

AN ABSTRACT OF THE THESIS OF

Edward J. Smith for the degree of Master of Science

in Animal Science presented on May 23, 1989

Title EVALUATION OF RESPONSES TO SELECTION AND ASSOCIATION AMONG SPECIFIC TRAITS IN THREE POPULATIONS OF SWINE

Abstract approved

*Redacted for Privacy*

D. C. England

Oregon State University swine herd records of 456 litters farrowed between 1962-73 in three populations were analyzed on a generation basis to compare changes in performance of a Composite population to parental Berkshire and Yorkshire breeds. Analysis was performed in six discrete and overlapping generations on backfat thickness, loin eye area and litter size (number born alive and dead); litter size was the primary trait of emphasis in the selection scheme. Phenotypic correlations adjusted for different environmental effects were estimated along with heritability for the traits considered.

Phenotypic correlation between backfat thickness and loin eye area was moderate and showed a negative trend in

both parental and Composite populations. Correlations between litter size and loin eye area or backfat thickness were not consistent; litter size had, where significant, a moderate negative association with loin eye area. The phenotypic correlation between litter size and backfat thickness was non-significant.

The increased number of pigs born to Composite dams over parental Yorkshire and Berkshire dams, was significant only in earlier generations. The differences among the breeds for backfat thickness and loin eye area in the generations were small and mostly non-significant.

Heritability estimates for each of the three traits in each of the three populations were within the usual values found in other studies and they indicate positive response in relation to selection differentials. Among other possible explanations for similarity of responses within each of the three populations is the long history of coadapted direction of selection in the populations used.

**Evaluation of Responses to Selection and Association  
Among Specific Traits in Three Populations of Swine**

**by**

**Edward J. M.S. Smith**

**A THESIS**

**submitted to**

**Oregon State University**

**in partial fulfillment of  
the requirements for the  
degree of**

**Master of Science**

**Completed May 23, 1989**

**Commencement June 1990**

APPROVED:

*Redacted for Privacy*

Professor of Animal Science in charge of major

*Redacted for Privacy*

Head of department of Animal Science

*Redacted for Privacy*

Dean of Graduate School

Date thesis is presented May 23, 1989

Typed by Bethany Fisher for Edward J. Smith

## ACKNOWLEDGEMENT

This has been a long road and many helped to make it less rocky. To these I would like to offer my sincere gratitude:

The African American Institute without whose financial support this study would not have been possible.

Dr. David C. England my major professor who against all odds believed in me and always urged to do my best. His un-ending energy, patience and familiarity with diverse topics kept me highly motivated.

Dr. Paul Bellaty, whose statistical ingenuity and knowledge of computers helped set this project in a more comfortable direction.

Jim Pratt, a graduate student in Statistics who helped in writing the computer programs and fitting the models.

My committee members, Drs. P. Cheeke, T. Beddell, R. Petersen and T. F. Savage for their patience and editorial capabilities especially in getting the manuscript to final form.

My many friends who were there for both scientific and emotional support particularly Gliceria Pimentel and Wilhelmina Kwansa for their comments during preparations for my defense, Roslyn Fullilove, for being very understanding and Hugh Lefcourt for just being there.

Dr. Marvin Durham my foreign student advisor, who always found the time to talk about other things outside of school, an indication that he cares.

And last but not least, my family, especially my mom for hanging on to life with the loss of her daughter and the sons being away, Ye Yema I think and pray for you everyday.

# **DEDICATION**

**To the memory of my sister Ngo Princess  
who died in the struggle to see us,  
her brothers, succeed.**

## Table of Contents

	<u>Page</u>
1. INTRODUCTION	1
2. REVIEW OF LITERATURE	4
Recombination of Traits	4
Selection	5
Selection Response	7
Phenotypic Correlations and and Correlated Responses	10
Genetic Progress	12
Breed and Environmental Variables	14
Inbreeding	16
3. MATERIALS AND METHODS	19
4. RESULTS	30
5. DISCUSSION	55
6. SUMMARY AND CONCLUSIONS	71
7. BIBLIOGRAPHY	75



## Lists of Tables

<u>Table</u>		<u>Page</u>
3.1	Generations determined from crosses made within Yorkshire, Berkshire and Composite breeds	22
3.2	Sib analysis of variance by GLM procedure	27
4.1	Summary of adjusted data: Mean and standard deviation of backfat thickness, loin eye area and litter size within overlapping generations in three breeds of swine	38
4.2	Correction factors for adjusting carcass traits and litter size for parity from a gilt to a sow equivalent, and loin eye area and backfat thickness to a barrow equivalent.	39
4.3	Mean and standard deviation of inbreeding coefficients in three populations of swine	40
4.4	Estimates of change in litter size as inbreeding of litter and dam increased by 10%	41
4.5	Multiple Comparisons of trait means in purebreds of data adjusted for inbreeding of dam, sire and litter, parity and weight at slaughter	42
4.6	Multiple Comparison of trait means for data adjusted for sex, season and year	43
4.7	Regression coefficients and p values from linear regression of factors affecting backfat, loin eye area and litter size in Berkshire	44
4.8	Regression coefficients and p values from linear regression of factors affecting backfat, loin eye area and litter size in Yorkshire	45
4.9	Regression coefficients and p values from linear regression of factors affecting backfat, loin eye area and litter size in Composite	46

4.10	Multiple Comparisons of Generation Means in BF, LEA and LS	47
4.11	Multiple comparison of breed means in generations 1, 0.5, 1.5, 2, 2.5 and 3 using Fisher's Protected Least Significant Differences	48
4.12	Phenotypic correlation, $r$ , between backfat, loin eye area and litter size in Berkshire, Yorkshire and Composite breeds	49
4.13	Genetic correlation between traits in purebreds on data adjusted to same season, year and sex	50
4.14	Heritability estimates in the unselected populations from sib analysis within generations 0.5, 1.5, 2, 2.5 and 3 in Berkshire, Yorkshire and Composite breeds	51
4.15	Heritability estimates from sib analysis in generations 0.5, 1.5, 2, 2.5 and 3 for Berkshire, Yorkshire and Composite breeds for adjusted data	52
4.16	Expected genetic progress from selection in generations 1, 0.5, 2, 1.5, 2.5 and 3 for litter size in the Composite, Berkshire and Yorkshire	53
4.17	Selection response and realized heritability estimates in litter size for Berkshire, Yorkshire and the Composite with correlated responses in backfat thickness and loin eye area	54
5.1	Heritability estimates reported in this study	70

# EVALUATION OF RESPONSES TO SELECTION AND ASSOCIATION AMONG SPECIFIC TRAITS IN THREE POPULATIONS OF SWINE

## 1. Introduction

In the swine industry, low genetic potential ranks high among reasons for low productivity in traditional, unimproved indigenous pigs (Cunningham, 1983; Fitzhugh, 1983 and Hallam, et al., 1983). If a person was to increase swine meat production, a breeding program should include, as a minimum priority, the upgrading of indigenous genotypes. Replacement of these breeds is most often not an effective solution as indigenous populations, unlike introduced breeds are better adapted to their environment and production systems, (Pathiraja, 1987). Besides the high capital investment required for such replacement programs, changes in the population structure might result in a significant reduction in very valuable genes (Polge, 1983).

Genetic recombination of traits from a crossbred foundation based on breed classes having contrasting trait superiorities would be expected to offer a potentially beneficial genetic basis for combining desired traits. A production oriented program involving use of two somewhat contrasting breeds and a population developed from a cross of these was begun at Oregon State University in 1961. The primary objective of this program was the use of a

low-cost breed developing technique to combine traits from diverse genotypes and improve performance. A Berkshire population with an average loin eye area (LEA) of 4.34 square inches and litter size of 8.07, was expected to contribute large LEA to a composite population developed from a Berkshire x Yorkshire and Yorkshire x Berkshire crossbred base. The Yorkshire's traits consisted of its large mean litter size 11.13 and a low LEA of 3.82 square inches (Krider et al., 1982). The resulting population from these two clones, hereafter referred to as Composite, would be expected to offer an opportunity to combine the superior traits of the parental breeds to mean levels greater than the average of the two.

The technique of recombination of traits used to develop the Composite breed was accompanied by a flexible selection system, which unlike conventional selection practices is not based on a constant weighting index. This flexibility allowed for more emphasis on some traits and less on others. In each generation animals were selected mainly for litter size, number of pigs weaned, growth rate and feed efficiency. Carcass traits including loin eye area, length, and backfat thickness were recorded from randomly slaughtered pigs in a litter, but less emphasized in selecting pigs to become parents in the next generation. The primary objective of this study was to evaluate the extent, if any, of genetic

relationship between litter size, loin eye area and backfat thickness. A correlation between these parameters would enable improvement in the non-selected traits and allow for a more efficient breeding program.

The objectives of this study designed to provide an understanding of the technique of recombination can be summarized as:

1. Compare the performance of a Composite population to parental Yorkshire and Berkshire breeds.
2. Evaluate the nature and extent of phenotypic correlations within generations between litter size, loin eye area and backfat thickness in each of the three populations.

## 2. REVIEW OF LITERATURE

### Recombination of Traits

If a population initially contains gametes of types AB and ab, recombination in AB/ab results in the production of new genotypes aB and Ab. Through these genotypes recombination between loci then becomes a source of new genetic variation between animals. Acting on this variation to increase performance in livestock is the major role of the breeder. The breeder's accuracy in choosing genetically superior animals from the variability is increased with detailed records on the performance of his herd. Adjustment of the performance traits to the same age basis, sex and other variables enables the breeder to make comparisons more accurately. It is important to note however that genetic variability from recombination does not come through new genes but from new genotypes which, unlike mutation can occur very rapidly (Falconer, 1981).

