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DAVID TUPPER SPURR for the Ph. D.
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Title: SOME GENETIC AND ENVIRONMENTAL FACTORS AFFECTING PERFORMANCE AND CARCASS MEASUREMENTS IN SWINE

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D. C. England

Data from 592 litters of pigs farrowed and raised at the Oregon Agricultural Experiment Station at Corvallis from the spring of 1961 through the spring of 1968 were analyzed for effects of year and season of birth, breed, sex, inbreeding and age of dam on measures of fecundity, growth rate and carcass merit. Hierarchal analysis of variance was done to find the effects of population structure and inbreeding on the components of phenotypic variance and heritability for measures of litter size and average daily gain.

The Oregon State University swine herd is composed of a partly closed line of Berkshires, a partly closed herd of Yorkshires, reciprocal crosses between these two breeds and a line developed from inter-se mating of F_1 and later generations. Significant differences among the various breed groups were found for number

of pigs born alive, number born alive plus dead, number born plus mummified fetuses, number weaned per litter, average daily gain, carcass length, average backfat thickness, loin eye area and ham weight. Differences among breeds were not significant for loin weight.

The level of performance did not increase, over the period studied, for any of the traits studied except loin eye area. The lack of increase in level of performance may be due to a lack of sufficient selection pressure, detrimental environmental effects or the depression in performance due to inbreeding.

Fall-farrowed pigs had lower average daily gains than spring-farrowed pigs but, in general, had more desirable carcasses. The differences in performance and carcass traits are attributed to the smaller proportion of males performance tested from fall-farrowed litters. Males gained 0.096 pounds per day faster than females but carcasses were 0.264 inches shorter, had 0.067 inches more average backfat, had ham and loin weights that were 0.798 and 0.516 pounds less respectively and had loin eye areas that were 0.382 square inches smaller.

Negative regressions for the effects of inbreeding of the dam on litter size at birth and weaning and positive regressions for the effect of inbreeding on litter size at birth were found but most effects were not statistically significant. The number of mummified fetuses and stillbirths was not affected by inbreeding but mortality between birth and weaning increased significantly when inbreeding of the dam rose above a threshold of ten percent.

Both linear and quadratic components of age of dam had highly significant effects on the litter size at birth and on the number of pigs weaned with a peak in sow productivity occurring at about three years of age. Age of dam effects were thought to be due almost entirely to differences in ovulation rate or early embryo survival as the number of mummified fetuses, stillbirths or pre-weaning deaths were not related to age of dam.

Environmental variation of litter size and average daily gain increased with increasing levels of inbreeding, indicating that inbred individuals were unable to buffer themselves against fluctuations in environment. Heritability of average daily gain decreased with inbreeding because of lower genetic variance and higher environmental variance. Heritability estimates of litter size were quite variable due to the limited number of sire groups available but, in general, were quite low and generally not significantly different from zero. Estimates of heritability of average daily gain were more than twice as high as most estimates reported in the literature. These high estimates were thought to be biased due to the cumulative effects of a number of characteristics of the population and of the data.

A line developed from a Berkshire-Yorkshire crossbred foundation should have more alleles segregating and therefore should have a higher additive genetic variance than the parental breeds. However, no differences between breed groups were observed in the magnitude of genetic variance, environmental variance or heritability estimates.

Some Genetic and Environmental Factors Affecting Performance and Carcass Measurements in Swine

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Associate Professor of Animal Science
in charge of major

Redacted for Privacy

Chairman of Genetics Board

Redacted for Privacy

Dean of Graduate School

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SOME GENETIC AND ENVIRONMENTAL FACTORS AFFECTING PERFORMANCE AND CARCASS MEASUREMENTS IN SWINE

I. INTRODUCTION

Performance merit in livestock is determined by their capacity for economical reproduction and production. In swine this is a composite of fecundity, liveability, rate of gain, efficiency of feed utilization and carcass quality. By careful selection of breeding stock a breeder may bring about genetic improvement in one or more of the traits that constitute performance merit. The amount of genetic improvement depends on the intensity of selection, the generation interval and the accuracy with which one can estimate the breeding value of the animals. The breeding value of an animal is a function of the heritabilities (correlations between the phenotype and genotype) of the various traits and their economic importance. The selection intensity depends on the proportion of the offspring needed for replacement, the average genetic superiority of the selected animals over that of the generation from which they were raised and on the amount of genetic variation in the population.

It is obvious that selection can be effective only in the presence of genetic variation among individuals or populations. Genetic variability springs from segregation and recombination and is affected by such forces as mutation, chromosomal rearrangement, hybridization, inbreeding and random drift in gene frequencies.

It has generally been found that inbreeding, even at a slow rate, results in a reduction of performance at some level of inbreeding. Inbreeding decline is especially pronounced in lowly heritable traits. In certain situations inbreeding is an unavoidable consequence of the breeding plan. Among these would be herds closed to prevent the introduction of diseased animals, in linebreeding programs, herd thought to be of such high merit that breeding animals of higher merit can be found within the herd than in other herds and herds closed because an accurate assessment of the genetic merit of outside animals becomes very difficult.

The first objective of the present study was to determine the effects of year and season of birth, sex, age of dam and inbreeding on various measures of performance and carcass characteristics in swine. From the information related to the effects of years, certain inferences can be made about the effectiveness of selection in the partly closed sub-populations within the Oregon State University swine herd. Measures of the effects of season of birth, sex, age of dam and inbreeding can be used to develop corrections for these effects and thus improve the evaluation of the genetic value of the animal from its phenotype.

A gene pool developed from a cross of two or more breeds should contain more genetic variability than would be in a population from within a single breed. Inbreeding, on the other hand, would be expected to reduce the amount of the genetic variation in a population and may change the amount of environmental variation. Changes in the relative proportions of these two components of variance may change the effectiveness of selection. Little experimental work has been done on the effect of inbreeding on genetic and environmental variance in populations of economically important species of animals. The second objective of this study was to find the direction and magnitude of change in genetic and phenotypic variation for such lowly heritable traits as measures of fecundity and for a more highly heritable trait, rate of gain, resulting from inbreeding and from crossbreeding.

II. REVIEW OF LITERATURE

Selection and Swine Improvement

The genetic improvement of farm animals is a process of replacing an existing population of genotypes with another which is superior in some particular feature or features of net productive merit. Any method for improving the performance ability of an animal or plant species, including selection methods, must be based on genetic principles. Artificial selection is largely dependent on the ability to classify animals as to their genotype or genetic worth. Accurate classification is complicated by the fact that the phenotype is dependent on both genetic and environmental factors. The breeding value of an animal is therefore a function of the heritabilities or correlations between the phenotypes and genotypes for the various traits.

Heritability

Heritability, in a narrow sense, is defined as the regression of the additive genetic effects on the phenotype, or as that portion of the total phenotypic variance that is due to additive genetic effects. This is essentially the same as the expected average genetic progress made in the next generation when superior individuals are selected as parents. In a broad sense it may be defined as that portion of the total phenotypic variance that is due to hereditary differences between individuals and includes variation that is due to dominance, epistasis, maternal environment and genetic-environmental interaction in addition to additive effects.

Heritability estimates have been made for a number of performance and carcass characteristics and of certain live animal measurements for all species of livestock. A complete review of all heritability estimates is beyond the scope of this discussion, but a summary of some of the estimates in swine found in the literature is presented (Table 1). Estimates of heritability for various productivity traits in swine have varied widely depending on the population used and the method of analysis. Lush (1948) states that heritability estimates are a description of a particular characteristic in a certain population at a certain moment. The ranges found in heritability estimates may represent genuine differences in the populations studied but allowance must be made for sampling errors and/or the possibility of bias due to inclusion of unmeasured non-genetic effects. All methods of estimating heritability are based on resemblance between relatives and include some variance due to epistasis, dominance, maternal influences and genetic-environmental interactions; the proportions depend on the technique used. Dickerson (1960) and Becker (1964) discuss the various components of phenotypic variance that are included in estimates of heritability by various types of

Table 1. Heritability estimates of various conformation, performance and carcass characteristics of swine.[1]

	h^2	
	Range	Approx. avg.
Conformation measurements		
Body length	40-81	59
Leg length	51-75	65
Number of vertebrae	74	74
Conformation score	10-35	29
Nipple number	39	39
Leg weakness scores	-16-56	6
Performance measurements		
Litter size (farrowed)	-11-24	15
Litter size (weaned)	- 9-32	12
Litter wt. at weaning	3-37	17
Wt. at 5-6 months	3-66	20
Growth rate	14-58	29
Economy of gain	2-72	31
Carcass measurements		
Length	40-81	59
Loin eye area	16-79	48
Back fat thickness	12-80	49
Belly thickness	39-72	52
Percent ham	51-65	58
Percent shoulder	38-56	47
Percent fat cuts	42-69	63
Percent lean cuts	14-76	31
Carcass score	35-67	46
Size and shape of ham (score)	61	61
Firmness of fat (score)	40	40

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[1] From Allen, Tribble and Lasley (1959), Craft (1958), Fredeen (1958), Johansson and Kirkman (1951), and Smith (1966).

analysis.

Bradford and Van Vleck (1964) examined 5740 first lactation dam-daughter pairs to determine if the heritable fraction of total variation is related to selection differential and found that heritability was essentially constant over the entire range of phenotypes. Selection response should then be linearly related to selection differential for milk production in diary cattle. Heritability estimates, however, have not always been good predictors of the ability of a population to respond to selection. This may be due to the method of calculation or to the interpretation of the results. Work in Denmark with swine (Fredeen and Jonsson, 1957) and dairy cattle (Hinks, 1968) has shown that the conditions under which the data are collected can affect heritability estimates. Fredeen and Johsson found that elimination of intra-litter competition by individual feeding reduces the within-litter-variation in growth rate and correspondingly increased the estimate of heritability for this trait. Hinks reported a higher heritability for milk yield from test station data than from farm data.

In general, characters associated with reproductive fitness, such as litter size, survival, longevity, and milk production have low heritabilities. Such characters as conformation, fat deposition and many of the measures of carcass merit are more extensively affected by additive genetic effects. Natural and artificial selection has generally been in one direction for characters associated with reproductive fitness, while selection pressure has been mild or in opposite directions at different times for characters such as body conformation (Fredeen, 1958). Intense selection pressure in one direction for a number of generations will increase the degree of homozygosity for loci having additive effects in the traits selected and decrease the proportion of additive genetic variation in a population. However, selection for a trait such as litter size may have been toward intermediate levels because as natural selection will be directed towards the combinations and levels of components that give the highest overall reproductive efficiency.

Genetic Correlations and Correlated Response

Heritability is not the only important genetic parameter that needs to be considered in a breeding program. Genetic correlations between traits should also be considered (Hazel, 1943). Estimates of genetic associations between various traits have generally supported the idea of little or no genetic antagonism between important traits (Hazel, Baker, and Reinmiller, 1943; Dickerson and Grimes, 1947; Johansson and Korkman, 1950; Fredeen, 1953; Fredeen and Jonsson, 1957; King, 1957; Ward, Rempel and Enfield, 1964; Groenwold, 1953; Stockhausen and Boylan, 1966; and Roy, Boylan and Seale, 1968). One exception is Dickerson and Grimes (1947) conclusion that rapid fat deposition, low feed requirements and poor suckling ability tend to be caused by the same genes. Fredeen and Jonsson (1957), however, disputed the antagonism between fat deposition and feed requirements. The concept of genetic correlations makes it possible to consider indirect selection and correlated responses. Searle (1965) discussed the theoretical relationships between heritabilities and genetic correlations and the conditions in which indirect selection for a correlated trait with high heritability might be more effective in improving a trait than direct selection for that trait.

Effectiveness of Selection in Swine

Given the necessary estimates of genetic parameters and the conditions under which a population is maintained, one can make certain predictions as to how the population will change over time. Verification of these predicted changes can be made by examining the results obtained from applying a known amount of selection pressure in experimental populations. Generally, selection has been ineffective for measures of prolificacy and viability, moderately successful for measures of rate of growth and efficiency of feed utilization and quite successful for carcass measurements as one can expect from knowledge of genetic parameters.

The existence of many conflicting reports in the literature appears to result from the fact that most selection attempts were by-products of development of inbred lines and probably reflect difficulties in estimating trends due to inbreeding and environmental changes. Effective selection for litter size has been reported in inbred lines (Comstock and Winters, 1944; Fine and Winters, 1952; and Rempel and Winters, 1952) and in outbred lines (Damon and Winters, 1955) in spite of the low expected response. Dickerson _et al_. (1954), however, report a notable lack of effective selection for litter size in the development of 38 inbred lines of swine. Effective selection for post-weaning growth rate has been reported by Fine and Winters (1953) and for efficiency of feed conversion by Dickerson and Grimes (1947). Dickerson _et al_. (1954) again report a noticeable lack of selection response in growth rate in the formation of inbred lines but again this conflict may be due to bias in estimating the degree of depression due to inbreeding. One of the best examples of effective selection has been the selection for carcass traits under nation-wide field conditions in Denmark (Fredeen, 1958). Carcass length, backfat thickness and belly thickness have been slowly moving in the desired direction since before 1926. Furthermore, the use of official testing stations for genetic improvement of seed stock has greatly improved the national average for the various carcass traits in Denmark. In two lines of Poland China pigs selected for decreased backfat thickness at Missouri, Gray (1965) reported that backfat thickness was reduced by about 20 percent in five generations and that the realized heritability was 0.54 and 0.43 for the two lines. In addition, a correlated response in the desired direction was found in percent of the four lean cuts, loin eye area and percent fat trim. Hetzer and Harvey (1967) carried out selection for both high and low backfat thickness through ten generations in two Duroc lines and through eight generations in two Yorkshire lines. Differences between the high-fat and low-fat Duroc lines differed by 68 percent of the initial mean after ten generations. The corresponding difference between the two selected Yorkshire lines after eight generations was 44 percent. Realized heritabilities of 0.43 and 0.38 were reported for the low-fat and high-fat lines of Yorkshires respectively. Corresponding realized heritabilities for the Duroc lines were 0.48 and 0.47.

Inbreeding and Swine Improvement

Inbreeding is a generic term for mating systems in which individuals are mated to more closely related individuals than random members of the whole population. This above definition permits the establishment of base lines within a line, breed or species from which changes in degree of inbreeding may be measured. The essential consequence of two individuals having a common ancestor is that they both carry replicates of some of the alleles present in the ancestor and if they mate, they may pass on these replicates to their offspring. A method for calculating the coefficient of inbreeding "F" based on the correlation between uniting gametes was devised by Wright (1922). This was further clarified by Malecot (1948) in the development of essentially the same formulas based on the probability that two alleles at any one locus in an individual are identical by descent. Wright's "F" is an estimate of the expected degree of homozygosity over and above that of some specified or implied base population. Gill and Clemmens (1965) using Monte Carlo computer techniques found that both linkage and selection increased the rate of inbreeding in populations of a given size and that the effect of linkage was the greater of the two. Selection for heterozygotes, on the other hand, would cause Wright's "F" to be an overestimate of the degree of increased homozygosity.

Actual Consequences of Inbreeding

Most simply inherited abnormalities are a result of recessive alleles so one can expect an increase in abnormalities with inbreeding. Woodward and Clark (1959) reported a significantly higher number of still-born calves in an inbred population of beef cattle than in a test population, but this increase was not clearly shown to be due to specific simply inherited defects. Donald (1955) presented data to indicate that the frequency of defects in inbred lines of pigs is approximately double that observed in outbred lines. The most common defect was "kinky tail" with a percentage incidence of 4.6 in inbred and 2.1 in outbred lines. Various other abnormalities such as haemophilia, hernia, cryptorchidism and many others have been found in swine but very little information is available on the effects of inbreeding on these traits.

In all species of farm animals inbreeding decline is most severe and selection has been least effective for such traits as measures of reproductive efficiency. Traits of doubtful adaptive value to the animal, such as body measurements which have been under mild or varying selection, show little inbreeding depression and respond well to selection. In general, the more closely a character is related to biological fitness the more it is subject to inbreeding depression.

