through phenotypic selection for these traits will be slow.

The low coefficients of determinations found in the analyses of litter size ($R^2 = .27$) and within litter variance of birth weights ($R^2 = .06$) show that undefined temporary environmental factors are responsible for much of the variation in the performance of the traits of reproduction. Inasmuch as season effects failed to remove these environmental effects it is proposed that much of the observed variation in reproductive performance is the result of individual environment and gene-environment interactions. The individual environmental variation may
result from changes in social status of a sow within the herd as old sows are replaced by young gilts or changes in the grouping of sows that occur within the herd. The effects of such social phenomenon may be manifested in changes in the amount of stress (either increased or decreased) or harrassment during critical periods of gestation, especially the early embryonic period. A more direct gene-environment interaction mechanism would be a differential response within the herd to environmental stresses such as heat or quantitative or qualitative changes in the diet.

Further investigations to determine the nature of the environmental variables which presently constitute the unknown source of environmental variation will help to provide for management practices which bring about a more constant environment. Under such conditions it should be possible to reduce the environmental variance and thereby more accurately assess the magnitude of gene-environment interactions. Furthermore, a reduced environmental variance will increase the magnitude of the estimates of repeatability and heritability so that phenotypic selection will more accurately identify desired genotypes.

The rather marked effects of inbreeding of dam should be counteracted by employing a wider genetic base populations at the onset of a program of selection and
improvement. Slower rates of inbreeding than those employed in this herd during the time from which these data were taken will also help in offsetting the depressing effects of inbreeding by permitting a greater opportunity for segregation and recombination to occur with consequent increased opportunity for effective selection.
SUMMARY AND CONCLUSIONS

Analyses of genetic and environmental factors influencing the component traits of reproduction, namely, within litter variance of birth weights, litter size, mean birth weight and number of pigs born dead, were made utilizing the method of a stepwise multiple linear regression. From these analyses it was found that:

1. The estimate of within litter variance of birth weights was influenced significantly in a positive manner by litter weight and in a negative direction by inbreeding of litter. It was proposed that the model of fetal growth in multiparous species proposed by McLaren and Michie (24) best described the physiological causes of the observed relationship between litter size and within litter variance of birth weights. The negative effects of inbreeding of litter are explained on the basis of differences in growth capacity of inbred pigs and outbred pigs in the more favorable uterine positions.

2. Inbreeding of litter and inbreeding of dam effects were the only significant variables influencing litter size. The unusual positive relationship between litter size and inbreeding of litter found in this study in addition to the negative effects of inbreeding of dam leads to the conclusion that the size of litter is more strongly
influenced by the genotype of the dam than by the genotype of the offspring within a litter.

3. The positive effects of litter size upon number of pigs born dead is in agreement with other studies cited in the review of literature. The unexpected positive curvilinear effect of age-of-dam is explained as a character of the population from which the data are taken.

4. The average birth weight of pigs within litters was smaller in large litters. This weight is significantly decreased as the inbreeding of dam increases.

An analysis of variance was used to derive estimates of repeatability and heritability for within litter variance of birth weights, litter size and litter weight. From these sib analyses it was found that:

a. Within litter variance has a very low repeatability and does not appear to be a permanent character of the individual sow.

b. The repeatabilities of litter size and weight are 20.8 and 13.5 respectively. From these estimates it was concluded that selection for improvement of these traits would be slow and that genotypes could be better identified by stabilizing temporary environmental factors. The possible role and importance of gene-environmental interactions was also discussed.
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