New breeds have been synthesized by employing various techniques of recombination from foundation stocks consisting of diverse genotypes. These are generally developed to correct inabilities of existing breeds. The Santa Gertrudis beef breed, for example, was developed in South-Eastern United States to increase beef yield as the Hereford and Shorthorn could not profitably do this under

the harsh environments of that region. The Santa Gertrudis, approximately 3/8 Brahman and 5/8 Shorthorn, have been widely acclaimed as a hardy beef breed, performing profitably in diverse geographic area environments in Africa, Asia and Central America (SGBI, 1979 and Takalashi et al., 1988). The technique of recombination for developing new pig breeds in the United States has been most widely used by the U. S. Department of Agriculture and by L.M. Winters at the University of Minnesota and his students thereafter. The Minnesota No. 1, No. 2 (Winters et.al., 1944), Hormel Miniature pig (England et. al., 1954) and the Hanford Miniature Swine (Bustad et.al., 1965) are all breeds developed through recombination from foundation stocks of diverse genotypes.

Genetic progress from recombination of traits can be accelerated when accompanied by selection. Planned programs involving selection for developing new stable populations by recombination of traits based on two or more complementary existing populations have potential for providing more useful populations than presently existing ones.

### SELECTION

Recombination followed by selection results in disequilibrium in a population (Dickerson, 1969, and Falconer, 1981) with the favored genotypes increasing at

the expense of others. The simplest and most direct selection method used to improve farm animals is mass selection (Fredeen and Mikami, 1986a). This system involves selecting parents for the next generation based on their phenotype. The flexible selection system developed and widely practiced by L. M. Winters and students thereafter is a modification of the mass selection method. As reported by England et.al. (1954), the system does not use a constant index and only the best with respect to high performance for a trait or traits are chosen; within the chosen population, mating is done in a manner judged to best meet needs for enhancing relative merit of the various traits in each generation. No set pattern of relationships among mated pairs is adhered to (England, 1952); merit rather than pre-designated relationship guides choice of specific mating pairs between least related animals. In addition to choosing individuals based on their own phenotype, their progeny can also be chosen based on performance of parents under the flexible selection system. The effect of selection ultimately comes through change in genotype frequencies as reflected in changes of the population mean in subsequent generations. This effect has been called Response to Selection (Falconer, 1981). It is defined as the difference in means between the offspring of selected parents and the whole of parental generation.



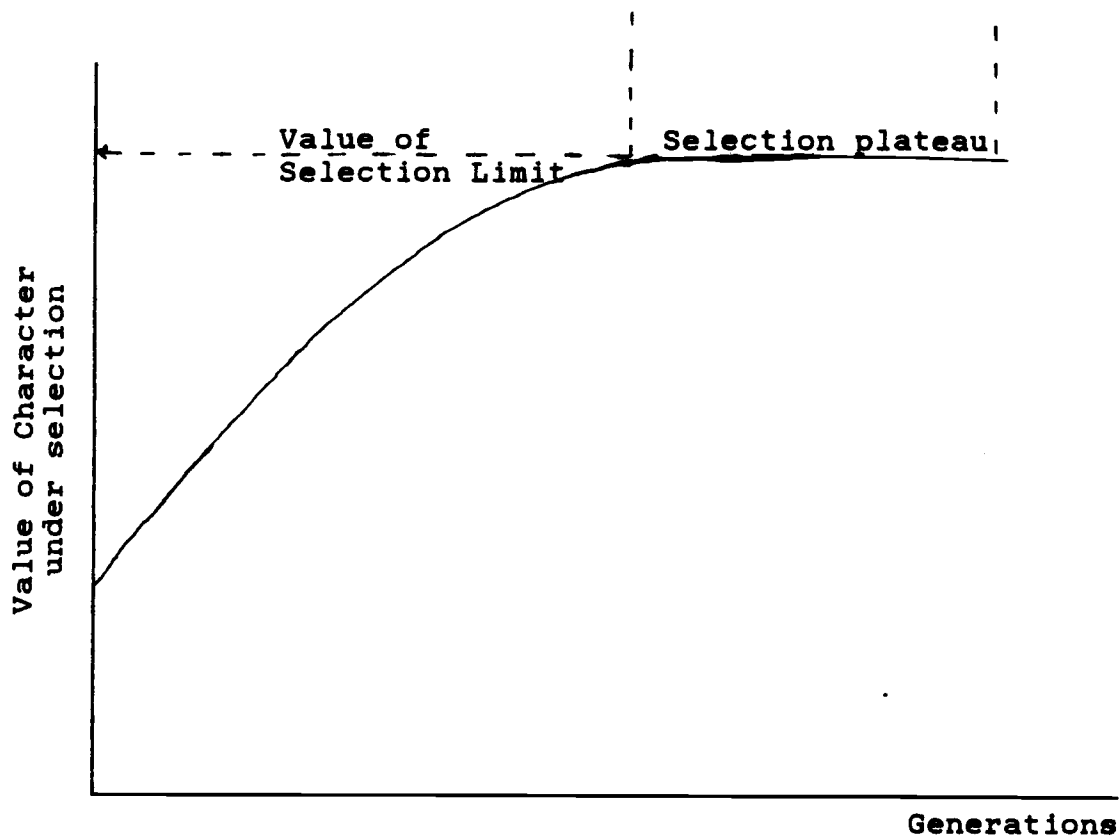
### Selection Response

In discrete generations actual response to selection follows the curve in Fig. 1 (Bowman, 1984). Selection differential in discrete generations is a measure then (Warwick & Legates, 1979) of phenotypic values of individuals selected as parents expressed as deviation from the generation mean before selection. The ratio of selection response to selection differential is the heritability of the trait. Heritability is a statistical tool that provides breeders with guidelines as to progress that can be made from selection.

Heritability estimates are essential in making effective breeding plans. When heritability is high as with carcass measurements mass selection emphasizing individual performance can be highly successful (Craft, 1958). On the other hand if heritability is low, as in reproductive traits including litter size, pig birth weight and weaning weight, use of information from pedigree and progeny performance is necessary to accomplish significant genetic progress from selection (Dickerson, 1969a).

In overlapping generations, reproduction in the dam or sire continues over an extended period relative to the age at first breeding (Richard et.al., 1973). For these generations the response to selection  $R$ , defined by Falconer (1961) as a heritability  $\times$  selection differential

Fig. 2.1 Long term response to selection in a single selected population.



for discrete generations is much more complex. Considered the average genetic superiority of selected individuals in overlapping generations,  $R$ , according to Bichard et.al. (1973), Hill (1972, 1977 and 1979) can be computed as

$$d(1 - h^2)$$

where  $d$  is number of phenotypic standard deviations determined from Fisher and Yates (1963) table of probits. The genetic change  $G$  from such overlapping generations of selection would be

$$G = \frac{(S_m + S_f)(1 - h^2)}{4(L_m + L_f)}$$

where:  $S_m$ ,  $L_m$  and  $S_f$ ,  $L_f$  are selection differentials and generation intervals for males and females, respectively.

It is generally agreed (Dickerson and Hazel, 1944, Bichard et al., 1973 and Hill, 1979) that genetic progress made in overlapping generations is slower due to limited selection pressure. The genetic improvement in the selected group in one year is not immediately passed through the population as happens in discrete generations. All the methods used for computing genetic progress, predict that response from selection in overlapping generations is reached asymptotically. In all of these studies, age structure of the population forms a very important component in determining response to selection.

### Phenotypic Correlations and Correlated Responses

Success in breeding programs through selection can be helped by knowledge of genetic relationships existing among the economic traits (Roy et.al., 1968). Phenotypic correlation, an example of such relationships among traits, provides such knowledge. Correlated characters are important to breeders, for the changes brought about by selection through improvement in one character will cause simultaneous changes in other characters. Correlation can be genetic or environmental (Bowman, 1984). The genetic cause of correlation is either through pleiotropy or from linkage of genes in populations derived from crosses between divergent strains. Pleiotropic cause of correlation is the property of a gene, so that in segregating, it causes simultaneous variation in the characters it (they) affects (Falconer, 1981). The correlation arising from pleiotropy is the overall effect of all the segregating genes that influence the correlated characters. Some of the genes may increase one or more traits while reducing the other. The former is a positive genetic correlation and the latter a negative one. Environmental factors cause correlation between two traits if these traits are influenced by the same differences in environmental conditions (Yamada, 1962). Many workers have reported a high positive correlation between growth rate and feed conversion in swine

(Dickerson and Grimes, 1947, and Rempel and Enfield, 1964). By selecting for growth rate, one would indirectly be selecting for feed efficiency. Negative phenotypic correlation has been reported (Dickerson and Grimes, 1947) between rapid fat deposition, low feed requirements and poor suckling ability; all are believed to be caused by the same genes. Such correlations are only valid for a few discrete generations and estimates are subject to more error than heritability estimates for the same amount of data in overlapping generations. This is due normally to the relatively small changes of gene frequency occurring in overlapping generations.

The concept of genetic correlations makes it possible to consider indirect selection and correlated responses. Indirect selection for a correlated trait with high heritability might be more effective in improving a trait than direct selection for that trait. Estimates of genetic correlations are subject to large sampling errors, with true relationships differing between breeds, management and nutritional conditions. This is reflected in the considerable variation in results reported of different studies on the relationships among traits in swine. Hetzer and Miller (1973) reported a negative genetic correlation between growth rate and fatness for Duroc in 13 generations of selection for high and low backfat, while a positive relationship was observed for

Yorkshire in the same study. In most of these studies, the experiments involved lines that were not replicated, and the relationship observed might as well be due to random genetic drift.