Reduced litter size at birth and a general reduction of vigor and rate of growth especially in early post-natal periods are characteristic effects of inbreeding in swine. Inbreeding of the dam and inbreeding of the zygote both generally show a depression in measures of litter size (Bradford, Chapman and Grummer, 1958a; Dickerson et al., 1954; and Stewart, 1945). Some reports, however, have shown that only inbreeding of the dam reduced litter size (Bereskin et al., 1968 and Chapman, 1963) while others showed that inbreeding of the litter exhibited a detrimental effect (Godbey and

Godley, 1961). Chapman showed a positive but non-significant regression of inbreeding of the litter on number born but this was explained by the character of the population from which the date were taken. Litter weights and individual birth weights of pigs at farrowing are also affected by inbreeding of the dam and of the litter (Bereskin _et al._, 1968). Nonlinearity of inbreeding depression tends to show up in measures of litter and pig weights (Godbey and Godley, 1961; Bereskin _et al._, 1968). At low levels of inbreeding the depressing effect is not great and the effect tends to level off at higher levels of inbreeding to give a sigmoid regression line. The form of the response curve suggests that the trait resists the detrimental effects of homozygosity at early stages of inbreeding which Lush calls the "margin of safety" effect (Bereskin _et al._, 1968). Bereskin _et al._ (1968) discuss the mechanisms that might be involved to give a sigmoid-shaped curve.

The effect of inbreeding of the litter tends to become more important than inbreeding of the dam for measures of litter size and weight at weaning and this trend continues to later measurements, such as at 154 days or market weight. In general, inbreeding depression is not as pronounced for measures of litter size and weights, pig weights, and body measurements at the older ages. Bradford _et al._ (1958), however, reported that a ten percent increase in inbreeding of the litter decreased the number of pigs raised by

0.45 and reduced the 154 day litter weight by 75 pounds. Bereskin *et al.* (1968) reported that inbreeding of the dam still had a significant effect on 154 day litter weight in addition to its indirect influence on litter weights at farrowing.

Numerous studies have been directed at finding out if inbreeding of the sire depresses the number of offspring in a litter. Hauser et al. (1949) reported that crossbred boars had 30 percent higher body and testes weights at 150 days of age and a 31 percent larger epididimal size than did inbred boars. Inbreeding and line or breed both appear to affect the age at which spermatogenesis first occurs in boars but after the first fertile mating, no differences are found in fertilization rate (Andrews and Warwick, 1949, and Hauser *et al.*, 1952). England (1952), however, obtained results that more heterozygous boars tend to sire larger litters than do inbred boars, but this effect was not definitely evinced. Bereskin *et al.* (1966) reported that among boars that sired at least one live pig, inbreeding of the sire showed no sifnificant effects on litter size at farrowing. If inbreeding does affect reproductive performance of boars, it probably has an all or none effect on the quality or quantity of semen produced.

Effectiveness of Selection during Inbreeding

Early inbreeding experiments with swine and other species have indicated that selection could not overcome the decline in product traits and vigor associated with rapid inbreeding. Assuming that inbreeding depression results from homozygosity of undesirable, recessive alleles, selection should overcome inbreeding depression if the rate of inbreeding is quite slow. This procedure was used in some of the more than 100 lines and crossbred foundations established by the ten Mid-western experiment stations associated with the Regional Swine Breeding Laboratory (Craft, 1953). The technique of selection during inbreeding appears to have been quite successful in some populations but was noted for its lack of success in other populations.

Baker and Reinmiller (1942) reported that no loss in merit occurred in four lines of Duroc Jerseys at Nebraska in spite of the fact that average inbreeding of the lines rose from seven to 30 percent in five years. One measure, 180 day weight actually increased over the period studied. Winters et al. (1943) reported that certain lines in which inbreeding rose 30 percent in five years were at least equal or superior to foundation animals. Comstock and Winters (1944) developed a method for contrasting the expected decline due to inbreeding with the gains expected from selection and found that litter size was more difficult to maintain than rate of gain in inbred lines. Later work with the Minnesota lines (Fine and Winters, 1952, 1953; and Rempel and Winters, 1952) showed that conformation measurements and rate of gain were actually improved while litter size was maintained reasonably well by selection. Another notable example of successfully improving even lowly heritable traits in an inbred line is the Uark line of Poland China swine at Arkansas (Noland, Gifford and Brown, 1964). Litter size, litter birth weight and litter weaning weights were larger in the later years (1955-60) when inbreeding of the dams averaged 60 percent.

Dickerson _et_ _al_. (1954) studied the effectiveness of selection during the development of 38 mildly inbred lines of swine and concluded that even after removing the effects of inbreeding, selection during the development of these inbred lines generally failed to improve any of the measures of performance merit of the lines. Bradford _et_ _al_. (1958) also found that in five inbred lines of swine at Wisconsin, even after adjustment for estimated inbreeding effects, selection for performance during development of inbred lines was apparently ineffective. The disagreement between these two groups of findings appears to result from differences in the populations and in the interpretations of the findings. The estimates of decline caused by inbreeding that were used to correct for inbreeding effects were greater in the Minnesota work than in the work reported by Dickerson _et_ _al_. (1954) and by Bradford _et_ _al_. (1958). The lines studied by Fine and Winters (1952, 1953) were started as crossbred foundations which probably showed a large degree of inbreeding depression or loss of heterosis in the early stages so the larger corrections were probably justified. The Uark line (Noland *et al.*, 1964) was started with inbred animals that were probably screened for undesirable recessives quite well prior to closing the line to outside breeding. The lack of success reported by Dickerson *et al.* (1954) and Bradford *et al.* (1958) may well have resulted from bias due to the time trend method of examining the data or because most of the selection in these lines was automatic rather than deliverate. On the other hand, the Minnesota workers may have overestimated the degree of success because of sampling errors in calculation of heritabilities and degree of depression on inbreeding. Research workers are somewhat hampered by the lack of unbiased methods for examining data for selection in closed lines. In general, however, selection was least effective and inbreeding depression most severe for lowly heritable traits such as litter size and viability. Body conformation at the opposite extreme is little affected by inbreeding and may improve under selection in small closed lines of swine. Growth appears to be intermediate, and shows some decline with increased inbreeding that may be moderated by selection.

Interrelationships Among Genetic Diversity, Inbreeding, Heterosis and Variation

Genetic diversity has long been recognized as a requirement for the expression of heterosis to be manifest in a cross of two lines or breeds and the amount of heterosis exhibited by a cross is customarily used as a measure of the genetic divergence of the parent stock. England and Winters (1953) recorded the heterotic responses resulting from the crossing of inbred lines of swine and found that the amount of heterosis expressed increased as the genetic divergence of the parents increased. Similar evidence has been shown in Drosophila (Wallace, 1955) and in corn (Paterniani and Lonnquist, 1963). In spite of a high correlation between genetic diversity and the degree of heterotic response, individual crosses may not perform as well as expected. Genetic divergence in the parents is needed for heterosis to be manifest in a cross but a large degree of genetic divergence does not always give a heterotic response. The negative heterotic contributions of some loci may cancel positive responses at other loci so that little deviation from the midparent mean results, even though the parent strains have a large degree of divergence (Cress, 1966).

All biological models explaining the phenomena of heterosis are based on the existence of loci having non-additive gene action and on the increase in heterozygosity at these loci that results from outbreeding. Inbreeding depression is assumed to result from increasing homozygosity for loci having non-additive gene action. Heterosis can then be considered to be an antithesis of inbreeding depression.

Very little interest has been given to the effects of inbreeding on phenotypic and genetic variation in populations. Inbreeding causes a redistribution of genetic variance so that between-line variance increases and within-line variance decreases. In other words, it causes genetic differentiation between lines and genetic uniformity within lines. The extent that genetic variance changes is somewhat difficult to calculate as the degree of change depends on gene frequencies and the type of gene action involved (Falconer, 1960). In spite of the fact that genetic variance within lines theoretically should decrease with inbreeding, uniformity of phenotype is not always attained. Fausch (1953) reported a general trend for variation of various production traits in swine to increase in groups of animals having the highest coefficient of inbreeding. Inbred animals may lose the ability to buffer themselves against fluctuations in environment. In many production traits the proportion of additive genetic variance is small relative to the environmental variance so inbreeding may increase the phenotypic variability by increasing the environmental variance more then the genetic variance is decreased. Dickerson _et al._ (1954) presented data that indicated that increased levels of inbreeding in swine caused a decrease in phenotypic variance for highly heritable traits such as conformation scores and that variance remained unchanged for litter size, viability and growth rate. This indicates a difference in gene action between the two classes of performance traits, if we can assume that homozygosity leads to genetic uniformity. Chapman (1963) reported that inbreeding of the litter decreased the within-litter variance of birth weights of pigs. The degree to which inbreeding causes a loss of ability to buffer environmental effects and to increase phenotypic variation appears to be a function of the population, the heritability of the trait and the types of gene action involved.

If the magnitude of genetic and environmental variation changes with increasing homozygosity within a line, we can then expect changes in heritability estimates with inbreeding. Noland _et_ _al._ (1966) used the sire component of variance to investigate the effect of time trends on heritability of various production traits in swine. Heritability of birth weight of pigs that survived to weaning and of weaning weight were found to be much higher for the latter time periods when inbreeding was higher.

Workers at Minnesota investigated the effect of the broadness of the genetic base on heritability estimates (El-Issawi and Rempel, 1961 and Boylan, Rempel and Comstock, 1961). Heritability estimates of growth rate and litter size were no higher in the Minnesota No. 3 line than in the Minnesota No. 1 and No. 2 lines, in spite of the fact that the Minnesota No. 3 was more recently established and was from a broader genetic base. The amount of initial heterozygosity in the establishment of a line does not appear to affect heritability estimates.

Effect of Environmental Variables on Performance Characteristics of Swine

Season, year, location and type of housing have all been reported to affect performance characteristics of swine. Reddy *et al.* (1959) reported that pigs farrowed in the fall have an average of 0.43 mm. more backfat and a rate of gain of 0.14 pound per day lower than pigs farrowed in the spring.

Johansson and Korkman (1950), in an analysis of data from Swedish progeny testing stations using 3036 Swedish Landrace and Large White litters, demonstrated significant ($P < 0.05$) and important station differences in age at slaughter and firmness of fat but not for other performance and carcass characteristics, except for a barely significant difference in backfat thickness. Stothart (1938), using data from 81 litters of Canadian Yorkshires from seven Advanced Registry test stations, demonstrated important station differences in feed economy, length of carcass and loin area. These differences could result from strain differences within the Yorkshire breed in Canada or from the varied climatic conditions found between stations. However, Fredeen (1964) found no evidence of strain formation in the Yorkshire breed in Canada. Station differences are likely caused by the large environmental differences between stations or by variations in pre-test environment as indicated by a wide variation in age of pigs starting test.

Reddy, Lasley and Tribble (1959) reported that pigs reared on pasture in the summer averaged 1.56 mm. more in backfat thickness and 0.24 pound per day more gain per day than those reared on dry lot. This does not agree with the work of Diggs, Baker and Rogers (1965) who reported that pigs on concrete had smaller loin eye areas, more ham fat, a higher loin marbling score and more soft, watery hams than pigs raised on pasture. They found no significant difference in backfat thickness or color of loins between pasture and dry lot fed pigs. Bowland and Berg (1959b) reported differences due to type of housing in pre-and post-weaning performance, but they found no major difference in measures of carcass merit between pigs raised inside and pigs raised outside.

It has been well established that restriction of feed intake, especially for pigs over 100 pounds, results in reduced rate of gain, increased feed efficienty, and leaner carcasses. McMeekan (1940) produced pigs conforming to a predetermined growth curve by controlling the plane of nutrition. Growth of skeleton and muscle was encouraged by keeping pigs on a high plane of nutrition early in the feeding period and then putting them on a low plane of nutrition. This caused the production of a "bacon-type" pig. Restriction of feed early in the feeding period and keeping pigs on a high plane of nutrition later in the fattening period greatly increased the deposition of subcutaneous fat to produce a "lard-type" hog. In another study (Gregory and Dickerson, 1952) limiting of feed intake to an average of 87 percent of that under full feeding caused no detectable change in digestability of dry matter, reduced daily gain by eight percent, decreased feed required per unit of gain by seven percent and produced carcasses with six percent higher scores for quality. Work at the University of Alberta (Berg and Bowland, 1958) has shown that restricting feed intake by allowing pigs to have access to feed for either a one-hour or two one-hour periods per day reduced the growth rate but increased feed efficiency and measures of carcass merit. Salmela _et al._ (1960, 1963), using different breeds and three levels of feeding (liberal feeding, feed restricted to 85 percent of liberal feeding, and feed restricted by adding 20 percent roughage), noticed that restricted feeding had a significant, favorable influence on feed per 100 pound gain, on carcass length and on the proportion of the five trimmed primal cuts. Restriction of feed, however, reduced daily rate of gain and increased age at 200 pounds.

Breed x treatment interactions were found in average daily gains, age at 200 pounds, carcass length, ham weight and loin eye area.

The age of the dam at the time the litter is born has been reported to be more important than either inbreeding of the dam or of the litter in the determination of seven measures of sow productivity (Blunn and Baker, 1947). Lush and Molln (1942) found that litter size increased from an average of eight pigs per litter for gilts to an average of almost ten pigs per litter when the sows were three years of age. Litter size remained at approximately ten pigs per litter until the sows were five years of age and then began to decline. Godbey and Godley (1961) reported peaks in sow age at 24 to 36 months for litter size and weight at birth, birth weight and for many body measurements. Bereskin _et_ _al_. (1968) showed that the effect of age of dam was curvilinear even for first litters from dams aged ten to 19 months.

Most reports show that age of dam does not affect survival from birth to weaning (Godbey and Godley, 1961; Bereskin _et_ _al_., 1968; and Tanhueco and Rigor, 1964). However, Bauman _et_ _al_. (1966) reported higher pre-weaning mortality in the second litter. This may have been due to a relationship between mortality and litter size as both Bauman, Kadlec and Powlen (1966) and Berruecos (1965) reported that mortality increases with litter size. Age of dam appears to have a slight effect on pre-weaning growth as

Bereskin et al. (1968) reported that, although age of dam had practically no effect on number of pigs weaned over the indirect effect on number born, it did have an effect on average weaning weight per pig.

Effect of Sex on Performance Characteristics of Swine

It is generally recognized that in most species males tend to be heavier at any given age than females. This is true in swine as well as in other farm animals where males gain more rapidly and have a larger mature size. Even at birth, male pigs have been reported to be significantly heavier than female pigs (Godbey and Godley, 1961). Craig et al. (1956) reported that males were approximately five percent heavier at birth and three percent heavier at 56 days of age than females. Reddy et al. (1959) in a comparison of 272 gilts and 234 barrows found that gilts had a significantly slower average daily rate of gain than barrows.

Research in Canada by Bennett and Coles (1946) on 281 Yorkshire pigs revealed that gilts took longer to reach market weight but averaged 0.34 inches more in carcass length, 0.78 square inches larger in loin eye area and 0.15 inches less in average backfat depth than barrows. Percent shoulder and ham were 0.5 and 0.4 more respectively for gilts. This agrees with the work of Fredeen (1953) who analyzed data from 12,084 pigs raised at Canadian

Advanced Registry test stations. Females required 5.4 days longer to reach market weight but produced carcass that averaged 0.23 inches more in length, 0.11 inches less in shoulder fat, 0.12 inches less in backfat and 0.11 inches less in loin fat. Loin eye area was 0.53 square inches larger and percent ham and shoulder were 0.12 and 0.57 more respectively for females than for males.

The superiority of carcasses from gilts over those from barrows because of increased length, decreased backfat and greater loin eye area has been confirmed by numerous other studies in Canada (Freedeen and Lambroughton, 1956; Bowland and Berg, 1959a; Fredeen and Plank, 1963; Fredeen *et al.*, 1964), in the United States (Reddy *et al.*, 1959), in the United Kingdom (Buck, Harrington and Johnson, 1962) and in Sweden (Johansson and Korkman, 1950). Fredeen and Plank (1963) reported an unexplained relationship between the number of pigs weaned and fat deposition. Among pigs from large litters, the sex difference in backfat thickness was greater than among pigs from small litters.

A few studies have been carried out to compare performance and carcass characteristics of boars with those of gilts and barrows, although boars are seldom marketed for meat production in most countries because of the problem of adverse meat flavor. Hetzer, Zeller and Hankins (1956) found that the rate of total fat deposition in boars and gilts was essentially the same, but barrows had a much faster rate of deposition of subcutaneous fat. Backfat thickness was greater in barrows than in boars at 175, 200 and 225 pounds, but not at 150 pounds. Gilts were found to have thicker backfat than boars at all four weights but had thicker backfat than barrows only at 150 and 175 pounds. This agrees with earlier work (Comstock, Winter and Cummings, 1944) where not only a sex difference was noticed in rate of liveweight gain but a sex x breed interaction was also found. The earlier maturing Minnesota No. 1 line showed a greater sex difference than did the inbred lines of Poland China. This sex difference was attributed to the suppression of growth rate in the gilts due to the sexual activity at the onset of puberty which occurred at an earlier age in the No. 1 line. Prescott and Lamming (1967) reported that rate of gain from 50 to 250 pounds was very similar for boars and barrows, but boars had a lower dressing percentage and less fat, more lean, bone and skin than did barrows.