Though genetic relationships between maternal traits of sows (conception rate, litter size and litter weaning weight) and carcass characters have not been well defined, some studies report a low negative genetic correlation between backfat thickness and litter size (Morris, 1974). Young et al., 1977 reported a low positive genetic correlation between growth rate and ovulation rate of gilts. Fahmy and Bernard (1972) looked at changes in litter size after 10 generations for Yorkshire selected for leanness and feed utilization. Trends in litter size were small and inconsistent in both the high and low backfat lines.

### Genetic Progress

When individual selection is practiced, computation of selection differential (the difference between performance of those individuals selected to be parents and the mean of their generation) is relatively easy. Selection differential reflects the amount of selection pressure applied for a particular trait. The larger the selection differential the more progress could be expected to be made from selection (Bulmer, 1971). Selection

differential is affected by number of animals kept for replacement purposes and number of traits selected for. Since fewer males are normally needed for breeding purposes, the selection differential for males is most often larger than for females. The more traits selected for, the lower the selection differential for any one of them. Average level of performance in a trait also affects the size of the selection differential. If selection for a trait has been practiced for many years and the average for that particular trait is very high, it becomes more difficult to find individuals for breeding purposes that greatly exceed this average.

Like selection differential, heritability estimates indicate the amount of progress that can be made from selection in one generation (Strang and Smith, 1979). Selection for a trait that is lowly heritable, like litter size (15 to 17 percent), makes little progress. When heritability is moderate to high as with carcass traits (backfat thickness, loin eye area and carcass length), and post-weaning rate of gain in swine, selection should result in more progress. In the broad sense, heritability determines the extent to which individuals' phenotypes are determined by their genotypes. In livestock breeding programs heritability in the narrow sense is of more interest, as it determines the degree of resemblance between relatives; it expresses the extent to which

phenotypes are determined by the genes transmitted from the parents (Smith et al., 1962).

Selection differential and heritability (realized) would theoretically estimate response to selection. This response is the difference of mean phenotypic value between the offspring of selected parents and the whole of the parental generation. Work with mice (Falconer, 1953) selected over ten generations for body weight showed that measurement of response to selection introduces several procedural problems. The erratic fluctuation of generation means, weighting selection differential to remove differences in litter size among animals in a generation and realized heritability are among the primary problems in evaluating response to selection.

#### Breed and Environmental Variables:

Most existing pig breeds are evaluated based on their relative performance in economic traits (Drewry, 1973). On a scheme provided by the National Swine Improvement Federation and reported by Warwick and Legates (1979), Yorkshire ranked first in litter size but sixth in backfat thickness and fifth for loin eye area amongst nine breeds. Hacker et al., (1970) reported significant differences between breeds for litter size both at birth and weaning. Differences have also been reported between breeds in percent of stillborn pigs per litter, ovulation



rate and embryo survival (Pond, et al., 1960 and England and Chapman, 1962). The number of Corpora lutea for Berkshire and Yorkshire sows is approximately 14.6 and 19.2 respectively, whilst the number of embryos is 9.6 and 15.2 (Johnson and Zimmerman, 1986).

Sex differences within breeds in most performance traits have long been established. 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. Within Yorkshire pigs, Bennett and Coles (1946) revealed that gilts took longer to reach market weight but averaged 0.34 inches more carcass length, 0.78 square inches larger loin eye area and 0.15 inches less backfat thickness than barrows. Sex differences within the Minnesota No. 1 for backfat depth was found to be greater than that in inbred lines of Poland China (England and Winters, 1953). Pigs from large litters generally have greater sex differences in backfat thickness.

Season and year of farrowing have been reported to affect performance in swine. Reddy et al., (1959) reported that fall farrowed pigs have an average of 0.43 mm more backfat than spring farrowed pigs. Summer raised pigs on pasture were found to average more backfat, 1.56mm, than those raised on dry lot.

Age of dam at farrowing has been reported to be as important a source of effect on performance as inbreeding of dam (Lush and Molln, 1942). Studies by Olbrycht (1943) involving 156 sows for ten litters found that litter size increased until the third litter, remains at peak until fifth parity and then declines. Literature reports on the effect of age of dam on birthweight, embryo mortality and pig survival are inconsistent. Godbey and Grodley, (1961) and Bereskin et al., (1968) reported that age of dam had no effect on pig survival; Bauman et al., (1966) however reported otherwise.

#### Inbreeding

Inbreeding involves the mating of animals more closely related than the average members of the breed or population being inter-mated. The flexible mass selection system results, through its basic structure of mating best-to-best, in some inadvertent inbreeding (England and Winters, 1953). Whilst this causes the accumulation of desirable genes, it also has the unfavorable effect of uncovering phenotypes resulting from deleterious recessive alleles (Pirchner, 1983).

Inbreeding coefficient,  $F_x$ , is the probability that two alleles at any locus in an individual are alike by descent (Wright, 1922 and Malecot, 1948). With values ranging from 0 to 1, it represents the probable increase of homozygosity resulting from the mating of individuals

more closely related. The coefficient can only be quantified in relative terms with reference to some particular generation of a population. The base population is normally regarded as having a zero coefficient. Increase in the coefficient indicates increase in expected homozygosity, departing from the average heterozygosity assumed in the base generation.

Inbreeding depression, a phenotypic consequence of inbreeding, is absent where traits lack dominance and epistatic effect, in which case the mean is expected to stay unchanged (Hill and Robertson, 1968 and Falconer, 1981).

Where traits are influenced more by non-additive genes and environmental variation, the detrimental and favorable effects of inbreeding become of interest to breeders. Inbreeding of dam or litter generally shows a depression of litter size (Craft, 1958, and Bereskin et al., 1968). For each ten percent increase in inbreeding of the dam, reduction in litter size for different swine populations average 0.2 to 0.3 pigs. Though some studies have refuted reports that inbreeding of litter reduces litter size (Noland et al., 1964, Bereskin et al., 1969), there is a general consensus that a decline in vigor affects number of pigs weaned and average weaning weight. Inbreeding of sire has been shown to delay testicular development and depress libido but has no direct effect on litter size or

litter traits. England (1952), however, reported larger litters sired by heterozygote boars than those sired by homozygotes.

Carcass traits are genetically affected mainly by additive gene action. Inbreeding has been shown to have only minor effects on these (King and Roberts, 1959; Warwick and Legates, 1979 and Falconer, 1981). The incidence of abnormalities such as hernias, cryptorchidism and kinky tail is about 9.4 percent in inbred pigs and only 4.01 percent in outbred swine. Though the formation of new breeds of swine involves some inbreeding, it is generally recommended that it not be practiced in commercial herds. However, for traits like backfat thickness and loin eye area mild inbreeding remains a valuable technique for improvement of different lines or breeds.

### 3. Materials and Methods

Oregon State University swine herd records for litters farrowed between 1962 and 1973 are the source of data for this study. Berkshire, Yorkshire and a composite from these two breeds were used. The composite is a result of *inter se* mating of Berkshire X Yorkshire crossbreds in the F1 and subsequent generations. Berkshire females were mated to Yorkshire males and Yorkshire females to Berkshire males to establish a foundation population; thus the composite from this population, through recombination, is assumed to have equal proportions of Yorkshire and Berkshire genes.

The animals used in this study were raised under a Specific Pathogen-Free type environment. Gilts were selected as broodstock animals at approximately seven months of age, and subsequently exposed to boars for mating at third estrus. Gilts and sows that conceived were transferred to farrowing crates at 110 days. Pigs were weaned at 56 days when dams were removed to the broodstock barn and rebred on first estrus. A total of 488 animals from 140 litters for Berkshire, 512 from 153 litters from Yorkshires and 514 animals from 163 litters for the composite breed was used in the analysis. Litters were farrowed mainly in the spring and fall seasons. Data were used from 157 Berkshires in generation

1, 98 in generation 0.5, 61 in generation 2, 45 in generation 1.5, 74 in generation 3 and 59 in generation 2.5. In the Composite, 172 animals were used from generation 1, 86 from generation 0.5, 93 from generation 2, 90 from generation 1.5, 40 from generation 3 and 63 from generation 2.5. For corresponding generations of Yorkshire there were 145, 71, 63, 75, 95 and 89 animals, respectively, used in the analyses. Only litters having three or more animals with backfat and loin measurements were used in the analyses.

Litter size was determined as the total number of pigs born alive and dead by a dam at a specific farrowing. This was adjusted to a sow equivalent basis to remove parity effects. Adjusting to sow equivalence involved the use of observed differences between gilts and sows of each breed type. The average difference (residual) adjusted by least squares estimate was added to observed values for all gilt litters. This is based on the assumption that the differences between gilts and sows are mainly environmental. Backfat and loin eye area measurements were made on randomly selected animals from a litter. Backfat was measured using a calibrated probe as described by Hazel and Kline (1952) as an average of three measurements on the back at the shoulder, at the mid-back and at an estimated location of the last lumbar vertebrae. The outline of the cross sectional surface loin eye muscle

between the tenth and eleventh ribs was traced on acetate paper and the area was calculated to the nearest tenth of a square inch using a compensating polar planimeter.

Generations, both discrete and overlapping, were determined on the basis of generational advance from the foundation stocks. Mating of foundation (0 generation) animals produced generation 1 offspring; a foundation sire or dam mated to a generation 1 animal produced generation 0.5. Mating types and offspring generations produced from these are shown in Table 3.1.

Adjustments were made for inbreeding of sire, dam and litter from mean coefficient values calculated for the populations from pedigree and effective population size. In computing inbreeding coefficients for individuals within a breed, the foundation stock was considered to have a coefficient of zero; effective population size was used to approximate inbreeding coefficient in generations.

Individual inbreeding coefficients were calculated by the co-ancestry method reported by Malecot (1948) and modified by Emik and Terrill (1949). It was assumed that the inbreeding coefficient of an individual depends on the amount of common ancestry in its two parents. The amount of common ancestry, it is assumed, determines the inbreeding coefficient of the progeny, and is the probability that two gametes, one from each parent will

contain the same alleles that are identical by descent (Wright, 1922).

Table 3.1: Generations determined from crosses made within Yorkshire, Berkshire and Composite breeds

Matings		Generation of Progeny
Foundation	x Foundation	1
Generation 1	x Foundation or Foundation x Generation 1	0.5
Generation 1	x Generation 1	2
Generation 1	x Generation 2 or Generation 2 x Generation 1	1.5
Generation 2	x Generation 2	3
Generation 2	x Generation 3 or Generation 3 x Generation 2	2.5

#### Statistical Analysis:

Outliers detected by plotting studentized residuals against predicted values generated from regression analysis were eliminated to give better estimates of the effects of generation, sex and season on backfat, loin eye area and litter size within breeds.

The method of least squares (Harvey, 1975) was used to analyze the data. Dependent variables used in this study were litter size, backfat thickness and loin eye area.



Preliminary analyses were used to examine the effects of weight at slaughter, parity and inbreeding of dam, litter and sire on appropriate traits. The model used for the preliminary analysis was:

$$I. Y_i = \mu + b_1x_1 + b_2x_2 + b_3x_3 + b_4x_4 + b_5x_5 + e_i$$

where

$Y_i$	is the performance of the $i$ th individual (backfat, loin eye area and litter size)
$\mu$	is the overall mean when $x_1$ , $x_2$ , $x_3$ , $x_4$ and $x_5$ are equal to zero.
$b_1$ - $b_5$	are least square estimates indicating the extent of the linear relationship between $Y_i$ and the predictor variables $x_1$ - $x_5$ ;
$x_1$ - $x_5$	are weight at slaughter, inbreeding of dam, litter and sire and parity.

The model used for analysis of backfat (BF), loin eye area (LEA) and litter size (LS) by multiple regression analyses for each breed after adjusting for significant effects as determined in the model for preliminary analysis was of the general form:

$$II. Y_{ijkl} = \mu + F_i + J_j + S_k + G_l + (FG)_{il} + (JG)_{jl} + (SG)_{kl} + e_{ijkl}$$

Where:

$Y_{ijkl}$	is the merit of the $i$ th season, the $j$ th year, $k$ th sex and $l$ th generation.
------------	---

$\mu$	the overall mean at standard slaughter weight and zero inbreeding (for litter size) and parity effect.
$F_i$	is the effect of the $i^{\text{th}}$ farrowing season ( $i$ =fall, spring).
$J_j$	is the effect of $j^{\text{th}}$ year ( $j$ =1962-73)
$S_k$	is the effect of $k^{\text{th}}$ sex ( $k$ =male, female).
$G_l$	is the effect of the $l^{\text{th}}$ generation ( $l = 0.5-3$ )
$(FG)_{il}$	is the interaction of farrowing season with generation of progeny
$(JG)_{jl}$	is the interaction of year with generation
$(SG)_{kl}$	is the interaction of sex with generation
$e_{ijkl}$	random error accounting for variation in back fat, loin eye area or litter size due to other factors.

Coefficient  $\beta_0$ , the intercept representing backfat, loin eye area and litter size when all the effects are zero was not computed. In each generation for each breed, the means for the animals within each litter, rather than separate value for each animal in the litter was used to give independence before determining the effects of different factors on loin eye area and backfat thickness.

When adjusted for different significant factors according to least square estimates from (Models I and II) generation effect on the traits for each population was

further analyzed using the General Linear Model procedure of the Statistical Analysis System (SAS) (Barr, et al., 1987). In this analysis means were compared using Duncan's Multiple range test and least significant differences were also computed to compare trait means within generations among breeds.

Phenotypic correlations were first determined from computations based on direct measurements of backfat, loin eye area and litter size adjusted for factors determined to be significant in Model I. After adjusting the data to a standard year, season and sex where significant as determined by Model II, the correlations were again determined.

Phenotypic correlations among traits, on data adjusted for effects found significant on Model I were calculated on an intra-generation basis using Pearson's true product moment correlation of the Statistical Analysis System (SAS) (Barr, et al., 1987)

The formula used in the computation was:

$$r_{xy} = \frac{\sum xy}{\sqrt{(\sum x^2)(\sum y^2)}} \quad \text{or} \quad \frac{\sigma_{xy}}{\sqrt{\sigma_x^2 \sigma_y^2}}$$

Where:

$r_{xy}$

is the phenotypic correlation between litter size and backfat thickness or loin eye area, or between loin eye area and backfat thickness.

x and y            deviations of individual  
measure from the mean of  
either litter size, loin eye  
area or backfat thickness.

In each generation for each breed the data adjusted to a uniform weight at slaughter and to remove seasonal, sex and yearly effects provided the basis for estimate of additive genetic variance.

Phenotypic correlations on data adjusted to factors significant in Model II were computed using covariances between relatives for the traits considered according to the equation (Becker, 1984):

$$r_{xy} = \frac{\text{Cov}(xy)}{\sqrt{\text{Cov}_{xx} \text{Cov}_{yy}}}$$

The procedure involved analysis of litter size, backfat thickness and loin eye area on sibs with the covariance obtained for 1 trait in one relative and for trait 2 in the second relative. This is intended to reflect a greater genetic component of the association.

Heritability was computed in discrete and overlapping generations using analysis of variances partitioned between sibs on the assumption that the data can be treated as a hierarchical design (Snedecor and Cochran, 1967; Flock, 1970; Rutzmozer and Pirchner 1979). It was assumed that dominance and epistatic effects on backfat

and loin eye area were negligible (Bellaty, 1987) in both discrete and overlapping generations. It was further assumed that environmental deviation and genotypic value were not correlated in that treatment or management conditions were not designed to favor a superior or inferior genotype. The phenotypic variance was divided between sires ( $\sigma_S^2$  or within dams) and between dams ( $\sigma_D^2$ ) or within progenies ( $\sigma_W^2$ ) components. The form of the analysis as produced by the general linear model of the Statistical Analysis System (SAS) is presented in Table 3.2.  $s$  is the number of sires each mated to  $d$  dams which produce  $k$  offspring.

Table 3.2: Sib Analysis of Variance by GLM Procedure

Source of Variation	df	Mean Square	Component of Variance
Between Sires	$S-1$	$MS_S$	$\sigma^2 = \frac{1}{S} (MS_S - MS_D)$ $\frac{1}{dk}$
Within Sires (Between Dams)	$s(d-1)$	$MS_D$	$\sigma^2 = \frac{1}{D} (MS_D - MS_W)$ $\frac{1}{k}$
Within progenies	$sd(k-1)$	$MS_W$	$\sigma^2 = MS_W$ $W$
$\sigma_T = \text{Total variance} = \sigma_S^2 + \sigma_D^2 + \sigma_W^2 = \sigma_p^2 \text{ or } V_p$			

Heritability estimate from sib analysis was made from a sire component of variance as:

$$h^2 = \frac{4\sigma_S^2}{\sigma_T^2}$$

based on reports that the dam component of variance is much more influenced by the environment.

Selection differential, for litter size in each generation of selection was computed to estimate the change in the population mean. Males and females had different average selection differentials; the selection differential  $S$  in a generation was calculated as:

$$S = \frac{1}{2}(S_M + S_F)$$

In generation 0.5  $S$  is computed as either  $\frac{1}{2}S_F$  or  $\frac{1}{2}S_M$  as in this overlapping generation only females or males are selected.

Expected Genetic Change for litter size ( $\Delta G$ ) was determined to provide an estimate of possible genetic progress for each generation of selection using (Falconer, 1981)

$$\Delta G_t = h^2 S$$

where	$\Delta G_t$	=	Expected genetic change in litter size from selection in generation $t$
	$h^2$	=	heritability estimate for litter size
	$S$	=	Selection differential weighted by $1/\sqrt{n}$

Realized heritability in each generation was computed from the ratio of selection response to selection differential

(Falconer, 1981). Selection response (SR) was computed (Hetzler and Harvey, 1967) as

$$SR = \bar{P}_s - \bar{P}_o$$

where

$\bar{P}_s$  is mean performance of selected parents

$\bar{P}_o$  is mean performance of offspring of selected parents.

Correlated response in backfat thickness and loin eye area was computed from the estimated heritabilities and genetic correlation in each generation as (Fredeen and Mikami, 1986b)

$$CR_y = i h_x h_y r_g \sigma_y$$

where

$CR_y$  is correlated response in backfat thickness or loin eye area

$i$  is selection intensity

$h_x$  square root of heritability of litter size

$h_y$  square root of heritability of either backfat thickness or loin eye area

$r_g$  is the genetic correlation between the traits

$\sigma_y$  is phenotypic standard deviation in backfat or loin eye area

#### 4. RESULTS

Breed averages were determined on the basis of data adjusted to remove the influences of different factors on variation of backfat thickness, loin eye area and litter size. Litter size was adjusted for effect of inbreeding of dam and litter and to a sow equivalent. \*A summary of the data used to determine generation effect after adjusting for factors found significant (Tables 4.7-4.9,  $p \leq .05$ ) in each population is presented in Table 4.1. The data set was also adjusted for inbreeding of dam and litter for estimates of litter size as these variables changed. For an increase of 10% in inbreeding of dam, litter size changed by -0.07 for Berkshire, -0.50 for Yorkshire and -1.16 for Composite. With 10% inbreeding of litter, litter size was changed by -0.51 for Berkshire, -0.10 for Yorkshire and -0.12 for Composite (Table 4.3).