III. EXPERIMENTAL

Source of the Data

Data presented were taken from the swine herd maintained at the Oregon Agriculture Experiment Station at Corvallis, Oregon, using records of 568 litters of known ancestry born during the spring- and fall-farrowing seasons from the spring of 1961 through the spring of 1968. The herd consisted of a Yorkshire line, a Berkshire line and a line developed from crosses between the Yorkshires and Berkshires. In this manuscript the term "inter-se" crosses is used to designate animals in the F_2 and later generations. This term is used to avoid any confusion on the part of the reader as the term crossbred my imply F_1 animals rather than later generations. The original herd of 1960 was composed of animals that were not inbred. No breeding stock was introduced into the Berkshire line after the spring of the 1961 farrowing except for one boar used to sire eight litters born in the spring of 1963 and one boar used to sire three litters in the spring of 1966. The Yorkshire line has been closed since prior to 1961 except for one boar used to sire one litter born in the spring of 1963, another used to sire three litters born in the fall of 1964 and semen from another used to sire one litter in the spring of 1967. Berkshire x Yorkshire F_1 pigs have been introduced into the inter-se crossbred line on numerous occasions throughout the period under study.

In 1961 the Oregon State swine herd was established free of major diseases and has been so maintained since that time. Any outbreeding was done by laborious methods to prevent the introduced boars from introducing contagious diseases into the herd.

Management of the herd has been similar from year to year except that the swine herd was moved to new facilities in December, 1965. These new facilities consisted of barns designed for complete confinement of all animals including the breeding herd and they make use of slotted floors and a lagoon for manure disposal. Nutrient content of the rations was quite similar throughout the study but ingredients used in the rations changed to take advantage of changes in relative prices of feedstuffs.

Selection for traits of economic importance was based on a method called the "flexible" system by Winters (1952). An attempt was made to keep animals that were outstanding in one or more traits, with greatest selection emphasis being placed on correcting the weaknesses of the herd at the time. This method attampts to insure that the herd carries desirable genes for all traits but does not require that any one animal be outstanding for all traits. Abnormalities and inherited defects were considered on a minimum culling basis. An electronic computer was used to develop coancestry charts and inbreeding coefficients. Attempts were made to reduce the rate of inbreeding in the herd by mating sows to the least related boar within the line where possible.

Pigs were "ear notched" for identification and weighed at birth and were weaned at approximately eight weeks of age. Weaning weights were recorded, adjusted to 56 days using correction factors as described by Whatley and Quaife (1937). Pigs were kept as litter groups in 8' x 10' pens from birth to market. Occasionally, two or more closely related small litters were maintained in the same pen from weaning to market to make better use of the physical facilities. Boars were usually left uncastrated until their performance indicated a low probability of being selected for use. By 150 pounds all except the top candidates were castrated. Pigs were weighed every two weeks from weaning until they reached 200 pounds. Weekly weights were kept as pigs approached 60 pounds and again as they approached 200 pounds. Average daily gain was recorded from the weekly weights nearest to 60 and to 200 pounds.

Statistical Treatment of the Data

The method of least squares was used to evaluate the effects of various genetic and environmental factors on performance and carcass characteristics. Specific models will be described with the appropriate results.

Sib analyses were used to estimate the heritability of four measures of litter size and of growth rate. The hierarchal analysis of variance for measures of litter size was done using the following model:

$$Y_{ijklm} = \mu + b_i + S_{ij} + d_{ijk} + e_{ijklm}$$

where:

Y_{ijklm}	is the size of the mth litter from the lth individual from the kth dam mated to the jth sire of the ith breed,
μ	is the common mean,
b_i	is the effect of the ith breed,
S_{ij}	is the effect of the jth sire,
d_{ijk}	is the effect of the kth dam,
e_{ijklm}	is the error due to the failure of the model to completely specify all factors affecting Y_{ijklm}.

The litters were divided into inbreeding groups of 0-5, 5-10, 10-15 and over 15 percent inbreeding of dam of the litter. The three breed groups were litters from Berkshire dams, litters from Yorkshire dams and litters from F_1 and inter-se crossbred dams. Analyses of variance were done within each breed and inbreeding group, within inbreeding group but pooled over breed, within breed but pooled over inbreeding group and pooled over both inbreeding and breed groups. Expected mean squares for the hierarchal analyses of variance of litter size are given in Table 2a.

The analysis of variance used to estimate heritability of average daily gain was very similar, except that effects of sex were included in the model.

$$Y_{injkl} = \mu + b_i + C_{in} + S_{inj} + d_{injk} + e_{injkl}$$

where:

Y_{injkl} is the weight constant average daily gain of the l^{th} animal of the n^{th} sex from the k^{th} dam mated to the j^{th} sire in the i^{th} breed,

C_{in} is the effect of the n^{th} sex, and

other parameters are as described in the previous model.

The inbreeding and breed classifications of the l^{th} animal were assigned as for the previous model. Expected mean squares for the analysis of growth rate are given in Table 2b.

Table 2. Expected mean squares for hierarchal analysis of variance used for estimating heritability.

(a) Sib analyses of litter size.

Source of Variation	Expected Mean Square
Breed	$\sigma^2_E + k_3\sigma^2_D + k_5\sigma^2_s + k_6\sigma^2_B$
Sires/Breed	$\sigma^2_E + k_2\sigma^2_D + k_4\sigma^2_s$
Dams/Sire	$\sigma^2_E + k_1\sigma^2_D$
Within full-sib groups	σ^2_E
Total	

(b) Sib analyses of growth rate.

Source of Variation	Expected Mean Square
Breed	$\sigma^2_E + k_4\sigma^2_D + k_7\sigma^2_s + k_9\sigma^2_A + k_{10}\sigma^2_B$
Sex/Breed	$\sigma^2_E + k_3\sigma^2_D + k_6\sigma^2_s + k_8\sigma^2_A$
Sires/Sex	$\sigma^2_E + k_2\sigma^2_D + k_5\sigma^2_s$
Dams/Sire	$\sigma^2_E + k_1\sigma^2_D$
Within full-sib groups	σ^2_E

IV. ANALYSES AND RESULTS

Genetic and Environmental Factors Affecting Performance

Measures of Fecundity

Data from 546 litters of pigs born from the spring of 1961 through the spring of 1968 were used to study the effects of year, season of birth, breed, inbreeding and age of dam on three measures of litter size. These measurements were:

a. number of pigs born alive,

b. number of pigs born alive plus stillborn pigs, called number of pigs born, and

c. number of pigs born plus number of decomposing fetuses or "mummified" fetuses.

The following model was used for analysis by the least squares method.

$$Y_{ijkl} = \mu + y_i + c_j + B_k + b_1F_x + b_2F_D + b_3A + b_4A^2 + e_{ijkl}$$

where:

Y_{ijkl} is the performance of the l^{th} litter from the k^{th} breed, the j^{th} season and the i^{th} year.

μ is the overall mean when F_x, F_D and A are equal to zero,

y_i is the effect of the i^{th} year ($i = 61 - 68$)

c_j	is the effect of the j^{th} season of birth (j = spring, fall),
B_x	is the effect of the k^{th} breed (k = Berkshire, Yorkshire, inter-se and reciprocal F_1's)
b_1, b_2, b_3, b_4	are regression coefficients which furnish a measure of linear relationship between the dependent variable Y_{ijkl} and the continuous independent variables F_x, F_D, A and A^2,
F_x	is the inbreeding coefficient of the litter,
F_D	is the inbreeding coefficient of the dam,
A	is the age of the dam, and
e_{ijkl}	is the error due to the failure of the model to completely specify all factors affecting Y_{ijkl}.

A least squares analysis of variance using a similar model was carried out on data from 490 litters to find the effects of the same independent variables considered in the first model on the number of pigs weaned. In this analysis the 56 litters born in the spring of 1968 were not used.

Least squares constants for the factors affecting the three measures of litter size at birth (Table 3) and litter size at weaning (Table 4) are presented. Year of birth was found to have a significant effect on the number of pigs born alive and the number of pigs weaned ($P < 0.05$) but did not affect the number of pigs born or the number of pigs born plus regressing retuses. There does not appear to be an

Table 3. Least squares constants for the effect of year, season, breed, inbreeding and age of dam on litter size.

	No. of litters	No. born alive	No. born alive + dead	No. born plus mummified fetuses
Over-all mean[1]	546	9.756	10.454	10.626
Year of Birth				
1961	51	.341	-.033	.024
1962	47	-.144	-.506	-.189
1963	79	-.709	-.340	-.160
1964	67	.115	.016	.302
1965	82	.494	.733	-.490
1966	84	-.405	-.214	-.064
1967	80	.224	.261	.337
1968	56	.087	.082	.237
Season of Birth				
Spring	338	-.190	-.178	-.135
Fall	208	.190	.178	.135
Breed of Litter				
Berkshire (1)	149	-2.447	-1.994	-2.090
Yorkshire (2)	181	.237	.235	.332
Inter-se crosses	161	.532	.236	.267
1 ♂ x 2 ♀	19	1.785	1.703	1.722
2 ♂ x 1 ♀	37	-.106	-.182	-.231
Inbreeding	Average			
F_x of litter	10.36	.0135	.0129	.0115
F_x of dam	6.99	-.0297	-.0412	-.0353
Age of dam				
Age	20.32	.192	.194	.225
Age^2	506.37	-.00261	-.00236	-.00281

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[1] Mean adjusted to zero inbreeding and average age of dam.

Table 4. Least squares constants for the effects of year, season, breed, inbreeding and age of dam on litter size at weaning.

	No. of litters	No. weaned
Over-all mean[1]	490	7.766
Year of birth		
1961	51	-.224
1962	47	.490
1963	79	-.987
1964	67	.359
1965	82	.416
1966	84	-.067
1967	80	.015
Season of birth		
Spring	282	-.309
Fall	208	.309
Breed		
Berkshires (1)	132	-2.127
Yorkshires (2)	163	-.203
Inter-se crosses	141	1.062
1 ♂ x 2 ♀	18	1.271
2 ♂ x 1 ♀	36	-.001
Inbreeding	Average	
F_x of litter	10.09	-.0171
F_x of dam	6.97	-.0193
Age of dam		
Age (mo.)	20.27	.208
Age^2 (mo.)	478.94	-.00304

[1] Mean adjusted to zero inbreeding and average age of dam.

Table 5. Mean squares for four measures of litter size.

	df	No. born alive	No. born alive + dead	No. born + mummified fetuses	df	No. weaned
Year	7	15.828*	10.911	12.585	6	18.023*
Season	1	15.878	7,998	13.862	1	41.527*
Breed	4	192.644**	150.630**	130.039**	4	145.386**
F_x of litter	1	3.225	2.354	2.956	1	4.723
F_D of dam	1	20.737	29.318	39.998*	1	7.950
Age of dam	1	104.183**	143.410**	106.357**	1	106.961**
Age^2 of dam	1	64.644**	75.310**	53.163*	1	78.012**
Residual	529	7.852	8.612	8.219	474	8.194
Total	545				489	

* $P < 0.05$

** $P < 0.01$

increase in litter size in the later years, indicating that selection was ineffective. Selection for litter characteristics would occur even if pigs were chosen at random from the population due to differences in litter size. This is referred to as automatic selection. The difference between this and the total selection differential is defined as deliberate selection. Selection pressure for these traits may not have been very intense and automatic rather than deliberate selection may have accounted for nearly all of the selection pressure. Also, detrimental environmental effects on litter size may account for a failure of an increase in later years. However, it may be noted that all of the effects of year were positive for number of pigs born alive and number of pigs weaned after 1963 except for the year 1966. This was the first year of farrowing in the new confinement facilities and some management problems associated with moving to new facilities may have been a factor. Evidence that response to selection was either effective or ineffective can only be substantiated by a comparison of response to the selection actually practiced.

Farrowing was carried out twice a year with the majority of the spring pigs being born in a two month period (March and April) and most of the fall pigs were born during September and October. For convenience in analyzing the data, pigs born in the first half of the year were designated as spring pigs and those born in the last half of the year were designated as fall pigs. Although all four measures of litter size were smaller in the spring-farrowed litters, only the number of pigs weaned was found to be significantly affected by season of birth ($P < 0.05$). This would indicate a possible difference in survival between the spring- and fall-farrowed pigs that could be due to management or other environmental differences.

Analyses were done separately on the Berkshire litters, the Yorkshire litters and on the combination of the inter-se crossbred and F_1 litters using the previously described model with breed effects excluded. These analyses were done on the number of pigs alive at birth (Table 6) and at weaning (Table 7) to find if the effects of year and season of birth, inbreeding and age of dam were different for these three groups of animals.

No significant year and season effects (Table 8) were found in number of pigs alive at birth and at weaning for the Berkshire and Yorkshire litters. There was a slight increase in litter size in the Yorkshires in the later years. This might indicate that selection may have improved prolificacy in this breed even though the effect of years was not statistically significant. Year effects were significant for number of pigs born alive ($P < 0.05$) and for number of pigs weaned ($P < 0.01$) in the crossbred group. Consistent patterns in year effects, however, were not found since superior and inferior years were scattered throughout the period studied. Season effects were not significant in the inter-se crosses.

Table 6. Least squares analysis of variance for number of pigs born alive.

Source of Variation	Berkshires df	Berkshires Mean square	Yorkshires df	Yorkshires Mean square	Inter-se Crosses+F_1s df	Inter-se Crosses+F_1s Mean square
Year	7	.686	7	14.108	7	17.700*
Season	1	10.727	1	38.852	1	15.537
Inbreeding of litter	1	.843	1	.508	1	17.773
Inbreeding of dam	1	1.789	1	71.413**	1	6.178
Age of dam	1	35.828	1	37.633	1	15.298
Age^2 of dam	1	24.730*	1	26.173	1	7.563
Residual	136	6.610	168	10.312	203	6.881
Total	148		180		215	

* $P < 0.05$
** $P < 0.01$

Table 7. Least squares analysis of variance for number of pigs weaned.

Source of Variation	Berkshires df	Berkshires Mean square	Yorkshires df	Yorkshires Mean square	Inter-se Crosses+F_1s df	Inter-se Crosses+F_1s Mean square
Year	6	9.925	6	9.326	6	22.632**
Season	1	.585	1	23.087	1	16.566
Inbreeding of litter	1	.116	1	1.794	1	30.468*
Inbreeding of dam	1	12.545	1	38.277*	1	.018
Age of dam	1	42.501**	1	109.360**	1	23.271
Age^2 of dam	1	33.753*	1	98.135**	1	17.706
Residual	121	6.144	151	9.845	182	7.702
Total	132		162		193	

* $P < 0.05$
** $P < 0.01$

Table 8. Least squares constants for the effect of year, season, inbreeding and age of dam on litter size with breeds separated.

	Berkshire Litters				Yorkshire Litters				Inter-se crossbred and F_1 Litters			
	No. of litters	No. born alive	No. of litters[2]	No. weaned	No. of litters	No. born alive	No. of litters	No. weaned	No. of litters	No. born alive	No. of litters	No. weaned
Over-all mean[1]	149	7.322	133	4.989	181	10.481	163	8.589	216	9.515	194	5.320
Year of birth												
1961	33	.219	33	- .394	17	- .397	17	- .756	1	- .490	1	- .380
1962	9	- 0.20	9	-1.210	18	- .639	18	.850	20	.799	20	1.076
1963	20	- .298	20	- .804	24	- .927	24	-1.010	35	- .314	35	-1.122
1964	13	- .295	13	.863	25	.056	25	.032	29	.825	29	.306
1965	19	.222	19	.722	28	.188	28	.226	35	1.251	35	.480
1966	20	.113	20	.754	28	.055	28	.685	36	- .975	36	- .246
1967	19	.085	19	.068	23	1.512	23	- .025	38	-1.395	38	- .110
1968	16	- .027	9		18	.152	0		22	.298	0	
Season of birth												
Spring	98	.304	82	- .071	113	- .528	97	- .409	127	- .297	105	- .308
Fall	51	-..304	51	.071	68	.528	68	.409	89	.297	89	.308
Inbreeding	Avg.		Avg.		Avg.		Avg.		Avg.		Avg.	
F_x of litter	9.72	.0125	9.75	.0048	14.88	- .0271	14.62	- .0170	7.03	.0634	6.52	.0928
F_x of dam	6.47	- .0159	6.22	.0442	9.82	- .0916	9.99	- .0728	4.97	.0394	4.95	.0023
Age of dam												
Age (mo.)	24.82	.198	24.81	.240	18.07	.304	18.01	.537	19.10	.171	19.04	.221
Age^2 (mo.)	777.6	- .00252	776.2	- .00325	374.0	- .00524	371.3	- .01045	430.2	- .00242	428.0	- .00387

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[1] Mean adjusted to zero inbreeding and average age of dam.