Significance of differences among breed means were determined by Duncan's multiple range test. Backfat thickness and loin eye area were adjusted for weight and to a common sex basis at slaughter; Berkshires and Composites did not differ significantly for backfat thickness but both were larger than Yorkshire ( $p \leq .05$ ). Loin eye area for Berkshires was significantly greater than Yorkshire and Composites; Yorkshires and Composites did not differ significantly in this trait ( $p > .05$ ). The three breeds differed from each other for litter size,



with Berkshires having the smallest litter size, Yorkshires intermediate and Composite having the largest (Tables 4.5-4.6).

In Table 4.7 - 4.9 are presented regression coefficients and probability values showing the effects of sex, farrowing season, year of farrowing and generation on backfat thickness, loin eye area and litter size for each population. Adjustment factors for differences between sow and gilt means as determined from parity effects for litter size, and between gilts and barrows for loin eye area and backfat thickness are presented in Table 4.2. Mean barrow and gilt differences in backfat thickness were small and ranged from 0.09 inches for Berkshire to 0.17 inches for the Composite. Litter size differences between gilts and sows were largest for Berkshire with 2.43 more pigs for sows, intermediate for Composite with 1.04 and lowest for Yorkshire with 0.83 more pigs for sows than for gilts.

Regression coefficient for sex effect (Tables 4.7-4.9) on backfat thickness was significant ( $p \leq .05$ ) for the Composite; Composite females had an average BF of 1.34 and males 1.45 inches. Differences were not significant in the other two breeds. For loin eye area, sex effect was highly significant ( $p \leq .01$ ) in all breeds. Berkshire females had an average LEA of 4.51 square inches and the males had 4.32. In Yorkshires, females had 3.99 square

inches and the males had 3.71. In the Composite breed, females had 4.28 square inches of LEA and the males had 3.85.

Seasonal effect on BF (Tables 4.7-4.9) was significant ( $p \leq .05$ ) for Composite but not for Berkshire and Yorkshire. Spring farrowed Composite pigs had a higher backfat thickness of 1.53 inches than fall pigs with 1.39. For all the breeds, season of farrowing had no significant effect on loin eye area; however fall farrowed Berkshire pigs had a loin eye area of 4.33 square inches, Yorkshires had 3.98, Composite 4.02 square inches whilst spring Berkshire pigs had 4.45, Yorkshires 4.01 and Composite pigs had an average LEA of 4.05 square inches. In Yorkshsire and Composite the interaction between season and sex for backfat and also loin eye area was significant ( $p \leq .01$ ). Spring farrowed female pigs for all breeds had a higher average LEA and lower BF than spring farrowed males and also for fall farrowed pigs. The effect of season of farrow on subsequent litter size was only significant ( $p \leq .01$ ) for Berkshire. Berkshire litters farrowed in spring had on average 0.86 more pigs than those farrowed in the fall.

In Berkshires, year of farrowing had a significant ( $p \leq .01$ ) effect on backfat thickness and number of pigs born but none on LEA. On average 0.14 more pigs were farrowed each year, spanning the study period. Backfat on the

other hand was reduced in this period by 0.045 inches/year. Year of farrowing also significantly affected BF and LS in Yorkshires ( $p \leq .01$ ) but not for LEA. Backfat was reduced on average by 0.03 inches each year whilst LS was increased by 0.16 pigs. Both loin eye area and backfat of Composite pigs were not significantly affected by year of farrowing but litter size varied significantly ( $p \leq .05$ ).

Weight at slaughter had a highly significant ( $p \leq .01$ ) effect on backfat thickness and loin eye area in all the breeds. For analysis, backfat thickness was adjusted to 210 lbs. live weight at slaughter and loin eye area to 216 lbs.

Generation effect was significant ( $p \leq .01$ ) only for loin eye area in Berkshire, but was not for either backfat or litter size (Table 4.10).

As shown in Table 4.10, generation effect on both LS and LEA for the Composite was highly significant ( $p \leq .01$ ). The decrease in litter size after generation 1.5 may indicate a substantial loss in heterosis during development of Composite population from crossbreds. In essence a similar result occurs with inbreeding of a purebred population but generally of lesser magnitude. In the Composite breed there is an increase, though not significant ( $p \leq .05$ ), in generation 0.5 from generation 1 of 11.62 and 12.28% in loin eye area and litter size

respectively. Backfat thickness is increased significantly by 12.69% in generation 0.5; the increase in backfat depth in generations 1.5, 3 and 2.5 over generations 1 were not significant.

Backfat thickness was highest ( $p \leq .05$ ) in generation 1.5 for Berkshires (Table 4.10). It decreased by 3.7% from generation 1 to 0.5 or by 4.7% from generation 0.5 to 2 and by 1.52% from generation 3 to 2.5. Measures of loin eye area for Berkshires in generation 0.5, 1.5, 3 and 2.5 are significantly higher ( $p \leq .05$ ) than generation 1. The differences represent an increase of 18.23, 31.39, 22.53 and 21.01% respectively. Generations 3 and 2.5 represent reduction in LEA of 6.74 and 7.9% over generation 1.5 with a LEA of 5.19 square inches.

Though not significant ( $p > .05$ ), there was a decrease in backfat thickness in generations 1.5 and 3 of 5.2 and 3.7% over generation 1 in the Yorkshire (Table 4.10). Litter size was increased ( $p \leq .05$ ) by 23.73% in generation 0.5 to 11.89 pigs from 9.61 in generation 1.

Breed differences within generations for backfat thickness, loin eye area and litter size are presented in Table 4.11. In generation 1 the composite had a significantly ( $p \leq .05$ ) lower loin eye area of 3.53 square inches than for both Yorkshire with 3.76 and Berkshire with 3.95 square inches. In generation 1, the differences between the breeds were not significant ( $p > .05$ ) for

litter size and backfat thickness. In generation 2 and 1.5, Composite dams had more pigs ( $p \leq .05$ ) than Yorkshire and Berkshire dams; the differences between the breeds were not significant in generation 3 and 2.5.

Phenotypic correlations ( $r$ ) presented in Table 4.12 are data adjusted for inbreeding of sire, dam and litter parity and weight at slaughter for all the traits in the 3 breeds. In Table 4.13 are  $r$  values when the data was adjusted according to significance of the regression coefficients reported in Tables 4.7 - 4.9. The association between backfat and loin eye area in the 1st generation of selection was highly significant in Yorkshire and Composite ( $p \leq .01$ ) with a negative correlation in both the data adjusted for inbreeding and parity effects (Table 4.12) and that adjusted to same year and season of farrow (Table 4.13). In the Berkshire the relationship between LEA and LS was not significant ( $p > .05$ ) in generation 1. The negative correlation between BF and LEA was significant in both generations 1.5 and 3 for the unadjusted data. In the data adjusted for sex, season and years there was no association. The negative correlation between backfat thickness and loin eye area in Yorkshire was significant in generation 0.5, 2, 3 and 2.5. Generation 2 had the only significant association between LEA and BF in the Composite breed.

The phenotypic correlation with data adjusted for season and year effects (Table 4.13) between BF and LS was not statistically significant in all the breeds for all the generations except in generation 1 and 1.5 in Composite and generation 2 in Yorkshire with  $r$  of 0.36, -0.25 and -0.51 respectively. For the correlation between loin eye area and litter size only generations 1, 2 and 2.5 for Berkshire, 2 for Yorkshire and Composite were significant. Adjusting the data generally weakened the correlations that were significant in the data adjusted only for inbreeding, weight at slaughter and parity (Table 4.12).

Table 4.14 presents progeny phenotypic variances within and between dams and sires, and estimates of heritability from these, using data adjusted for inbreeding, parity and weight at slaughter. Heritability estimates for data adjusted to remove sex, year and seasonal effects are presented (Table 4.15). Heritability for litter size in the Composite varied from 16% in generation 3 to 23% in generation 2.5 (Table 4.14). Loin eye area heritability varied from 37% in generation 1.5 to 57% in generation 2.5. In the Yorkshire, heritability estimate was lowest in generation 1.5 with 39% and highest in 2.5 with 66% for loin eye area; litter size heritability estimate varied from 18% in generations 2 and 3 to 27% in generation 1.5. For Berkshire

heritability estimates for backfat thickness varied from 43% in generations 2 to 66% in generation 3.

Expected genetic progress in litter size estimated in generations (overlapping and discrete) are presented in Table 4.16 as computed from heritability values (Table 4.15) and realized selection differential. The Composite, except in generation 2 and 2.5, had a greater selection differential than either Yorkshire or Berkshire. With a 22% decrease in litter size over generation 2, generation 3 in the Composite is most affected by generation change. The genetic response is quite variable, reaching peak in generation 1.5 and then declines with subsequent selection to 0.29 in generation 2.5 and 0.61 in generation 2. The selection differentials in generation 0.5 ranged from 0.01 for Berkshire, to 0.04 for Yorkshire and 0.14 for the Composite breed.

The reduction in variance through the generations as presented in Table 4.14 and 4.15 are inconsistent; variance estimated for siblings from different sires are much higher than those between dams. Between sire variances are much higher for litter size than for loin eye area and backfat thickness.

Realized heritability estimates for litter size in generations 0.5, 1.5, 2, 2.5 and 3 are presented (Table 4.17) along with selection and correlated responses determined in the progeny generations.

Table 4.1: Summary of adjusted data, mean and standard deviations of BF<sup>1</sup>, LEA<sup>2</sup> and LS<sup>3</sup> within overlapping generations in three breeds of swine:

GEN	TRAIT	Breed					
		N	BERKSHIRE	N	YORKSHIRE	N	COMPOSITE
1	BF	157	1.38 ± 0.14	145	1.35 ± 0.22	172	1.43 ± 0.21
	LEA	157	4.25 ± 0.67	145	3.82 ± 0.56	172	3.95 ± 0.71
	LS	34	8.84 ± 2.31	38	10.10 ± 2.71	46	10.92 ± 2.33
0.5	BF	98	1.37 ± 0.16	71	1.35 ± 0.21	86	1.48 ± 0.18
	LEA	98	4.70 ± 0.60	71	3.88 ± 0.63	86	3.96 ± 0.51
	LS	33	8.95 ± 2.31	23	12.27 ± 3.03	26	11.53 ± 3.52
2	BF	61	1.29 ± 0.06	63	1.40 ± 0.23	93	1.36 ± 0.17
	LEA	61	4.37 ± 0.46	63	3.53 ± 0.64	93	4.18 ± 0.67
	LS	17	9.5 ± 1.64	28	10.47 ± 3.55	25	11.09 ± 2.6
1.5	BF	45	1.43 ± 0.11	59	1.27 ± 0.19	90	1.37 ± 0.17
	LEA	45	5.19 ± 0.45	59	3.88 ± 0.68	90	4.15 ± 0.53
	LS	15	8.45 ± 1.34	119	10.48 ± 4.55	28	12. ± 1.66
3	BF	74	1.23 ± 0.24	85	1.24 ± 0.22	68	1.37 ± 0.13
	LEA	74	4.83 ± 0.35	85	3.94 ± 0.53	68	3.93 ± 0.38
	LS	23	8.90 ± 1.39	28	10.24 ± 2.55	18	9.5 ± 0.54
2.5	BF	59	1.36 ± 0.14	89	1.22 ± 0.14	71	1.4 ± 0.19
	LEA	59	3.90 ± 0.51	89	3.75 ± 0.43	71	4.28 ± 0.84
	LS	18	9.24 ± 1.35	25	11.85 ± 2.83	20	9.2 ± 2.19

<sup>1</sup>BF: Backfat thickness in inches

<sup>2</sup>LEA: Loin eye area in square inches

<sup>3</sup>LS: Litter size (number of pigs born alive and dead at a particular farrowing).



**Table 4.2:** Correction factors for adjusting carcass traits and litter size for parity from a gilt to a sow equivalent, and loin eye area and backfat thickness to a barrow equivalent.

Trait	Breed		
	BERKSHIRE	YORKSHIRE	COMPOSITE
Litter Size (number of pigs born alive and dead)	2.43	0.83	1.04
Loin Eye Area (Square Inches)	-0.14	-0.23	-0.22
Backfat (inches)	0.09	0.12	0.17

**Table 4.3:** Mean and standard deviation of inbreeding coefficients in three populations of swine

Variable \ Breed	BERKSHIRE	YORKSHIRE	COMPOSITE
Inbreeding of dam	.0614 $\pm$ .0632	.1274 $\pm$ .0778	.1331 $\pm$ .0403
Inbreeding of litter	.0893 $\pm$ .0670	.1338 $\pm$ .0809	.1342 $\pm$ .0546
Inbreeding of sire	.0789 $\pm$ .0678	.1112 $\pm$ .0870	.1280 $\pm$ .0585

**Table 4.4:** Estimates of change in litter size as inbreeding of litter and dam increased by 10%

Variable	Breed of Dam		
	Berkshire	Yorkshire	Composite
Inbreeding of litter	-.51	-.10	-.12
Inbreeding of dam	-.06	-.50	-1.24

Table 4.5: Multiple comparison of trait means in purebreds of data adjusted for inbreeding of dam, sire and litter, parity and weight at slaughter:

Breed	Trait			
	N	BACKFAT	LOIN EYE AREA	LITTER SIZE
BERKSHIRE	488	1.36 <sup>a</sup>	4.51 <sup>a</sup>	9.17 <sup>a</sup>
YORKSHIRE	512	1.29 <sup>b</sup>	3.99 <sup>b</sup>	10.27 <sup>b</sup>
COMPOSITE	514	1.34 <sup>a</sup>	4.28 <sup>c</sup>	11.30 <sup>c</sup>

Means in the same column with same superscript are not significantly different ( $p > .05$ ).

N is total number of pigs used from each breed

Table 4.6: Multiple comparison of trait means for data adjusted for sex, season and year.

Breed	Trait			
	N	Backfat	Loin Eye Area	Litter Size
BERKSHIRE	488	1.33 <sup>a</sup>	4.50 <sup>a</sup>	8.32 <sup>a</sup>
YORKSHIRE	512	1.28 <sup>b</sup>	4.01 <sup>b</sup>	9.45 <sup>b</sup>
COMPOSITE	514	1.34 <sup>a</sup>	4.12 <sup>b</sup>	10.82 <sup>c</sup>

Means in the same column with same superscript are not significantly different ( $p > .05$ )

**Table 4.7** Regression coefficients and p values from linear regression of factors affecting backfat, loin eye area and litter size in Berkshire.

Independent Variable \ Trait	Backfat (inches)	Loin Eye Area (square inches)	Litter Size
Sex p <sup>1</sup>	0.006 ± 0.02 NS <sup>2</sup>	0.28 ± 0.1 0.007	---
Season p	0.006 ± 0.013 NS	0.03 ± 0.06 NS	0.70 ± 0.20 0.0006
Year p	-0.017 ± 0.005 0.002	-0.008 ± 0.02 NS	0.16 ± 0.08 0.05
Generation p	-0.0003 ± 0.002 NS	0.124 ± 0.016 0.001	-0.04 ± 0.01 NS
Sex (Generation) p	0.18 ± 0.04 NS	0.26 ± 0.17 0.01	---
Season (Generation) p	0.02 ± 0.05 NS	0.17 ± 0.09 0.02	0.81 ± 0.42 0.002
Year (Generation) p	-0.13 ± 0.09 0.02	0.02 ± 0.01 0.04	0.16 ± 0.11 NS

<sup>1</sup>p is level of significance.

<sup>2</sup>Not significant (p > .05)

**Table 4.8:** Regression coefficients and p values from linear regression of factors affecting backfat, loin eye area and litter size in Yorkshire.

Independent Variable	Trait		
	Backfat (inches)	Loin Eye Area (square inches)	Litter Size
Sex p <sup>1</sup>	-0.05 ± 0.03 0.07	0.38 ± 0.07 0.0001	---
Season p	0.015 ± 0.015 NS <sup>2</sup>	0.059 ± 0.04 NS	0.40 ± 0.24 NS
Year p	-0.027 ± 0.009 0.002	0.02 ± 0.03 NS	0.44 ± 0.14 0.002
Generation p	0.004 ± 0.03 NS	0.06 ± 0.04 NS	0.14 ± 0.11 0.0002
Sex (Generation) p	-0.05 ± 0.02 NS	0.39 ± 0.14 0.0011	---
Season (Generation) p	-0.034 ± 0.04 NS	0.06 ± 0.01 NS	0.46 ± 0.17 0.014
Year (Generation) p	-0.02 ± 0.01 0.006	0.09 ± 0.02 NS	0.46 ± 0.13 0.0001

<sup>1</sup>level of significance.

<sup>2</sup>Not significant (p > .05)

**Table 4.9:** Regression coefficients and p values from linear regression of factors affecting backfat, loin eye area and litter size in Composite.

Independent Variable \ Trait	Backfat (inches)	Loin Eye Area (square inches)	Litter Size
Sex p <sup>1</sup>	-0.07 ± 0.02 0.0001	0.49 ± 0.07 0.0001	---
Season p	0.03 ± 0.01 0.02	0.02 ± 0.05 NS <sup>2</sup>	0.26 ± 0.18 NS
Year p	0.01 ± 0.01 NS	0.03 ± 0.03 NS	0.24 ± 0.11 0.02
Generation p	0.13 ± 0.06 0.03	0.16 ± 0.11 0.0002	0.21 ± 0.17 0.0001
Sex (Generation) p	-0.02 ± 0.01 0.0001	0.21 ± 0.04 0.0001	---
Season (Generation) p	0.09 ± 0.01 0.02	0.17 ± 0.08 0.001	0.20 ± 0.12 0.0001
Year (Generation) p	0.09 ± 0.03 NS	0.15 ± 0.11 0.006	0.16 ± 0.07 0.009

<sup>1</sup>Level of significance.

<sup>2</sup>Not significant (p = .05)



**Table 4.10: Multiple comparisons of generation means in BF, LEA and LS**

Generation	Breed								
	BERKSHIRE			YORKSHIRE			COMPOSITE		
	BF	LEA	LS	BF	LEA	LS	BF	LEA	LS
1	1.40 <sup>a</sup>	3.95 <sup>c</sup>	9.82 <sup>ab</sup>	1.34 <sup>ab</sup>	3.76	9.61 <sup>b</sup>	1.34 <sup>b</sup>	3.53 <sup>c</sup>	9.69 <sup>b</sup>
0.5	1.35 <sup>a</sup>	4.67 <sup>ab</sup>	8.78 <sup>a</sup>	1.33 <sup>ab</sup>	3.84	11.89 <sup>a</sup>	1.51 <sup>a</sup>	3.94 <sup>abc</sup>	10.88 <sup>ab</sup>
2	1.29 <sup>a</sup>	4.37 <sup>bc</sup>	9.50 <sup>ab</sup>	1.44 <sup>a</sup>	3.53	10.47 <sup>ab</sup>	1.34 <sup>b</sup>	3.75 <sup>bc</sup>	12.53 <sup>a</sup>
1.5	1.49 <sup>b</sup>	5.19 <sup>a</sup>	10.20 <sup>b</sup>	1.27 <sup>b</sup>	3.63	10.63 <sup>ab</sup>	1.35 <sup>b</sup>	4.14 <sup>ab</sup>	12.43 <sup>a</sup>
3	1.30 <sup>a</sup>	4.84 <sup>ab</sup>	8.65 <sup>ab</sup>	1.29 <sup>b</sup>	3.85	10.53 <sup>ab</sup>	1.40 <sup>ab</sup>	4.00 <sup>ab</sup>	9.67 <sup>b</sup>
2.5	1.32 <sup>a</sup>	4.78 <sup>ab</sup>	9.61 <sup>ab</sup>	1.34 <sup>b</sup>	3.78	10.25 <sup>ab</sup>	1.40 <sup>ab</sup>	4.28 <sup>a</sup>	10.50 <sup>b</sup>
*P <sub>Gen</sub>	0.19	0.0010	0.09	0.33	0.26	0.0002	0.02	0.0002	0.0001
**R <sup>2</sup>	0.047	0.3326	0.026	0.021	0.024	0.1139	0.0856	0.1488	0.2863

Means in the same column with same superscript are not significantly different ( $p = .05$ )

\* P<sub>Gen</sub> is level of significance showing effect of generations on each trait in each breed.