[2] Litters born in the spring of 1968 were not included in the analysis of number of pigs weaned.

Differences among breed groups were found to be highly significant ($P < 0.01$) for all four measures of fecundity. Berkshire litters were significantly smaller than the other breed groups at birth and at weaning. The F_1 litters out of Yorkshire dams exceeded the other four groups in all measures of litter size but differences between this group and other groups were not always significant. The litters from the Berkshire ♂x Yorkshire ♀ matings significantly exceeded those from the Yorkshire ♂x Berkshire ♀ matings for the three measures of litter size at birth but did not significantly exceed them in number of pigs weaned.

The effect of heterozygosity and resulting hybrid vigor was clearly evident for survival of embryos in the early stages of gestation. The F_1 litters from Yorkshire dams were significantly larger than the purebred Yorkshire litters and the F_1 litters from Berkshire dams were significantly larger than the purebred Berkshire litters for all measures of litter size. The number of ovulations could be assumed to be similar for the purebred and F_1 litters. If we could assume that fertilization rate is the same for both groups of litters, then the difference in litter size must be due to the fact that crossbred embryos are better able to survive. This difference in the ability to survive must occur in the early embryonic stages as the number of pigs born plus mummified fetuses followed a similar pattern to all other measures of litter size and the presence of mummified fetuses indicates mortality in the late embryonic stages.

Litter size at birth in the inter-se crossbred population did not differ significantly from that in either of the two classes of F_1 litters. This may indicate that selection for increased litter size offset the inbreeding depression or loss of hybrid vigor that was exhibited in the F_1 litters. There was a slight tendency for the inter-se crosses to have larger litters than F_1s at weaning, indicating that inter-se crosses were more easily able to survive to weaning age.

Yorkshire litters did not differ significantly from the inter-se crossbred litters or from the F_1 litters out of Berkshire dams for the four measures of litter size. Litter size at birth and weaning was significantly smaller in the Yorkshire litters than in the F_1 litters out of Yorkshire dams.

Chi-square analysis was done on pigs from 592 litters to find the effect of breed of the dam on mortality of pigs at different stages (Table 9a). The litters used in this analysis were those used for the least squares analysis plus litters resulting from backcrosses involving animals from the inter-se crosses and Yorkshire or Berkshire parents. The number of mummified fetuses was used as an indication of fetal mortality, the number of stillborn pigs as a measure of mortality at parturition and the number that died between birth and weaning as a measure of ability to survive after birth. This analysis is not directly comparable with the analysis of variance as the data

Table 9. Reproductive performance of various sub classes of pigs in the Oregon State University swine herd.

(a) Breed of dam	No. of Litters	No. Weaned	Pre-weaning Deaths	No. born Alive	No. of Stillbirths	No. Born	Mummified Fetuses	Total Born
Berkshire	176	1042	319	1361	189	1553	24	1574
Yorkshire	213	1576	531	2107	171	2278	70	2348
Inter-se crossbred	203	1754	355	2089	108	2197	55	2252
Total	592	4372	1185	5557	468	6025	149	6174
Chi-square			57.35**		67.50**		84.92**	

(b) Inbreeding of dam	No. of Litters	No. Weaned	Pre-weaning Deaths	No. born Alive	No. of Stillbirths	No. Born	Mummified Fetuses	Total Born
0-5%	288	2165	529	2694	235	2929	47	2976
5-10%	125	962	228	1190	83	1273	58	1331
10-15%	121	890	271	1161	102	1263	34	1297
>15%	58	355	157	512	48	560	10	570
Total	592	4372	1185	5557	468	6025	149	6174
Chi-square			37.32**		3.71		35.50**	

** P <0.01

were divided into three groups according to breed of dam rather than five groups according to breed of litter.

The breed of the dam had a significant effect on the number of mummified fetuses (χ^2 = 84.92, 2df) on the number of stillbirths (χ^2 = 67.50, 2df) and on the number of pigs that died between birth and weaning (χ^2 = 57.35, 2df). The number of mummified fetuses from Berkshire, Yorkshire and inter-se crosses and crossbred dams was 1.52, 2.98 and 2.44 percent respectively of the total number born. Stillbirths accounted for 12.19, 7.51 and 4.92 percent of the pigs born from the Berkshire, Yorkshire and inter-se crosses and crossbred dams respectively. In addition to the fact that Berkshires had a smaller number of pigs born, they had a larger number of stillbirths. The crossbred females had litter sizes almost identical to those of the Yorkshires but had a reduced number of stillbirths to give a larger number of pigs born alive. Moreover, crossbred dams were able to raise 83.96 percent of the pigs born alive to weaning age as compared to 76.56 and 74.80 percent for the Berkshires and Yorkshires respectively.

In the least squares analysis, regression coefficients were positive for the effects of inbreeding of the litter on the three measures of litter size at birth and were negative for the effect of inbreeding of the litter on the number of pigs weaned. This would indicate that prolificacy increases with inbreeding of the litter but that survival from birth to weaning is adversely affected by inbreeding. But, the effects of inbreeding of the litter, however, were not significant for any of the four measures of fecundity. Regression coefficients were negative for the effects of inbreeding of the dam on all four of the measures of litter size indicating that litter size decreases with increasing inbreeding of the dam. However, of these four regression coefficients only the effect of inbreeding of the dam on the number of pigs born plus regressing fetuses was significant ($P < 0.05$).

In the analyses of the three separate breed groups the regression coefficient (Table 8) of inbreeding of the litter on number of pigs weaned was positive and found to be significantly different from zero ($P < 0.05$) for the crossbred plus F_1s but was not significant for number born alive. For each ten percent increase in inbreeding of the litter, litter size at weaning increased by 0.928 pigs. No logical explanation is at hand to explain this positive regression.

A ten percent increase in inbreeding of the dam depressed litter size at birth by 0.916 pigs born alive ($P < 0.01$) and 0.728 pigs weaned ($P < 0.05$) in the Yorkshires. The regression coefficients for inbreeding of the dam on litter size at birth and at weaning were not significant for the Berkshires and for the inter-se crossbreds plus F_1s. These data would indicate that inbreeding effects differ among the three groups being studied.

Chi-square analysis was used to study the effect of inbreeding of the dam on mortality of pigs at different stages (Table 9b). In this analysis 6025 pigs born from 592 litters were used as described previously. The data were divided into four groups of 0-5, 5-10, 10-15 and over 15 percent inbreeding.

Inbreeding of the dam had a significant effect on the number of mummified retuses ($\chi^2 = 31.50$, 3df). However, this effect was largely due to a higher percentage of mummified fetuses in litters from Yorkshire dams having intermediate levels of inbreeding. Mummified fetuses accounted for 1.58, 4.36, 2.62 and 1.76 percent of the total for 0-5, 5-10, 10-15 and over 15 percent inbreeding respectively.

The number of stillborn pigs was not found to be associated with inbreeding ($\chi^2 = 3.71$, 3df). Stillbirths accounted for 8.02, 6.52, 8.08 and 8.57 percent of the number of pigs born for the four levels of inbreeding of the dam.

Inbreeding of the dam had a significant effect on the number of pigs that died between birth and weaning ($\chi^2 = 37.32$, 2df). Dams, having inbreeding coefficients of 0-5 and 5-10 percent, raised 80.36 and 80.84 percent of their pigs respectively while dams with 10-15 and over 15 percent raised only 76.66 and 69.34 percent respectively.

Inbreeding does not appear to affect the dam's ability to conceive and to give birth to pigs but does have an adverse effect on the ability of the dam to raise the pigs born alive to a weaning age of eight weeks. There appears to be a non-linear relationship between inbreeding of the dam and survival. The percentages of pigs that survived were nearly identical in the two groups having the lowest levels of inbreeding. This indicates that the genotype resists the detrimental effects of homozygosity in the early stages of inbreeding and that a threshold is not reached below the ten percent level of inbreeding.

Both the linear and quadratic components of age of dam had highly significant effects ($P < 0.01$) on the three measures of litter size at birth and on the number of pigs weaned. The peak productivity of sows appears to occur at about three years of age or at the time they farrowed their fifth litter (Figure 1). Consideration of the three breed groups independently showed that the Yorkshire sows tended to have an earlier peak of performance and that litter size declined more drastically in the older sows of this breed (Figure 2). The differences among these three breed groups in regard to the effect of age of dam on number of pigs born alive and number of pigs weaned can probably be attributed to the particular structure of the populations. The age of dam at farrowing time was somewhat less in the Yorkshire litters than it was in the Berkshire and inter-se crossbred litters. The absence of disqualifying features, such as blind or inverted nipples, in the Yorkshire line made it easier to

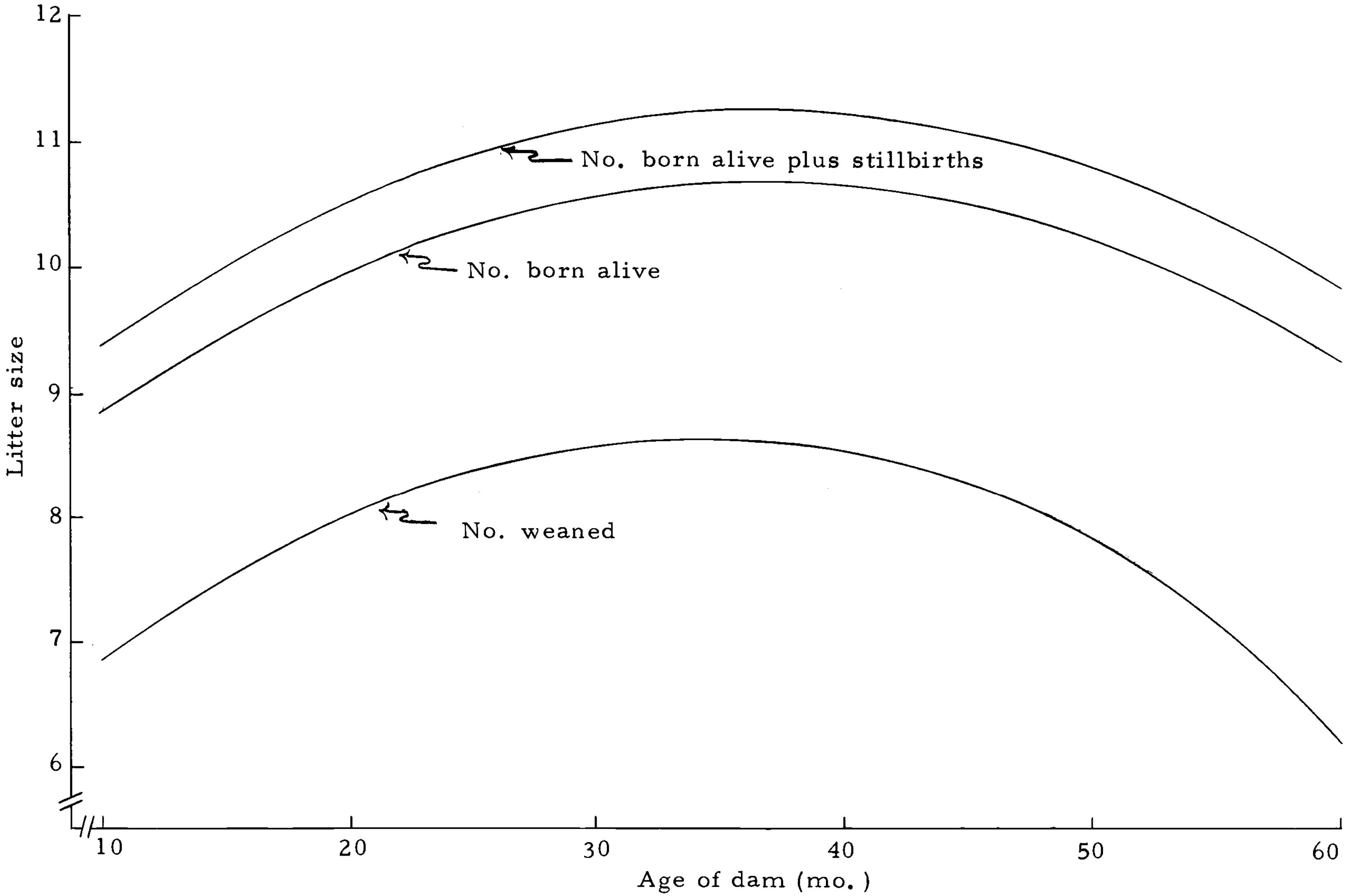

Figure 1. Relationship between age of dam and litter size.

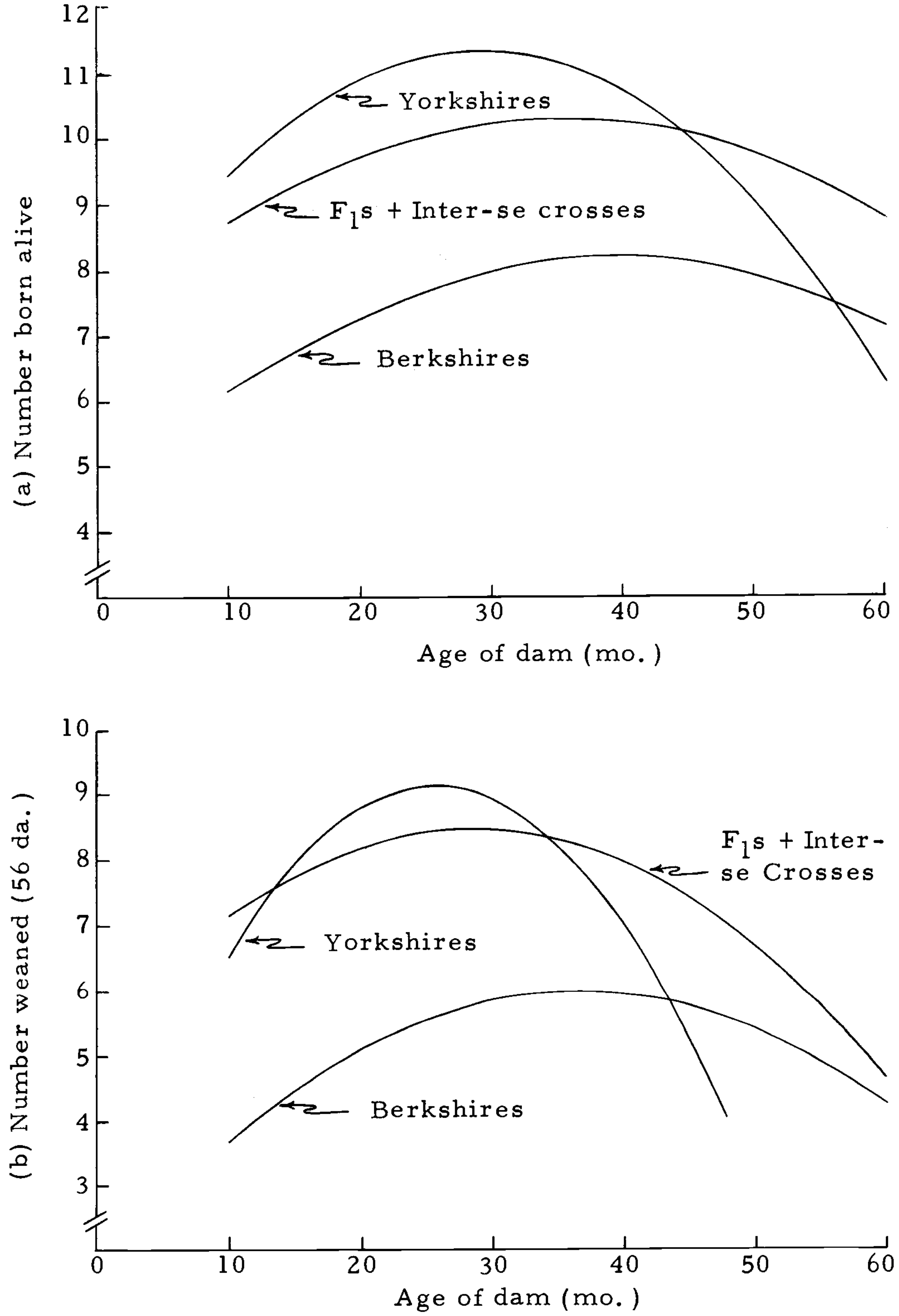

Figure 2. Relationship between age of dam and liter size at birth and at weaning; breeds separated.

replace older animals in the breeding herd with young animals having more desirable performance records. The lack of data from the older Yorkshire dams probably accounts for the drop in Yorkshire regression line at older ages.

Age of dam does not appear to affect the number of stillbirths or the number of pigs that died between birth and weaning (Figure 1) as the regression lines for different measures of litter size follow the same pattern.

Growth Rate

Data from 1764 pigs born from the fall of 1962 through the fall of 1967 were used to estimate the effects of year and season of birth, breed, sex, inbreeding and age of dam on growth rate. Average daily gain was computed on a weight-constant basis using the weekly weight nearest 60 pounds and the weekly weight nearest 200 pounds. Growth rate prior to the fall of 1962 was recorded on an age-constant basis (56 to 154 days of age) and weights were not available to calculate growth rate on a weight-constant basis. Age-constant average daily gains were considered to be a different variable from weight-constant growth rate and so were not included in the analysis.

Of 3117 animals weaned in the various groups considered in this analysis, only 1764 had complete data from which average daily gain could be calculated. Data were not available on the remainder of the animals for a number of reasons, some of which may have biased the results. Death losses and removal of animals from the performance test pens because of injury, excessive tail chewing or illness accounted for some of the missing data. Many animals were removed from the breeding herd soon after weaning and used for various nutrition and production experiments.

The following model was used for analysis by the least squares method:

$$Y_{ijklm} = \mu + y_i + c_j + B_k + S_l + b_1 F_x + b_2 F_D + b_3 A + e_{ijklm}$$

where:

Y_{ijklm}	is the average daily gain of the m^{th} pig from the l^{th} sex, the k^{th} breed group, the j^{th} season and the i^{th} year,
μ	is the over-all mean when F_x, F_D and A are equal to zero,
y_i	is the effect of the i^{th} year (i = 1962-67),
c_j	is the effect of the j^{th} season of birth (j = spring, fall),
B_k	is the effect of the k^{th} breed group (k = Berkshire, Yorkshire, Inter-se crossbred and reciprocal F_1s),
S_l	is the effect of the l^{th} sex (l = male, female),
b_1, b_2, b_3	are regression coefficients which furnish a measure of linear relationship between the dependent variable

Y_{ijklm} and the continuous independent variables F_x, F_D and A,

F_x is the inbreeding coefficient of the pig,

F_D is the inbreeding coefficient of the dam,

A is the age of the dam, and

e_{ijklm} is the error due to the failure of the model to completely specify all factors affecting Y_{ijklm}.

Least squares constants for the factors affecting average daily gain are presented in Table 10. Analysis of variance for average daily gain is recorded in Table 11. Year of birth was found to have a highly significant effect ($P < 0.01$) on rate of growth. The poor growth rate in the later years was probably due to various environmental factors connected with the moving of the swine herd to new facilities in December 1965, rather than to effective selection in the undesirable direction. Pigs removed from the barn normally used for performance testing work since 1965 to another barn for nutrition experiments had consistently higher growth rates than the pigs used in this analysis, suggesting that some undesirable environmental factor(s) exists in the performance testing pens used since December 1965.

The highly significant ($P < 0.01$) effect of season of birth probably resulted from part of the sex effect being included as a season effect. Males gained 0.096 pounds per day more than females,

Table 10. Least squares constants for the effects of year, season, breed, sex, inbreeding and age of dam on average daily gain.

	No. of Pigs	Avg. daily gain (lb. /da.)
Over-all mean[1]	1764	1.661
Year of birth		
1962	42	.023
1963	221	-.018
1964	335	.037
1965	356	.047
1966	498	-.067
1967	312	-.024
Season of birth		
Spring	1197	.031
Fall	567	-.031
Breed		
Berkshire (1)	338	-.017
Yorkshire (2)	573	-.021
Inter-se crossbreds	768	.085
1 ♂ x 2 ♀	47	-.071
2 ♂ x 1 ♀	38	.023
Sex		
Males	854	.097
Females	910	-.097
Inbreeding	Average	
F_x of individual	10.24	.000004
F_x of dam	6.85	.002593
Age of dam (mo.)	21.13	.000100

---

[1] Mean corrected to zero inbreeding and average age of dam.

Table 11. Analysis of variance for average daily gain.

Source of Variation	df	Mean Square
Year	5	1.4678**
Season	1	1.0108**
Breed	4	1.0219**
Sex	1	16.3000**
Inbreeding of litter	1	.0000
Inbreeding of dam	1	.3651*
Age of dam	1	.0011
Error	1749	.08008
Total	1763	

* $P < 0.05$

** $P < 0.01$

a difference which is highly significant. Most nutritional studies with swine at Oregon State University are carried out during the winter months and usually are done using only barrow pigs. Removal of males from the test pens in the fall resulted in a higher proportion of data from females for this season.

The breed of the individual had a highly significant effect ($P < 0.01$) on growth rate. It is interesting that growth rate of both classes of F_1s was not significantly different from the two parental breeds, whereas the inter-se crossbreds had higher average daily rates of gain than either the Yorkshires or Berkshires. Also, the F_1 pigs out of Berkshire dams were significantly superior in average daily gain to the F_1 pigs out of Yorkshire dams.

Inbreeding of the individual was found to have no effect on average daily gain while inbreeding of the dam significantly ($P < 0.05$) affected growth rate but in a positive direction. For each increase of ten percent in inbreeding of the dam, average daily gain was increased by 0.026 pounds per day. No explanation for the positive regression of inbreeding of the dam on average daily gain can be given at this time.

Age of dam did not have a statistically significant effect on average daily gain.

Measures of Carcass Merit

Data from 981 pigs born from the spring of 1962 through the spring of 1967 were used to estimate the effects of year and season of birth, breed, sex, inbreeding and market weight on four measures of carcass merit. These measures were as follows: 1. an average of three carcass backfat measurements, 2. carcass length as measured from the anterior edge of the aitch bone to the anterior edge of the first rib, 3. ham weight and 4. loin weight. Ham weight was determined by weighing both untrimmed hams to the nearest tenth of a pound while loin weight was the weight of both loins skinned and trimmed to remove all but approximately 1/8 inch of the subcutaneous fat.

Of approximately 4500 animals weaned in the various subgroups considered, data from only 981 were available for this analysis. Data on the remainder of the animals were not available for a number of reasons. In addition to loss of animals due to death, injury, illness and the removal of animals for other experiments, as was the case for growth rate, some snimals were selected for replacement or sold for breeding stock. An attempt was made to collect data from a sample of at least two animals from each litter. This did not always occur as the data varied from no carcass data from some litters to carcass data from the entire litter. It seems probable that any bias present is not related to any subgroup.

The statistical model used for fitting constants by the least squares method was as follows:

$$Y_{ijklm} = \mu + y_i + c_j + B_k + s_l + b_1F_x + b_2F_D + b_3Wm + e_{ijklm}$$

where:

Y_{ijklm}	is the carcass measurement on the m^{th} animal of the l^{th} sex, the k^{th} breed group, the j^{th} season and the i^{th} year,
μ	is the over-all mean when F_x, F_D and Wm are equal to zero,
y_i	is the effect of the i^{th} year (i = 1962-67),
c_j	is the effect of the j^{th} season of birth (j = spring, fall),
B_k	is the effect of the k^{th} breed group (k = Berkshire, Yorkshire, Inter-se crossbred and reciprocal F_1s),
b_1, b_2, b_3	are regression coefficients which furnish a measure of linear relationship between the dependent variable Y_{ijklm} and the continuous independent variable F_x, F_D and Wm,
F_x	is the inbreeding of the individual,
F_D	is the inbreeding of the dam,
S_m	is the live weight at slaughter and,

e_{ijklm} is the error due to the failure of the model to specify completely all factors affecting Y_{ijklm}.

Loin aye area values as measured by using a planimeter on a tenth rib tracing were available on 761 of the 981 pigs described above. This same model was used to analyze the loin eye area data.

Least square constants of the factors affecting carcass traits are presented in Tables 12 and 13. Year effects were highly significant ($P < 0.01$) for loin eye area, average carcass backfat, ham weight and loin weight, and significant ($P < 0.05$) for carcass length (Table 14). In spite of the statistically significant effects due to year, there does not appear to have been a trend either upward or downward for the carcass traits except for loin eye area and possibly loin weight. Whenever possible, records of loin eye area of litter mates were examined before an animal was selected as a replacement boar or gilt. Loin eye area is more highly correlated phenotypically with loin weight than is carcass length (Harrington, 1958) so any selection pressure for increased loin eye area should cause an increase in loin weight.

The highly significant effect ($P < 0.01$) of season of birth on average carcass backfat, carcass length and loin weight may have been a true season effect or may have been due to a sex effect. Carcasses from females were 0.264 inches longer, had 0.067 inches less backfat thickness and had loin eye areas that were 0.382 square

Table 12. Least squares constants for the effects of year, season, breed, sex, inbreeding and market weight on various carcass measurements.

	No. of Pigs	Avg. carcass Backfat	Carcass Length	Ham Weight	Loin Weight
Over-all mean[1]	981	1.3857	30.772	29.699	23.786
Year of birth					
1962	100	.0108	.149	.589	.260
1963	42	-.0537	-.024	-.612	-1.478
1964	127	.0305	-.128	-1.085	-.818
1965	217	.0171	-.065	-1.54	.816
1966	292	-.0121	.119	1.303	1.208
1967	203	.0079	-.051	-.038	.011
Season of birth					
Spring	638	-.0266	.246	.185	.233
Fall	343	.0266	-.246	-.185	-.233
Breed					
Berkshire (1)	177	.0000	-.680	-1.027	.350
Yorkshire (2)	300	-.0358	.615	.542	.217
Inter-se crossbred	434	-.0072	.144	.479	-.135
1 ♂ x 2 ♀	42	.0538	-.149	.069	.392
2 ♂ x 1 ♀	28	-.0107	.067	-.064	-.040
Sex					
Males	511	.0334	-.132	-.399	-.258
Females	470	-.0334	.132	.399	.258
Inbreeding	Average				
F_x of individual	10.32	-.00022	.0039	-.0049	-.0199
F_x of dam	7.64	-.00233	-.0006	.0130	.0001
Live slaughter weight (lb.)	218.2	.00228	.0180	.0522	.0502

[1] Mean adjusted for zero inbreeding and average market weight.

Table 13. Least squares constants for the effects of year, season, sex, inbreeding and market weight in loin eye area.

	No. of Pigs	Loin eye area (in.^{2})
Over-all mean[1]	761	3.963
Year of birth		
1962	123	.166
1963	55	-.680
1964	126	-.127
1965	216	.241
1966	241	.307
1967	138	.096
Season		
Spring	453	-.021
Fall	308	.021
Breed		
Berkshire (1)	148	.319
Yorkshire (2)	239	-.323
Inter-se crossbred	309	-.076
1 ♂x 2 ♀	38	.057
2 ♂x 1 ♀	27	.025
Sex		
Males	377	-.191
Females	384	.191
Inbreeding	Average	
F_x of individual	10.54	.00862
F_x of dam	7.51	.00174
Live slaughter weight (lb.)	217.4	.00382

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[1] Mean corrected to zero inbreeding and average market weight.

Table 14. Least squares analysis of variance for measures of carcass merit.

Source of Variation	df	Loin eye area	df	Avg. carcass backfat	Carcass length	Ham weight	Loin weight
Year	5	1.0333**	5	.1401**	4.132*	119.708**	88.353**
Season	1	.2268	1	.4325**	37.143**	20.898	33.302**
Breed	4	7.8601**	4	.0958*	39.297**	80.259**	9.016
Sex	1	24.0553**	1	.9728**	15.258**	138.488**	58.089**
Inbreeding of individual	1	1.4898*	1	.0013	.409	.653	10.627
Inbreeding of dam	1	.0728	1	.1681*	.012	5.258	.000
Market weight	1	5.8628**	1	2.5202**	157.611**	1322.634**	1225.932**
Residual	746	.3137	966	.03286	1.737	9.555	4.467
Total	760		980				

* $P<0.05$

** $P<0.01$

inches larger than those from the males. Ham and loin weights were 0.798 and 0.516 pounds heavier respectively for the females. All sex differences were highly significant ($P < 0.01$). As mentioned previously, the data from the fall-farrowed litters consisted of a larger proportion of females because of removal of males for nutrition and production studies.

Significant breed effects were found for all of the carcass traits studied except loin weight (Tables 11 and 12). Differences among the two classes of F_1s and the inter-se crossbreds were not statistically significant for loin eye area and carcass length. Yorkshire pigs had significantly longer carcasses and significantly smaller loin eye areas than the inter-se crossbreds. Berkshires, on the other hand, had significantly shorter carcasses and significantly larger loin eye areas. Negative correlations between loin eye area and carcass length have been reported (Harrington, 1958). Shorter pigs tend to have larger loin eye areas. Thus increases in carcass length and loin eye area tend to cancel one another in effect on loin weight so that loin weight becomes primarily a function of the weight of the animal rather than of carcass length or size of loin eye area. Carcasses from Yorkshire pigs had significantly less average backfat than did those from F_1 pigs out of Yorkshire dams. No other differences among the breed groups were found in backfat thickness. Hams from Berkshire pigs were significantly lighter than those from

Yorkshire and inter-se crossbreds, but were not significantly lighter than those from the F_1 pigs.

There was a strong tendency for the measures of carcass merit of the F_1 pigs to be intermediate between the two parent breeds. This would be expected as heterosis is not generally manifested for highly heritable traits such as carcass measurements. Of the two parent breeds, Berkshires were superior in some measures of carcass merit and inter-se crossbreds were superior in others. Theoretically, a crossbred foundation developed from these two breeds would provide desirable genes for all measures of carcass merit. No evidence was found that selection was able to combine the desirable carcass characteristics of the two breeds in the inter-se crossbred population.

No significant effects of inbreeding of the individual or of the dam were found for average backfat thickness, carcass length or weights of the ham and loin.

Age of dam was not included in the model used in the analysis of carcass measurements.

Effect of Breed and Inbreeding on Phenotypic and Genetic Variance

Measures of Litter Size

Within breed sib-analysis was done for the three measures of litter size at birth and for the number of pigs weaned, using uncorrected data from 176 litters of Berkshires, 213 litters of Yorkshires and 203 litters from F_1 and inter-se crossbreds. The litters were divided into four groups of 0-5, 5-10, 10-15 and over 15 percent inbreeding of the dam. Analysis of variance was carried out within each of the inbreeding and breed groups, for data pooled over breeds, for data pooled over all levels of inbreeding and for data pooled over both inbreeding and breed groups. Breed, sire, dam and daughter components of variance were calculated. Paternal half-sib (PHS), maternal half-sib (MHS) and full-sib (FS) estimates of heritability were made using the following formula:

$$h^2_{PHS} = \frac{4\sigma^2_s}{\sigma^2_S + \sigma^2_D + \sigma^2_E}$$

$$h^2_{MHS} = \frac{4\sigma^2_D}{\sigma^2_S + \sigma^2_D + \sigma^2_E}$$

$$h^2_{FS} = \frac{2(\sigma^2_s + \sigma^2_D)}{\sigma^2_S + \sigma^2_D + \sigma^2_E}$$

The number of degrees of freedom for the hierarchal analyses of variance of the four measures of litter size are given in Table 15.

Estimates of sire, dam and daughter components of variance and of total phenotypic variance for each of the breed groups are

Table 15. Number of degrees of freedom used in hierarchal analysis of variance of litter size.