\*\* R<sup>2</sup> is amount of variation in trait due to generations.

**Table 4.1: Multiple comparison of breed means in generations 1, 0.5, 1.5, 2, 2.5 and 3 using Fisher's Protected Least Significant Differences**

Breed \ Trait	Generation 1			0.5			2			1.5			3			2.5		
	BF <sup>1</sup>	LEA <sup>2</sup>	LS <sup>3</sup>	BF	LEA	LS	BF	LEA	LS	BF	LEA	LS	BF	LEA	LS	BF	LEA	LS
Berkshire	1.40	3.95 <sup>a</sup>	9.82	1.35 <sup>a</sup>	4.67 <sup>a</sup>	8.78 <sup>a</sup>	1.29	4.32	9.50 <sup>a</sup>	1.49 <sup>a</sup>	5.19 <sup>a</sup>	10.20 <sup>a</sup>	1.30	4.84	8.65 <sup>a</sup>	1.32	4.78 <sup>a</sup>	9.61
Yorkshire	1.34	3.76 <sup>b</sup>	9.61	1.33 <sup>a</sup>	3.84 <sup>b</sup>	11.89 <sup>b</sup>	1.44	3.53	10.47 <sup>b</sup>	1.27 <sup>b</sup>	3.63 <sup>b</sup>	10.63 <sup>a</sup>	1.29	3.85	10.53 <sup>b</sup>	1.34	3.78 <sup>b</sup>	10.25
Composite	1.34	3.53 <sup>c</sup>	9.69	1.51 <sup>b</sup>	3.94 <sup>b</sup>	10.88 <sup>b</sup>	1.34	3.75	12.53 <sup>c</sup>	1.35 <sup>b</sup>	4.14 <sup>ab</sup>	12.43 <sup>b</sup>	1.40	4.00	9.67 <sup>a</sup>	1.40	4.28 <sup>a</sup>	10.50

Means in the same column with same superscript are not significantly different ( $\alpha = .025$ )

<sup>1</sup>BF is backfat thickness in inches

<sup>2</sup>LEA is loin eye area in square inches

<sup>3</sup>Litter size

Table 4.12: Phenotypic correlation,  $r$ , between backfat, loin eye area and litter size in Berkshire, Yorkshire and Composite breeds.

Correlation	GENERATION	BERKSHIRE		YORKSHIRE		COMPOSITE	
		$r^*$	P	$r$	P	$r$	P
BF*LEA	1	0.06	NS**	-0.29	0.0005	-0.23	0.008
BF*LS		-0.02	NS	0.08	NS	0.36	0.0001
LEA*LS		-0.23	0.02	0.003	NS	0.05	NS
BF*LEA	0.5	0.01	NS	-0.29	0.015	-0.1	NS
BF*LS		0.03	NS	0.0004	NS	-0.38	NS
LEA*LS		-0.17	NS	-0.07	NS	0.14	NS
BF*LEA	2	0.55	NS	-0.51	0.03	-0.22	0.04
BF*LS		-0.29	NS	0.55	0.01	0.008	NS
LEA*LS		-0.93	0.008	-0.49	0.04	-0.36	0.0005
BF*LEA	1.5	-0.22	0.04	-0.29	NS	-0.15	NS
BF*LS		0.06	NS	-0.02	NS	-0.25	0.02
LEA*LS		0.09	NS	-0.11	NS	0.15	NS
BF*LEA	3	-0.18	0.006	-0.34	0.02	-0.15	NS
BF*LS		0.44	NS	-0.04	NS	0.28	NS
LEA*LS		-0.43	NS	-0.06	NS	-0.16	NS
BF*LEA	2.5	-0.25	NS	-0.42	0.03	-0.53	NS
BF*LS		-0.31	NS	0.35	NS	0.24	NS
LEA*LS		-0.24	0.04	-0.54	NS	-0.76	NS

\*NS is non-significant ( $p > .05$ )

\*\* $r$  is phenotypic correlation

Table 4.13: Genetic correlation between traits in purebreds on data adjusted to same season, year and sex.

Correlation	GENERATION	BERKSHIRE		YORKSHIRE		COMPOSITE	
		r**	P	r	P	r	P
BF*LEA	1	0.11	NS*	0.19	NS	-0.22	0.03
BF*LS		0.19	NS	0.28	NS	0.36	0.03
LEA*LS		0.04	NS	0.31	NS	0.05	NS
BF*LEA	0.5	0.14	.04	-0.16	.03	0.12	NS
BF*LS		-0.21	NS	0.14	NS	-0.25	0.035
LEA*LS		0.20	NS	-0.07	NS	0.24	NS
BF*LEA	2	0.37	0.05	-0.21	NS	-0.34	0.02
BF*LS		0.19	NS	0.25	NS	0.006	NS
LEA*LS		-0.44	NS	-0.28	0.03	-0.46	0.003
BF*LEA	1.5	- 0.02	NS	-0.19	0.05	0.15	0.04
BF*LS		0.14	0.03	-0.04	NS	-0.35	NS
LEA*LS		0.07	NS	-0.31	.03	0.09	NS
BF*LEA	3	-0.25	0.04	-0.31	NS	0.25	0.04
BF*LS		0.14	NS	0.14	NS	0.18	NS
LEA*LS		-0.23	0.05	0.26	0.04	-0.26	NS
BF*LEA	2.5	-0.36	0.03	-0.22	NS	-0.23	0.03
BF*LS		-0.11	NS	0.15	0.02	0.14	NS
LEA*LS		-0.31	NS	-0.24	0.05	-0.46	NS

\*NS is non-significant ( $p > .05$ )

\*\*r is phenotypic correlation

**Table 4.14:** Heritability estimates in the unselected populations from sib analysis within generations 0.5, 1.5, 2, 2.5 and 3 in Berkshire, Yorkshire and Composite Breeds.

Breed		Berkshire					Yorkshire					Composite				
Gen	Trait	Source of Variation					Source of Variation					Source of Variation				
		$S^2_D$	$S^2_S$	$S^2_W$	$S^2_T$	$h^2$	$S^2_D$	$S^2_S$	$S^2_W$	$S^2_T$	$h^2$	$S^2_D$	$S^2_S$	$S^2_W$	$S^2_T$	$h^2$
	BF	0.74	0.12	0.16	1.02	0.47	0.91	0.22	0.31	1.44	0.61	1.62	0.48	0.85	2.95	0.65
0.5	LEA	1.35	0.26	0.09	1.7	0.61	2.66	0.84	0.81	4.31	0.78	1.24	0.75	0.34	4.33	0.68
	LS	1.94	0.90	0.35	2.39	0.15	2.34	0.21	0.61	3.16	0.27	1.85	0.11	0.86	2.82	0.16
	BF	1.93	0.43	0.25	2.61	0.66	0.69	0.11	0.29	1.09	0.48	0.81	0.08	0.15	1.04	0.31
1.5	LEA	1.64	0.51	0.98	3.13	0.65	0.91	0.16	0.51	1.58	0.41	1.64	0.19	0.08	1.91	0.40
	LS	2.01	0.24	0.86	3.11	0.31	1.61	0.12	0.62	2.35	0.20	2.51	0.13	0.81	3.45	0.15
	BF	0.65	0.14	0.31	1.10	0.51	0.41	0.13	0.22	0.76	0.68	0.77	0.11	0.11	0.99	0.44
2	LEA	1.73	0.66	0.78	3.17	0.83	1.02	0.16	0.62	1.8	0.36	0.86	0.12	0.24	1.38	0.36
	LS	1.58	0.12	0.98	2.78	0.17	2.67	0.12	0.94	3.73	0.13	1.74	0.08	0.72	2.54	0.13
	BF	0.63	0.21	0.55	1.39	0.68	0.87	0.28	0.29	1.44	0.78	0.82	0.15	0.21	1.18	0.51
2.5	LEA	1.14	0.23	0.34	1.71	0.54	1.75	0.24	0.48	2.47	0.38	1.15	0.21	0.23	1.59	0.53
	LS	2.45	0.21	0.95	3.61	0.23	2.06	0.19	0.85	3.10	0.25	2.02	0.19	0.79	3.00	0.25
	BF	0.71	0.15	0.16	1.02	0.47	0.83	0.13	0.25	1.21	0.43	0.70	0.10	0.27	1.07	0.37
3.0	LEA	1.02	0.27	0.53	1.82	0.59	1.63	0.49	0.97	3.09	0.83	1.12	0.19	0.29	1.6	0.48
	LS	1.84	0.23	0.83	2.90	0.32	2.63	0.14	0.85	3.62	0.16	2.16	0.14	0.96	3.26	0.17

**Table 4.15: Heritability estimates from sib analysis in generations 0.5, 1.5, 2, 2.5 and 3 for Berkshire, Yorkshire and Composite breeds for adjusted data.**