Level of Inbreeding of Daughters	Source of Variation	Berkshires		Yorkshires		Inter-se Crosses		Pooled over Breeds	
		B[1]	W[1]	B	W	B	W	B	W
$0 \leq F_x \leq 5$	Breed							2	2
	Sires	6	6	10	10	14	13	30	29
	Dams	12	12	8	8	7	6	27	26
	Daughters	92	84	53	52	83	81	228	217
$5 < F_x \leq 10$	Breed							2	2
	Sires	7	7	7	7	9	9	17	17
	Dams	3	3	0	0	4	3	7	6
	Daughters	16	14	24	23	58	57	98	94
$10 < F_x \leq 15$	Breed							2	2
	Sires	2	2	8	8	3	3	13	13
	Dams	6	5	4	4	1	1	11	10
	Daughters	15	14	58	57	21	21	94	92
$F_x > 15$	Breed							1	1
	Sires	13	13	8	8	0	0	10	10
	Dams	0	0	5	5	0	0	5	5
	Daughters	11	13	30	28	0	0	41	39
Pooled over all levels of inbreeding	Breed							2	2
	Sires	16	16	23	23	25	24	64	63
	Dams	25	24	23	23	15	13	63	60
	Daughters	134	123	166	161	162	159	462	443

[1] B = three measures of litter size at birth.

[2] W = litter size at weaning.

given in Table 16. Daughter components of variance are estimates of variance among full sibs. They were considered to be an estimate of environmental variance. Negative components of variance for sire and/or dam were present for some groups and were assumed to be zero in calculating the total phenotypic variance.

A gene pool developed from a crossbred foundation should theoretically have a larger number of alleles segregating than an inbred population or a gene pool composed of animals of one breed. Some of the segregating alleles would increase and some would decrease the genetic value of the animals. The genetic and phenotypic variation in measures of litter size would therefore be expected to be different among the inter-se crossbreds than among the Berkshires and Yorkshires. The degree of change in the components of phenotypic variance cannot be predicted as any change depends not only on the degree of genetic divergence between the parental breeds but also on the number of alleles segregating and on the type of gene action involved for the trait. In this study both the genetic and phenotypic variation among the inter-se crossbred dams were very similar to that of the Berkshire dams. The Yorkshires, on the other hand, were more variable in all measures of litter size. Use of the coefficient of variation rather than total variance did not cause a change in these trends.

Total phenotypic variance for the number of pigs born alive for

Table 16. Estimates of components of variance by breed groups for four measures of litter size.

Measure of Litter Size	Breed	Sire Component	Dam Component	Daughter Component	Total Phenotypic Variance
No. born alive	Berkshire	.0862	1.1551	6.3139	7.5552
	Yorkshire	.3946	.7003	9.3469	10.4419
	Inter-se crosses	-.2111	-.3990	7.9173	7.9173
	Pooled	.0711	.5563	7.9659	8.5933
No. born	Berkshire	-.0477	1.5525	6.2538	7.8063
	Yorkshire	.9299	.2537	8.7527	9.9363
	Inter-se crosses	-.4927	-.5974	8.8805	8.8805
	Pooled	.1365	.4750	8.0727	8.6842
No. born plus mummified fetuses	Berkshire	.0238	1.2071	6.7329	7.9638
	Yorkshire	.8068	.6824	8.8953	10.3845
	Inter-se crosses	-.3734	-.2655	8.7920	8.7920
	Pooled	.1319	.5915	8.2319	8.9553
No. weaned	Berkshire	-.3907	.8595	6.8696	7.7292
	Yorkshire	-.2688	1.2751	9.1094	10.3845
	Inter-se crosses	-.4066	.2864	7.9663	8.2527
	Pooled	-.3900	.8402	8.0772	8.9174

the most highly inbred group was 175 percent as it was for the group with the lowest inbreeding coefficients (Table 17). Comparable figures for the number born alive plus dead, the number born plus mummified fetuses and the number weaned were 174, 179 and 174 percent respecitvely. The fact that the variance of litter size from dams with inbreeding coefficients of over 15 percent were consistently about 1.75 times as great as they were for litter size of dams having inbreeding coefficients of five percent or less is quite interesting. This increase in variation in measures of litter size appears to be almost entirely due to an increase in environmental variation as there were consistent increases in daughter components of variance with increasing levels of inbreeding for all measures of litter size. Sire and dam components of litter size (Table 17) did not show any trends that were related to inbreeding of the dam. Paternal half-sib, maternal half-sib and full-sib estimates did not appear to change as inbreeding increased (Tables 18-21). However, standard errors of heritability estimates were quite large and estimates were generally not significantly different from zero.

Various methods based on the degree of resemblance between relatives have been developed for estimating heritability. The choice of the method used depends on:

1. which sets of relatives are available in sufficient numbers to give a reliable estimate of heritability,

Table 17. Estimates of components of variance by level of inbreeding for four measures of litter size.

Measure of Litter Size	Level of Inbreeding	Sire Component	Dam Component	Daughter Component	Total Phenotypic Variance
No. born alive	0-5	-.2327	0.6145	6.8392	7.4537
	5-10	1.3187	0.1509	6.4768	7.9464
	10-15	-.1041	-.1855	10.7169	10.7169
	>15	-.4886	1.4422	11.5973	13.0395
	Pooled	0.0711	0.5562	7.9659	8.5932
No. born	0-5	-.0991	0.4484	7.3302	7.7786
	5-10	-.2138	1.5528	7.2084	8.7612
	10-15	0.0878	0.2102	8.8360	9.1340
	>15	0.1202	0.7516	12.6335	13.5053
	Pooled	0.1366	0.4750	8.0727	8.6843
No. born plus mummified fetii	0-5	-.0761	0.5999	7.5195	8.1194
	5-10	-.1207	0.8364	8.1799	9.0663
	10-15	0.3512	0.5454	8.0696	8.9662
	>15	-.9006	1.6978	12.8507	14.5485
	Pooled	0.1319	0.5915	8.2319	8.9553
No. weaned	0-5	-.2364	0.2683	7.3064	7.5747
	5-10	-1.3870	1.2528	7.9307	9.1835
	10-15	0.1780	0.6714	8.7498	9.5992
	>15	1.8841	-1.6869	11.3088	13.1929
	Pooled	-.3900	0.8402	8.0772	8.9174

Table 18. Heritability estimates and standard errors of number of pigs born alive from sire, dam and full sib components, by breed and inbreeding groups.

Inbreeding	Method of Calculation	Berkshires	Yorkshires	Inter-se Crosses	Pooled over Breeds
0-5	PHS	-35.8 ± 36.6	46.8 ± 69.7	-21.7 ± 23.8	-12.9 ± 25.7
	MHS	92.9 ± 62.3	36.2 ± 54.8	-118.3 ± 22.8	34.0 ± 30.7
	FS	28.5 ± 21.6	41.5 ± 35.0	-70.0 ± 15.5	10.6 ± 11.7
5-10	PHS	88.6 ± 133.9		0.0 ± 66.5	66.4 ± 61.3
	MHS	7.5 ± 119.7		18.5 ± 58.3	7.6 ± 43.9
	FS	48.0 ± 58.1		9.3 ± 28.4	37.0 ± 27.3
10-15	PHS	36.8 ± 101.4	-9.6 ± 57.4	83.6 ± 202.5	-4.0 ± 36.1
	MHS	-25.9 ± 100.5	10.0 ± 66.1	40.0 ± 141.8	-7.1 ± 46.4
	FS	5.5 ± 59.7	.2 ± 18.1	21.8 ± 85.9	-5.6 ± 13.2
>15	PHS		9.8 ± 69.6		-15.6 ± 76.7
	MHS		-2.1 ± 145.8		45.9 ± 163.6
	FS		3.8 ± 99.9		15.2 ± 99.9
Pooled	PHS	4.5 ± 30.2	15.1 ± 27.0	-11.6 ± 20.7	3.3 ± 15.2
	MHS	61.1 ± 41.0	26.8 ± 34.8	-21.8 ± 28.3	25.9 ± 20.9
	FS	32.8 ± 17.4	21.0 ± 13.0	-16.7 ± 8.8	14.6 ± 7.3

Table 19. Heritability estimates and standard errors of number born alive and dead from sire, dam and full sib components, by breed and inbreeding group.

Inbreeding	Method of Calculation	Berkshires	Yorkshires	Inter-se Crosses	Pooled over Breeds
0-5	PHS	-26.8 ± 34.0	64.3 ± 75.0	-30.3 ± 21.8	-5.2 ± 24.5
	MHS	73.0 ± 55.0	39.4 ± 53.9	-105.4 ± 25.9	23.4 ± 28.1
	FS	23.1 ± 37.5	51.8 ± 37.5	-67.9 ± 14.1	9.1 ± 11.4
5-10	PHS	-179.8 ± 288.9		-22.5 ± 67.9	-10.0 ± 81.5
	MHS	337.9 ± 361.0		23.7 ± 64.0	72.7 ± 79.5
	FS	79.0 ± 65.0		0.5 ± 28.1	31.3 ± 30.7
10-15	PHS	21.3 ± 90.4	33.4 ± 57.9	-85.4 ± 85.3	3.8 ± 40.8
	MHS	99.1 ± 145.0	-10.6 ± 48.7	-26.6 ± 63.0	9.2 ± 50.1
	FS	38.9 ± 54.0	11.3 ± 24.5	-56.0 ± 37.5	6.5 ± 14.7
>15	PHS		1.2 ± 67.8		3.6 ± 72.6
	MHS		-32.9 ± 142.7		22.3 ± 150.9
	FS		-15.8 ± 99.9		12.9 ± 99.9
Pooled	PHS	2.4 ± 31.4	37.4 ± 28.6	-25.3 ± 18.2	6.3 ± 15.1
	MHS	80.0 ± 45.3	10.2 ± 29.7	-30.7 ± 27.1	21.9 ± 20.2
	FS	38.8 ± 18.2	23.8 ± 14.2	-28.0 ± 7.9	14.1 ± 7.3

Table 20. Heritability estimates and standard errors of number born plus mummified fetuses from sire, dam and full sib components, by breed and inbreeding groups.

Inbreeding Coefficient	Method of Calculation	Berkshires	Yorkshires	Inter-se Crosses	Pooled over Breeds
0-5%	PHS	-29.8 ± 33.5	63.8 ± 75.4	-19.8 ± 25.5	-3.7 ± 25.7
	MHS	74.5 ± 55.7	41.2 ± 54.6	-87.9 ± 28.8	29.8 ± 29.3
	FS	22.3 ± 19.8	52.5 ± 37.7	-53.9 ± 14.3	13.0 ± 12.0
5-10%	PHS	23.4 ± 154.2		-45.1 ± 88.4	-5.4 ± 66.9
	MHS	64.1 ± 166.6		57.1 ± 86.0	37.6 ± 64.7
	FS	43.7 ± 55.9		6.0 ± 35.5	16.1 ± 25.8
10-15%	PHS	-22.9 ± 81.4	51.3 ± 75.7	-57.4 ± 82.2	15.7 ± 47.5
	MHS	75.2 ± 139.4	21.5 ± 63.3	-26.6 ± 57.6	24.3 ± 53.1
	FS	26.1 ± 51.0	36.4 ± 31.0	-42.0 ± 36.8	20.0 ± 17.8
>15%	PHS		-1.9 ± 67.7		-26.4 ± 76.7
	MHS		-8.3 ± 148.9		49.8 ± 168.4
	FS		-5.1 ± 99.9		11.7 ± 99.9
Pooled	PHS	1.2 ± 29.3	31.1 ± 30.0	-18.3 ± 21.1	5.9 ± 15.5
	MHS	60.6 ± 41.1	26.3 ± 33.5	-13.3 ± 31.1	26.4 ± 20.8
	FS	30.9 ± 17.0	28.7 ± 14.6	-15.7 ± 8.2	16.2 ± 7.4

Table 21. Heritability estimates and standard errors of number weaned from sire, dam and full sib components, by breed and inbreeding groups.

Inbreeding	Method of Calculation	Berkshires	Yorkshires	Inter-se Crosses	Pooled over Breeds
0-5	PHS	1.7 ± 35.7	-55.3 ± 59.6	-5.2 ± 29.1	-12.9 ± 22.9
	MHS	32.3 ± 41.6	46.2 ± 70.7	-85.1 ± 25.9	14.6 ± 27.7
	FS	17.0 ± 19.9	-4.6 ± 30.2	-45.2 ± 15.9	.9 ± 10.6
5-10	PHS	42.2 ± 126.9		-117.4 ± 171.7	-71.2 ± 93.0
	MHS	-77.2 ± 111.0		110.9 ± 134.1	64.3 ± 84.6
	FS	-17.4 ± 65.4		-3.2 ± 74.3	-3.4 ± 36.8
10-15	PHS	88.3 ± 186.2	25.4 ± 68.6	45.7 ± 155.9	7.4 ± 50.2
	MHS	93.9 ± 118.9	31.8 ± 80.3	13.8 ± 85.2	28.0 ± 55.2
	FS	91.1 ± 93.8	3.2 ± 20.3	29.8 ± 71.2	17.7 ± 18.4
>15	PHS		83.9 ± 92.2		65.5 ± 79.6
	MHS		-68.7 ± 106.3		=58.6 ± 110.7
	FS		7.5 ± 41.5		3.4 ± 22.9
Pooled	PHS	-21.3 ± 24.7	-10.6 ± 27.2	-20.7 ± 27.6	-18.3 ± 15.4
	MHS	46.8 ± 41.5	50.4 ± 42.2	14.6 ± 38.9	39.4 ± 24.1
	FS	12.8 ± 15.4	19.9 ± 12.6	-3.1 ± 9.2	10.6 ± 7.0

2. the sampling error or statistical precision of the estimate and,
3. the accuracy of the method in terms of the amount of environmental and other non-additive sources of variance included in the estimate of additive genetic variance.

In the present study, paternal half-sib estimates of heritability of litter size were generally much lower than maternal half-sib estimates. In addition to the additive genetic variance included in paternal half-sib estimates, maternal half-sib estimates include additional sources of variation, such as dominance and epistatic variance and maternal effects. It is assumed that the maternal effects were relatively small in the sib analysis of the four measures of litter size because the maternal effects were actually maternal genetic and maternal environmental effects contributed by the maternal grand dam of the litter. The writer does not feel that maternal effects contributed by the dam would have a large effect on the ability of the daughters to produce and raise large litters. Therefore, differences between paternal half-sib and maternal half-sib estimates may be attributed to non-additive genetic effects. The epistatic and dominance variance appears to exceed the additive variance in this analysis. Heterosis and its "antithesis" inbreeding depression are often exhibited for measures of litter size and all models set up to explain heterosis are based on non-additive gene action. The large amount of non-additive genetic variance present for measures of litter size found in this study partly explains why heterosis and inbreeding depression is often manifest for these traits.

Growth Rate

Sib-analyses were done for weight-constant average daily gains (60-200 pound) using data from 349 Berkshire, 572 Yorkshire and 973 F_1 and inter-se crossbred pigs. The data were divided into inbreeding groups of 0-5, 5-10, 10-15 and over 15 percent. Analyses of variance were first carried out within breed and sex for each of the breed and inbreeding groups as described for measures of litter size. Similar analyses were carried out without removal of the effects of sex for reasons that will be discussed later. The number of degrees of freedom used for the hierarchal analysis of variance of average daily gain is given in Table 22. Sex, breed, sire, dam and individual within dam components of variance were calculated. Estimates of sire, dam and individual components of variance and of total phenotypic variance for some of the analyses are given in Table 23. Individual components of variance were considered to be estimates of environmental variance. Negative components for sire and/or dam were present for a few of the analyses where the numbers of degrees of freedom were small. These were

Table 22. Number of degrees of freedom used in the hierarchal analysis of variance of average daily gain.

Level of Inbreeding	Source of Variation	Berkshires		Yorkshires		Inter-se crosses		Pooled over Breeds	
		A[1]	B[2]	A	B	A	B	A	B
$0 \leq F_x \leq 5$	Breed							2	2
	Sex	1		1		1		3	
	Sire	10	5	11	6	30	16	51	27
	Dam	11	7	21	12	36	20	68	39
	Pigs	53	63	92	107	171	202	316	372
$5 < F_x \leq 10$	Breed							2	2
	Sex	1		1		1		3	
	Sire	18	9	5	3	50	26	73	38
	Dam	14	7	3	2	57	31	74	40
	Pigs	71	88	21	25	394	445	486	558
$10 < F_x \leq 15$	Breed							2	2
	Sex	1		1		1		3	
	Sire	8	4	20	11	18	10	46	25
	Dam	20	10	24	13	20	12	64	35
	Pigs	74	91	163	184	158	175	397	450
$15 < F_x$	Breed							2	2
	Sex	1		1		1		3	
	Sire	9	5	21	11	5	3	35	19
	Dam	14	8	34	17	4	2	52	27
	Pigs	37	48	147	175	22	27	206	250
Pooled over all levels of inbreeding	Breed							2	2
	Sex	1		1		1		3	
	Sire	32	16	41	22	68	35	141	73
	Dam	78	42	98	52	158	88	334	182
	Pigs	237	290	431	497	745	849	1413	1693

[1] A = Within sex sib-analysis

[2] B = Sib-analysis without removal of sex effects

Table 23. Estimates of components of variance by level of inbreeding for average daily gain.

Breed or Inbreeding Group	Sire Component	Dam Component	Pig Component	Total Phenotypic Variance
Berkshires	.008964	.010151	.023299	.042414
Yorkshires	.013648	.006899	.028554	.049101
Inter-se crosses	.002979	.013815	.022776	.039570
$0 \leq F_x \leq 5$	.017207	.009546	.022222	.048976
$5 < F_x \leq 10$	.006471	.009175	.023453	.039099
$10 < F_x \leq 15$	.008970	.011071	.026855	.046896
$15 < F_x$	.009678	.004650	.025427	.039755
Analysis of all animals	.007212	.011053	.024626	.042891

considered to be zero as was done in the analyses of the measures of litter size.

As stated previously, both genetic and phenotypic variation should be larger in a population derived from diverse parent stocks than it would be in a population with a narrow genetic base. Although dam components of variance of average daily gain were greater for the crossbred individuals in this study, sire components of variance and total phenotypic variance were both lower for the inter-se crossbreds than they were for either of the parent breeds (Table 23).

If differences in heritability exist among populations, then selection pressure would lead to more rapid changes in population mean in the population having the higher heritability. Heritability estimates for average daily gain did not appear to change with breed group in this study (Table 24). Although paternal half-sib and maternal half-sib estimates were quite inconsistant, full-sib estimates were very similar for all three breed groups.

Inbreeding should theoretically cause a reduction in genetic variance within lines (Falconer, 1960). In the present study there appeared to be a tendency for genetic variance of average daily gain to decrease with increasing levels of inbreeding of the individuals but the results were somewhat inconsistent (Table 23). The sire component of variance for average daily gain was found to be the greatest for the least highly inbred group while the dam component of variance was the lowest for the most highly inbred group. The sum of the sire and dam components of variance was higher for the group of animals having inbreeding coefficients of five percent or less than it was for the groups having inbreeding coefficients of over five percent and the sum of sire and dam components was the smallest for the group having inbreeding coefficients over 15 percent. There also was a tendency for within-litter or environmental variance to increase with increasing levels of inbreeding, indicating that inbreeding tends to lower the animal's ability to buffer itself against adverse environmental effects. Consistent decreases in paternal half-sib and maternal half-sib estimates of heritability of average daily gain with increasing levels of inbreeding were not found. However, full-sib estimates of heritability did show a consistent decrease with increasing inbreeding (Table 24) showing that selection would be less effective in an inbred population.

Heritability estimates of average daily gain were in general more than twice as high in this study as those reported in the literature. An attempt was made to find an explanation for these high estimates. The formulas used to calculate heritability were based on a genetic relationship of 0.25 between half-sibs and of 0.50 between full-sibs. Paternal half-sib estimates were made, for instance, using the formula:

Table 24. Heritability estimates and standard errors of average daily gain by breed and inbreeding groups (sex effect removed).

Inbreeding	Method of Calculation	Berkshires	Yorkshires	Inter-se Crosses	Pooled over Breed
0-5%	PHS	119.1 ± 99.6	218.6 ± 109.0	79.6 ± 45.8	140.5 ± 41.9
	MHS	85.7 ± 69.1	51.1 ± 27.8	100.9 ± 38.8	78.0 ± 22.9
	FS	102.4 ± 46.2	134.9 ± 54.8	90.3 ± 23.4	109.2 ± 21.1
5-10%	PHS	170.4 ± 74.4	258.8 ± 199.6	45.3 ± 29.7	66.2 ± 27.5
	MHS	-12.7 ± 32.7	-47.2 ± 19.7	113.2 ± 31.7	93.8 ± 25.5
	FS	78.8 ± 37.1	105.8 ± 100.2	79.3 ± 14.8	86.0 ± 13.4
10-15%	PHS	106.0 ± 91.4	83.4 ± 44.9	58.9 ± 58.1	76.5 ± 33.6
	MHS	134.2 ± 57.8	36.6 ± 29.0	129.1 ± 54.8	94.4 ± 26.4
	FS	120.1 ± 47.6	60.0 ± 22.7	94.0 ± 28.3	85.5 ± 16.9
> 15%	PHS	29.8 ± 61.0	115.1 ± 52.1	-268.3 ± 171.5	97.4 ± 39.4
	MHS	7.5 ± 67.7	45.9 ± 29.8	344.7 ± 354.4	46.8 ± 27.3
	FS	18.7 ± 34.8	80.5 ± 26.7	38.1 ± 99.9	75.1 ± 20.2
Pooled	PHS	84.5 ± 36.0	111.2 ± 33.2	30.1 ± 17.4	67.3 ± 14.8
	MHS	95.7 ± 28.0	56.2 ± 17.1	139.6 ± 22.2	103.1 ± 12.9
	FS	90.1 ± 19.8	83.7 ± 17.4	84.9 ± 10.8	85.2 ± 8.3

$$h^2 = \frac{\sigma_S^2}{0.25\,(\sigma_s^2 + \sigma_D^2 + \sigma_E^2)}$$

$$= \frac{4\sigma_S^2}{\sigma_S^2 + \sigma_D^2 + \sigma_E^2}$$

In this study the assumption of random mating was not fulfilled. Relationships between dams mated to the same sire and the relationships between sires and the dams were much higher than would be expected in a large randomly mating population. Relationships between half-sibs, therefore, ranged upward from 0.25 and relationships between full-sibs ranged upward from 0.50. The average relationships between half-sibs and between full-sibs should, therefore, be used to correct for deviations from random mating.

Assortative mating, or a tendency for parents to be more similar genetically than would be expected from a random sample of the population, often occurs in populations of farm animals. This would lead to a higher degree of homozygosity and an upward bias in sire and dam components of variance. Consequently, larger values for heritability estimates would result. A check was made for the existence of assortative mating by finding the simple phenotypic correlation between the average daily gains (60-200 pounds) of the sire and dam of 158 matings. A low but significant correlation of 0.17 was found indicating that positive assortative mating had been practiced in the Oregon State University swine herd.

In this study and in other studies reported in the literature, male pigs have consistently higher average daily gains than do females. Each litter or group of full-sibs then contains two groups of individuals, one with a rapid rate of gain and one with a slow rate of gain. In the within-sex-sib analysis used to calculate heritability estimates of rate of gain, each group of full-sibs was considered to be two groups, one of males and one of females. The within-full-sib or pig component of variance, therefore, would be less and heritability estimates would be higher than is characteristic of the population. Sib analysis was carried out without removal of the effect of sex and from this analysis sire, dam and individual components of variance were calculated (Table 25). No marked differences in sire and dam components of variance were observed between the two sib analyses of average daily gain. However, as would be expected, the individual component of variance and the total phenotypic variance were larger in the analysis where effect of sex was not removed. Of 60 estimates of heritability for average daily gain, only four were larger in the second analysis than they were in the first analysis. The full-sib estimate for the data pooled over all levels of inbreeding and breeds was 16.8 percent lower in the second analysis than it was in the first.

Table 25. Estimates of components of variance of average daily gain for some of the breed and inbreeding groups (sex effect not removed in the analysis).

Breed or Inbreeding Group	Sire Component	Dam Component	Pig Component	Total Phenotypic Variance
Berkshires	.08668	.010809	.032518	.051995
Yorkshires	.014130	.005686	.034163	.053979
Inter-se crosses	.003537	.012152	.030501	.046190
$0 \leq F_x \leq 5$	.015248	.009514	.029021	.053883
$5 < F_x \leq 10$	.007481	.007355	.031001	.045837
$10 < F_x \leq 15$	.007075	.012620	.035065	.054760
$15 < F_x$	.010704	.002694	.032012	.045410
Analysis of all animals	.007589	.009973	.031971	.049533

Table 26. Heritability estimates and standard errors of average daily gain by breed and inbreeding groups (sex effect not removed).

Inbreeding	Method of Calculation	Berkshires	Yorkshires	Inter-se Crosses	Pooled over Breed
0-5%	PHS	109.3 ± 109.8	188.7 ± 128.0	58.2 ± 45.2	113.4 ± 45.4
	MHS	65.4 ± 60.4	60.9 ± 34.2	80.4 ± 37.9	70.8 ± 23.8
	FS	87.3 ± 53.2	124.8 ± 64.6	69.3 ± 23.3	92.1 ± 23.0
5-10%	PHS	107.6 ± 66.0	144.6 ± 197.1	57.5 ± 32.7	65.3 ± 29.0
	MHS	-10.5 ± 24.1	51.0 ± 86.3	74.4 ± 27.1	64.2 ± 22.2
	FS	48.6 ± 32.7	97.8 ± 94.1	66.0 ± 16.5	64.7 ± 14.3
10-15%	PHS	69.4 ± 99.8	72.3 ± 47.1	34.5 ± 54.8	51.7 ± 34.6
	MHS	148.7 ± 78.0	29.8 ± 25.4	107.7 ± 56.3	92.2 ± 29.6
	FS	109.0 ± 53.9	51.1 ± 23.7	71.1 ± 27.4	71.9 ± 17.6
15%	PHS	13.9 ± 43.1	110.5 ± 61.1	-57.1 ± 128.4	94.2 ± 42.4
	MHS	-16.6 ± 41.0	27.4 ± 23.0	123.3 ± 199.0	23.7 ± 19.8
	FS	-1.4 ± 23.7	69.0 ± 30.3	33.1 ± 99.9	59.0 ± 21.4
Pooled	PHS	66.7 ± 38.2	104.7 ± 39.1	30.6 ± 18.5	61.3 ± 16.5
	MHS	83.2 ± 27.8	42.1 ± 15.0	105.2 ± 21.1	80.5 ± 12.3
	FS	74.9 ± 20.9	73.4 ± 20.1	67.9 ± 11.3	70.9 ± 9.1

V. DISCUSSION

Genetic and Environmental Factors Affecting Performance

Both induced and natural environmental factors operate to conceal genetic merit in domestic livestock and thereby confuse the breeder and obstruct his efforts to select those animals having the greatest breeding value. In many instances variations in environment can be controlled, but in others only adjustments or corrections for known effects may be used to place animals on a comparable basis. In the first part of this study the objectives were to determine the effects of year and season of birth, sex, age of dam and inbreeding on various measures of performance and of carcass merit.

It was concluded that true year effects exist for the number of pigs born alive, number of pigs weaned, average daily gain and all measures of carcass merit studied but not for the number of pigs born alive plus dead and the number of pigs born plus mummified fetuses. The lack of an increase in litter size in later years at first seems to indicate that selection pressure was insufficient to increase reproductive ability. Due to differences in litter size, selection for litter characteristics would occur even if pigs were chosen at random from the population. This is referred to as automatic selection. The difference between this and the total selection differential is defined as deliberate selection. Although it is thought that deliberate selection pressure may be quite low in this population, one can make inferences about the selection response only by comparing the response to the selection actually practiced. Changes in environment may make it appear that selection has been ineffective in the later years. The Oregon State University swine herd was moved to new facilities in December 1965. Uterine infections were quite prevalent in the breeding herd during both the spring and fall farrowing seasons of 1966. The inability to adjust management practices quickly enough to suit the complete confinement barns may have contributed to a high incidence of uterine infections and consequently smaller litters in 1966. The average level of inbreeding in the herd also increased time so that inbreeding depression may also have acted to decrease, or at least slow the increase, in litter size. The effect of season of birth did not significantly affect the three measures of litter size at birth but the average number of pigs weaned in the spring litters was significantly smaller than it was for fall-farrowed litters, indicating possible differences in environment or management that affect survival to weaning. Analyses were done separately on the Berkshire litters, the Yorkshire litters and the combination of the inter-se crossbred foundation and F_1 litters. No significant year and season effects were found for the Berkshire and Yorkshire litters but the Yorkshires showed a slight increase in litter size in the later years. Significant year effects for the inter-se crossbreds were found but no consistent trend in litter size was observed.

As stated before, poor growth rate in the later years was probably due to environmental factors associated with the moving of the swine herd to new facilities in December 1965, rather than to effective selection in the undesirable direction. Pigs removed from the barn normally used for performance testing work since 1965 to another barn for nutrition experiments had consistently higher growth rates than pigs used in this analysis, indicating that some environmental factor affects the rate of gain in the performance testing pens used since December 1965. The significantly slower rate of growth for fall-farrowed pigs as compared with spring-farrowed pigs was probably due to the lower proportion of males that were performance tested from fall-farrowed litters.

Significant year effects were found for average backfat thickness, carcass length, loin eye area and ham and loin weights. Of these five measures of carcass merit only loin eye area and possibly loin weight showed an increase with years. As stated before, selection pressure may have been greater for loin eye area than for other measures of carcass merit as records of loin eye areas of litter mates were examined, where possible, before an animal was selected as a replacement boar or gilt. Superior carcasses from the fall-farrowed pigs may have been partly due to a sex effect rather than to a true season effect.

It is generally recognized that average litter size is larger in some breeds than in other breeds. Breed differences in litter size are due to differences in ovulation rate, fertilization rate and embryonic death losses (Lasley *et al.*, 1961). In the present study, Berkshire litters were smaller at birth and at weaning than Yorkshire litters, the litters from the two classes of F_1s and litters from the inter-se crossbreds developed from Yorkshire-Berkshire crossbreds. Litters from Berkshire dams had a smaller number of mummified fetuses but had a larger number of stillbirths than did litters from Yorkshire and crossbred dams. The crossbred foundation had litters that were similar to the Yorkshires in number of pigs born alive, number born and number born plus mummified fetuses but the inter-se crossbreds had a slight advantage in number of pigs weaned. Crossbred dams raised 84.0 percent of the pigs born alive as compared with 76.6 and 74.8 percent for the Berkshire and Yorkshire dams respectively. Litter size in the inter-se crossbreds was intermediate between the two classes of F_1s for all measures of litter size but all differences between the inter-se crossbreds and both classes of F_1s were not significant.

Mortality in the early embryonic stages would result in complete resorption of fetuses while mortality in the later stages would be observed as mummified fetuses. Evidence for heterosis for survival in early embryonic stages was found. Crossbred litters out of Yorkshire dams were significantly larger at birth than purebred Yorkshire litters, and crossbred litters out of Berkshire dams were larger than purebred Berkshire litters. Ovulation and fertilization rates should be similar within a breed of dam regardless of the breed of sire used so any difference in litter size must therefore be due to differences in embryonic mortality.

Maternal influence is a term often used to refer to the environmental effect of the dam on her offspring from conception to weaning and does not include any influence contributed by genes transmitted to her offspring. One way of determining whether or not there is a maternal effect on certain traits in swine is to compare production and performance from the reciprocal crosses of two or more breeds. The F_1 litters out of Yorkshire dams had 1.89 more pigs born alive than did F_1 litters out of Berkshire dams ($P<0.05$) but the difference in number of pigs weaned was only 1.27 pigs per litter ($P<0.05$). It is believed that most of the differences in number born alive is due to differences in ovulation rate although it is possible that fertilization rate and embryo survival may also have been involved. The fact that differences in number of pigs weaned was not so great and not significant may be due to a positive relationship between litter size and pre-weaning mortality because of a larger proportion of small and weak pigs in larger litters causing a higher frequency of accidental deaths in the larger litters. The differences reported here are even greater than they were in a similar study done with Landrace and Poland reciprocal crosses (Pani et al., 1963).

A significant difference in average daily gain in favor of the Berkshire dams was found between the reciprocal classes of F_1s. This indicates that maternal effects are also present for average daily gain. No significant maternal effects were observed for the five measures of carcass merit studied.

Significant breed effects were found for all carcass measurements studied except loin weight. No evidence was found for heterotic responses in measures of carcass merit as reciprocal F_1s had measurements that were generally midway between those of the Yorkshires and Berkshires. Yorkshires were longer and had larger hams but smaller loin eye areas than did the Berkshires. In general, the inter-se crossbreds had carcass measurements that were similar to those of the F_1s, but were longer and had heavier hams than the Berkshires and had larger loin eye areas than the Yorkshires, thus showing an improvement in the weakest traits of the parental breeds. Selection for desirable characters from both of the parental breeds in the inter-se crosses was not sufficiently successful to increase the average carcass merit of the crossbred foundation above that of the F_1s.

There were significant differences between males and females for average daily gain and for all measures of carcass merit studied.

Males gained 0.096 pounds per day more than females which is in agreement with work done in Canada (Fredeen, 1953), in the United States (Hetzer *et al.*, 1956) and in Great Britain (Buck *et al.*, 1956). Females were found to produce carcasses that were 0.264 inches longer, 0.382 square inches larger in loin eye area and had 0.067 inches less average back fat. Hams and loins from females were 0.798 and 0.516 pounds heavier respectively than those from males. The present findings concerning sex are in agreement with the literature where it is generally reported that males gain more rapidly than females but females are superior for measures of carcass desirability.

Negative regression coefficients were found for the effects of inbreeding of the dam on all four measures of litter size but only the effect of inbreeding on the number of pigs plus mummified fetuses was significant ($P < 0.05$). Positive but non-significant regressions for the effect of inbreeding of the litter on the three measures of litter size at birth were found in this study. The unusual positive association between inbreeding of the litter and litter size (Tables 3, 4 and 8) is explained by the composition of the breeding herd and by the mating system used. Coancestry charts were used to prevent highly inbred dams from being mated to closely related sires. Also, high producing sows with low inbreeding coefficients were often mated to related boars with good performance records to produce litters with higher than average inbreeding coefficients.

The observed effects of inbreeding of the dam and inbreeding of the 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 conclusion is in agreement with findings of other studies (Chapman, 1963; Bereskin et al., 1968). A significant effect of inbreeding of the dam on the number of mummified fetuses was found. Intermediate levels of inbreeding resulted in a higher number of deaths in the late embryonic stages than did inbreeding levels of below five percent and above 15 percent. The number of stillbirths was not affected by the level of inbreeding of the dam but the ability of the sow to raise the pigs to weaning was strongly affected by inbreeding. There appeared to be a threshold at about the ten percent level of inbreeding. When inbreeding coefficients of the dam were above the ten percent level, the increase in the pre-weaning mortality became quite pronounced.

If most of the alleles that increase the value of the character are dominant over the alleles that reduce the value, then inbreeding will result in a reduction of the population mean in a linear fashion. If the reduction of the population mean is non-linear, we can assume that epistatic interactions between loci are important (Falconer, 1960). In the present study inbreeding of the individual did not affect average daily gain but each increase of ten percent in inbreeding of the dam increased the average daily gain by 0.026 pounds per day. Inbreeding of the individual usually becomes more important than inbreeding of the dam for weight and body measurements taken later in the animal's life (Bereskin _et_ _al._, 1968). However, in this study no explanation can be given for the positive regression of inbreeding of dam on average daily gain except that a negative relationship existed between the inbreeding of the dam and the inbreeding of the litter. Loin eye area increased in later years, probably as a result of selection pressure. This could explain the increase of 0.086 square inches in loin eye area for each ten percent increase in inbreeding of the individual. Inbreeding coefficients tended to be higher in the later years of the study. No significant effects of inbreeding of the individual or of the dam were found for average backfat thickness, carcass length or weights of the ham and loin.

Both linear and quadratic components of age of dam significantly affected all measures of litter size. This contradicts an earlier study on the same population (Chapman, 1963) where age of dam did not appear to affect litter size. Litter size reached a peak, in the present study, when dams were about three years of age or at the time when they had their fifth litter. Other workers (Lush and Molln, 1942; Godbey and Godley, 1961; Bereskin _et_ _al._, 1968) have observed pronounced curvilinear effects of age of dam on sow productivity and these reports are in general agreement with the present findings. The tendency for Yorkshire dams to reach peak productivity at earlier ages and for productivity to decline more drastically than for Berkshire and inter-se crossbred dams may be in part attributed to the particular structure of the population. Throughout the period studied, many Berkshire and inter-se crossbred gilts were eliminated as potential replacement animals because of disqualifying features such as blind or inverted nipples. The Berkshire and inter-se crossbred dams tended to be older than the Yorkshires and very few Yorkshire sows over three years old were used. The effect of age on sow productivity appears to be due almost entirely to increased ovulation and/or embryo survival as age of dam did not appear to affect the number of stillbirths or the number of pigs that died between birth and weaning. Most reports in the literature show that age of dam does not affect the number of pigs weaned over the indirect effect of number born (Godbey and Godley, 1961; Bereskin _et al._, 1968). Chapman (1963) reported a curvilinear effect of age of dam on the number of stillbirths which contradicts the findings in the present study. However, this contradiction can be explained on the basis of population structure. In the former study, the data from older sows were all from one sire group which had a larger proportion of stillbirths. Age of dam had no effect on average daily gain indicating that the effects of age on mothering ability if present do not carry over to affect the performance at older ages. Age of dam was not considered in the analysis of carcass measurements.

Effect of Inbreeding and Crossbreeding on the Distribution of Genetic and Environmental Variance

Numerous workers have reported differences between inbred and outbred populations in the amount of phenotypic variation (Fausch, 1953; Chai, 1957; and Robertson and Reeve, 1952). However, very little work has been done on the effect of population structure on the components of phenotypic variance in populations of animals. The objectives of the second part of this study were to find the direction and magnitude of changes in genetic and environmental variation resulting from crossbreeding and inbreeding.

Inbreeding, without selection, does not cause a change in frequencies of alleles in a population, but does cause a redistribution of alleles into families or lines. Within a line, gene frequencies at a single locus tend toward the extreme values of zero or one and the lines become differentiated in gene frequency under inbreeding. Rasmuson (1952) subjected a line of *Drosophila melanogaster* to 70 generations of full sib mating without artificial selection and found that the mean phenotypic values of lines drifted apart for bristle number. In addition to a drifting apart of mean genotypic values of lines, inbreeding causes a redistribution of genetic variance. Falconer (1960) shows that, for loci in which the genotypic value of the heterozygote is intermediate between that of the two homozygotes (i. e., additive genes), the genetic variance within lines decreases while the genetic variance between lines increases. If $\sigma^2_{A_o}$ is used to designate the original additive genetic variance, then the additive genetic variance lines after inbreeding ($\sigma^2_{A_w}$) is

$$\sigma^2_{A_w} = \sigma^2_{A_o} (1 - F)$$

and the genetic variance between lines becomes

$$\sigma^2_{A_b} = 2F\sigma^2_{A_o}$$

The total additive genetic variance then increases to

$$\sigma^2_{A_{w+b}} = (1 + F)\sigma^2_{A_o}$$

Changes in additive genetic variance as a result of inbreeding depends upon the average effect of a gene substitution. For loci exhibiting dominance, changes in genetic variance due to inbreeding depend upon the initial gene frequency. Variation within lines due to recessive genes will increase with inbreeding until an inbreeding coefficient of a little under 0.50 is reached in a population having recessive genes at a low frequency. Between-line components due to recessive genes will increase with inbreeding, reaching a maximum at 100 percent inbreeding. Where interactions are present between two or more loci (i. e., epistasis) changes in genetic variance depend not only on gene frequency but also on the type of interaction present (Kempthorne, 1957). Generalizations about changes in epistatic variance cannot be made as such changes do not appear to follow any pattern.

For quantitative traits such as measures of litter size and growth rate, it is not only impossible to determine gene frequencies at individual loci, it is also impossible to know how many loci affect the genotypic value or the types of gene action present. It is therefore difficult to predict the changes in genetic variance and heritability that would result from inbreeding. Only if we could safely assume that dominance and epistasis play but a minor role in determining the genotypic value of a trait, can we expect that the reduction in genetic variance and heritability within a line be directly related to the amount of inbreeding.

In the present study it was found that phenotypic variation in litter size in pigs increased with inbreeding of the dam and that this increase appeared to be a result of an increase in environmental variation rather than to a change in the amount of genetic variation. Environmental variance increased with increasing coefficients of inbreeding for the four measures of litter size used and for weight-constant average daily gain (60 to 200 pounds). Sire and dam components of variance for average daily gain tended to decrease with increasing levels of inbreeding but these components did not change for the four measures of litter size.

Many workers have found that inbred populations are more variable phenotypically than are outbred populations (Falconer, 1960). In many quantitative traits the proportion of the variance due to additive genetic effects is small and any reduction in this portion of the variance may be completely masked by the much larger environmental variance. Inbreeding should result in greater homozygosity and the more homozygous animals are more sensitive to environmental fluctuations. Inbred animals, therefore, may appear more variable than outbred animals.

A gene pool developed from a crossbred foundation should theoretically have a larger number of alleles segregating than an inbred population or a gene pool composed of animals of one breed. Some of these additional alleles would increase and some would decrease the genetic value of the animals. As the gene grequencies, number of loci involved, and the types of gene action are all unknown for a quantitative trait, it is not possible to predict the effect of crossing on the genetic, environmental and phenotypic variance. However, it is well established that hybrids tend to be more uniform than the parental lines. This uniformity and the often expressed heterosis presumably result from increased heterozygoxity for loci exhibiting non-additive types of gene action. In the present study we are concerned more with the effects of genetic divergence in a population rather than the uniformity of the first cross.

In the present study, the magnitude of genetic variance of measures of litter size, as measured by sire and dam components of variance, did not appear to follow any trend related to the genetic diversity within the three sub-populations. However, negative sire and dam components of variance were more frequent in the inter-se crossbreds than in the Berkshires and Yorkshires. These negative components could be due to some unknown peculiarities of the population, such as large negative environmental correlations between the sires and dams. It is believed that these negative components are probably due to sampling errors since the number of degrees of freedom was not sufficient to give ideal estimates of the variance components. Total phenotypic variation in litter size among the inter-se crosses was intermediate between that of the Berkshire and Yorkshire populations.

Although variance components and heritability estimates of average daily gain were quite variable they were not as variable as they were for litter size because more degrees of freedom were available to give better estimates. Dam components of variance for average daily gain were lower in the inter-se crosses than in the two parent breeds but sire components of variance and total phenotypic variance were larger in the inter-se crosses. Heritability estimates were similar for all breed groups indicating that the genetic divergence in the population developed from the crossbred foundation of Yorkshire-Berkshire hybrids was not sufficient to change the proportion of genetic variance.

The low heritability estimates for measures of reproductive efficiency indicate that progress by mass selection would be slow. However, wide differences in fecundity among breeds and lines exist and there appears to be considerable heterotic effects for these traits (Winters et al., 1935). This suggests that much of the genetic variation in reproductive efficiency may be due to non-additive gene action. In the present study dam components of variance for litter size were consistently greater than sire components indicating that non-additive and/or variance due to maternal effects was present. Because the dam exerts her effect early in the life of the daughter, it is felt that maternal effects would not have a large effect on the reproductive performance of the daughter; therefore, most of the difference between paternal and maternal half-sib estimates of heritability are thought to be due to non-additive genetic effects. Differences between sire and dam components were not as great for average daily gain as they were for litter size indicating that maternal effects and non-additive genetic effects were not as great for this trait.

In the present study, heritability estimates of average daily gain were in general more than twice as high as those normally found in the literature. This may have resulted from the cumulative effect of a number of factors.

1. The presence of assortative mating in a population will cause an upward bias in the sire and dam components of variance and evidence of assortative mating was found in this population.
2. Relationships between half-sibs and full sibs were greater than 0.25 and 0.50 respectively and no correction was made for this higher average relationship between sibs.
3. The hierarchal analysis of variance of average daily gain was first done in such a way that each full sib family was considered to be two groups, one of males and one of females. This would lower the estimate of environmental variance that existed in the population since males consistently grow faster than females.
4. Environmental effects may have been more uniform within sire groups than between sire groups. The data used to estimate heritability of average daily gain was collected over a period of six years (1962-1967 inclusive). A large proportion of the full-sib groups were composed of animals that were all born in the same year. Since year

effects were not removed in the sib-analysis some of the yearly and seasonal fluctuations in environment would therefore be included in the sire and dam components of variance.

5. Since heritability is a ratio of variances it is possible that the environment was uniform enough to give a higher than average estimate of genetic differences between individuals.

It is believed that the cumulative effects of all of these factors may have also affected the heritability estimates of measures of litter size as well.

The objective of doing this portion of the study was to find the effects of homozygostiy and genetic diversity on genetic variance and heritability. Factors causing an upward bias in heritability estimates should not affect the validity of inferences made about such effects.

VI. SUMMARY AND CONCLUSIONS

Data from 592 litters of pigs farrowed and raised at the Oregon Agriculture Experiment Station at Corvallis from the spring of 1961 through the spring of 1968 have been analyzed for effects of year and season of birth, breed, sex, inbreeding and age of dam on measures of fecundity, growth rate and carcass merit. Hierarchal analysis of variance was done to find the effect of population structure and inbreeding on the components of phenotypic variance and heritability for measures of litter size and average daily gain. From the results of the present study the following conclusions appear warranted.

1. There was no increase in the level of performance in the Oregon State University swine herd over the years of 1961 through 1968 in any of the traits studied except for loin eye area. The lack of an increase in level of performance may be due to lack of sufficient selection pressure, detrimental environmental changes or the depression in performance due to inbreeding.

2. Fall-farrowed pigs had lower average daily gains than spring-farrowed pigs, but in general they had more desirable carcasses. These differences are attributed to the larger proportion of females performance tested from fall-farrowed litters.

3. Males gained 0.096 pounds per day faster than females but carcasses were 0.264 inches shorter, had 0.067 inches more

average backfat, had ham and loin weights that were 0.798 and 0.516 pounds less respectively and had loin eye areas that were 0.382 square inches smaller.

4. Berkshire litters were smaller than Yorkshire, F_1 and inter-se crossbred litters in number born alive, number born, number born plus mummified fetuses and number weaned. Breed of dam was, in general, more important than breed of litter in determining litter size but evidence was found for heterotic response in the survival ability of the early embryos. Inter-se crossbreds were intermediate between the two classes of F_1s and similar to Yorkshires in litter size at birth but crossbred dams were able to raise a larger proportion of their pigs to weaning age.

5. Average daily gains of the two classes of F_1 pigs were not statistically different from those of the Yorkshire and Berkshire pigs. Inter-se crossbred pigs gained faster than those of the other four breed classifications. A difference between growth rate of the two classes of F_1 pigs indicated that maternal effects in favor of the Berkshire dams were present.

6. Berkshire carcasses were 1.30 inches shorter and had hams that were 1.57 pounds lighter but had loin eye areas that were 0.64 square inches larger than did Yorkshire carcasses. Both reciprocal F_1s and the inter-se crossbreds developed from the F_1s had carcass measurements that were midway between those of the

two parental breeds. This leads to the conclusion that attempts to combine the desirable carcass characteristics of the two parental breeds were not too successful.

7. Negative regressions for the effects of inbreeding of the dam on all four measures of litter size and positive regressions for the affect of inbreeding of the litter on the three measures of litter size at birth were found, but most effects were not statistically significant. The number of mummified fetuses and stillbirths did not increase with increasing levels of inbreeding but mortality between birth and weaning increased significantly when inbreeding of the dam rose above a threshold of ten percent.

8. Both linear and quadratic components of age of dam had highly significant effects on the three measures of litter size at birth and on the number of pigs weaned. The peak in sow productivity occurred at about three years of age. Age effects on sow productivity were thought to be due almost entirely to differences in ovulation rate or early embryo survival as the number of regressing fetuses, stillbirths or pre-weaning deaths were not related to age of dam.

9. Environmental variation of measures of litter size and average daily gain increased with increasing levels of inbreeding indicating that the more homozygous individuals are unable to buffer themselves against fluctuations in environment. Heritability of

daily gain decreased with inbreeding because of the lower genetic variance and higher environmental variance.

10. Heritability estimates of litter size were quite erratic due to the limited number of sire groups available but, in general, were quite low and generally not significantly different from zero. Heritability of litter size did not appear to change with the level of inbreeding, nor as a result of measuring the trait in three different ways.

11. Estimates of heritability of average daily gain were more than twice as high as most estimates found by previous workers. These high estimates were thought to be biased due to the cumulative effects of a number of characteristics of the population and of the data.

12. The inter-se crossbred foundation developed by crossing Berkshires and Yorkshires should have more alleles segregating and therefore should have a higher additive genetic variance than the parental breeds. In this study no differences were found among the inter-se crossbreds and the parental breeds in the magnitude of genetic variance, environmental variance or heritability estimates.

13. Paternal half sib estimates were generally much larger than maternal half sib estimates of heritability of litter size indicating that non-additive and/or maternal components were quite large. This would lead to an upward bias in heritability estimates calculated by the maternal half sib or full sib method. Differences

among the methods of estimating heritability of average daily gain were not great. Thus, full sib estimates should be used for this performance trait because of the increased precision of the estimates.

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