Breed		Berkshire					Yorkshire					Composite				
Gen	Trait	Source of Variation					Source of Variation					Source of Variation				
		$S_D^2$	$S_S^2$	$S_W^2$	$S_T^2$	$h^2$	$S_D^2$	$S_S^2$	$S_W^2$	$S_T^2$	$h^2$	$S_D^2$	$S_S^2$	$S_W^2$	$S_T^2$	$h^2$
0.5	BF	1.18	0.05	0.10	0.33	0.61	0.70	0.19	0.21	1.21	0.63	1.41	0.35	0.74	2.50	0.56
	LEA	0.95	0.16	0.19	1.20	0.53	1.47	0.76	0.06	2.75	0.06	0.96	0.16	0.31	1.43	0.45
	LS	1.14	0.10	0.75	1.99	0.20	2.16	0.14	0.52	2.82	0.20	0.01	0.05	0.66	1.55	0.21
1.5	BF	1.43	0.33	0.33	2.09	0.63	0.54	0.12	0.22	0.88	0.65	0.71	0.09	0.14	1.94	0.35
	LEA	1.44	0.49	0.94	2.87	0.60	0.88	0.14	0.44	1.46	0.39	1.44	0.16	0.15	1.73	0.37
	LS	1.01	0.14	0.96	2.11	0.27	1.11	0.11	0.42	1.64	0.27	1.74	0.13	0.06	2.73	0.19
2	BF	0.61	0.10	0.21	1.10	0.43	0.49	0.12	0.44	1.02	0.42	0.56	0.10	0.14	1.98	0.50
	LEA	1.61	0.36	0.74	2.17	0.53	0.68	0.14	0.40	1.30	0.43	0.74	0.09	0.10	0.93	0.39
	LS	1.64	0.19	0.71	2.54	0.30	1.43	0.10	0.66	2.19	0.10	1.21	0.09	0.66	1.96	0.18
2.5	BF	0.50	0.19	0.57	1.34	0.57	0.74	0.16	0.24	1.14	0.66	0.69	0.12	0.24	1.05	0.46
	LEA	0.91	0.14	0.22	0.27	0.44	1.02	0.21	0.46	1.19	0.49	0.14	0.18	0.16	1.28	0.57
	LS	2.15	0.20	0.55	3.20	0.26	1.76	0.16	0.65	2.57	0.24	1.02	0.16	0.71	2.63	0.23
3.0	BF	0.70	0.16	0.11	0.97	0.66	0.01	0.10	0.15	1.21	0.30	0.64	0.11	0.29	1.04	0.42
	LEA	0.81	0.17	0.46	1.44	0.47	1.22	0.31	0.96	2.49	0.50	0.90	0.17	0.28	1.35	0.50
	LS	1.73	0.17	0.4	2.54	0.27	1.03	0.13	0.71	3.62	0.10	1.07	0.12	0.07	2.06	0.16

**Table 4.16: Expected genetic progress from selection in generations 1, 0.5, 2, 1.5, 2.5 and 3 for litter size in the Composite, Berkshire and Yorkshire.**

Generation \ Breed	Berkshire			Yorkshire			Composite		
	$s^1$	$R^2$	$i^3$	S	R	i	S	R	i
1	1.21	---	0.53	1.98	---	0.73	1.64	---	0.70
0.5	1.03	0.21	0.45	2.04	0.41	0.67	1.14	0.24	0.32
1.5	0.91	0.25	0.68	2.13	0.58	0.47	1.78	0.34	1.07
2.5	1.36	0.34	1.01	2.12	0.51	0.75	1.29	0.30	0.59
2	2.14	0.64	1.30	1.19	0.21	0.34	1.91	0.34	0.74
3	1.16	0.31	0.84	2.22	0.40	0.87	1.38	0.22	2.56

<sup>1</sup>S is realized selection differential (weighted selection differential)

<sup>2</sup>R is expected genetic progress (in generation) from selecting for litter size

<sup>3</sup>i is standardized selection differential or selection intensity

Table 4.17: Selection response and realized heritability estimates in litter size for Be responses in backfat thickness and loin eye area.

Breed Generation	Berkshire				Yorkshire				Composite			
	SR*	$h^2$	CR <sub>B</sub>	CR <sub>L</sub>	SR	$h^2$	CR <sub>B</sub>	CR <sub>L</sub>	SR	$h^2$	CR <sub>B</sub>	CR <sub>L</sub>
0.5	0.05	0.05	-.004	.020	0.14	0.07	0.007	-0.011	0.21	0.18	0.001	0.012
1.5	0.16	0.18	.004	.009	0.17	0.08	0.007	-0.011	0.19	0.11	0.017	0.014
2	0.11	0.05	.005	-0.105	0.24	0.20	0.005	-0.017	0.26	0.10	0.009	-0.059
2.5	0.13	0.10	-0.054	-0.053	0.16	0.08	0.006	-0.027	0.25	0.19	0.006	-0.082
3	0.11	0.10	0.012	-0.024	0.23	0.10	0.007	0.036	0.22	0.16	-.013	-0.072

\*SR is selection response in a generation

$h^2$  is realized heritability estimate

CR is correlated response in B-backfat thickness and  
L- loin eye area



## 5. Discussion

The results from earlier studies on this data by Spurr (1969) and more recently by Bellaty (1987) are consistent with results of the present study in that the Composite has a significantly ( $p < .01$ ) larger litter size than either Berkshire or Yorkshire. For carcass measurements, this study reports an increase, though not significant ( $p > .05$ ) in backfat thickness and decrease in loin eye area for the Composite over parental breeds. Spur (1969) attributed the lack of significant improvement in loin eye area to low selection intensity; this might well be so, because the general philosophy in the development of the Composite, litter size and growth measures (feed efficiency, growth rate, etc.) were more emphasized. Generation analysis, however have shown here that the increase in litter size for the composite is only sustained to generation 2, with significant decrease in number of pigs born in generations 2.5 and 3 respectively. The decrease in latter generations is probably due to loss of heterozygote advantage, which the Composite would be expected to have over Berkshire and Yorkshire parental breeds. This result agrees with reports by Pirchner (1983) that gene frequency might stabilize through generations of selection in crossbred populations with intense mating increasing homozygosity and reducing heterosis. A synthetic breed, like the Composite, would therefore be

expected to retain only a smaller fraction of its heterosis relative to the base population. The nature of the flexible selection scheme within small closed populations makes such losses highly probable with the unavoidable inbreeding that comes with mating best to best. This loss in heterozygote advantage probably explains the significant decrease in difference between Yorkshire and the Composite in litter size in later generations. As noted by Bellaty (1987), the average number of pigs born by both Berkshire and Yorkshire sows in this study are above those reported in the literature (Drewry, 1973). Litter size for Berkshire and Yorkshire was hardly improved by selection in this study. This is in agreement with the literature in that heritability is low for this trait and marked improvement would require extended generations of effective selection.

Kricker et al., (1982) reported that Yorkshire has a BF measure of 1.45 in. and LEA of 4.33 in<sup>2</sup> and Berkshire 1.41 in. and 4.41 in<sup>2</sup>. The results reported here indicate moderate improvements in BF and LEA for both parental breeds over generation 1 measurements. For loin eye area, Composite has a larger measure than Yorkshire but lower than Berkshire in all the generations; showing an improvement in carcass quality over Yorkshire, fulfilling in part the breeding objective. Arguments could be raised that loin eye area alone is not enough to determine

carcass quality and justify selection solely based on it. Spurr (1969) in his study on this data reported a significant differences ( $p < .01$ ) between length of carcass and loin eye area justifying the use of only LEA in the present study.

Influence of environmental factors is reflected by the positive year effects on backfat and litter size for all three populations (Tables 4.7 - 4.9). The year effects are consistent with other studies (Page, 1976, and Miller et al., 1978). Different feeding trials during the period 1962-73 when the data used in this study were collected, might account for the positive yearly effect on both backfat and loin eye area. McMeekan (1940) reported that lowering feed quality increased backfat thickness but do not significantly affect loin eye area of growing pigs. Nielson (1964) however disputed this claim, observing that severe retardation from the environment, not temporary lowering of feed quality, is necessary to permanently inhibit lean growth. Except for the Berkshire population, season of farrow had no significant effect on number of pigs born per litter. Since litter size is a function of the dam and its environment, the lack of significance might suggest an above average management condition to buffer seasonal changes. Spurr (1969) reported non-significant seasonal effects in the Berkshire, Yorkshire and Composite for litter size and pig birth weight but

significant effects on average number of pigs weaned from spring farrowed litters. Significant year effect on litter size for Berkshire, Yorkshire and Composite were found in this study. The positive effect reported here was certainly not maintained, as generation analysis (Table 4.10) showed a decline for all 3 breeds in later years. Inbreeding depression as shown in Table 4.4 might have acted to decrease or slow any increase in litter size. Spur (1969) and Bellaty (1987) reported a decline in growth rate in all three populations after 1965. This general decline in performance may in part account for the decrease in litter size in subsequent generations.

Significant sex effects were found for loin eye area in all three populations, and for average backfat thickness in the Composite. That females had an average 0.30 square inches larger loin eye area and 0.11 inches less backfat thickness than males is consistent with results of other studies reported by Hetzer et al., (1956) and Krider et al., (1979). These studies reported 0.38 square inches more loin eye area and 0.07 less backfat thickness for females than for males. Studies generally indicate a trade-off in performance between sexes, with male pigs growing faster, reaching market weight 5.4 days earlier than females, but with larger average backfat and smaller loin eye area (Fredeen and Plank, 1963 and Bruner and Swiger, 1968). The effects of increased live weight

at slaughter reported here are in agreement with findings of other studies (Staun, 1978; NSIF, 1981)

A possible problem with recombination based on crosses of diverse types is the breakdown of epistasis amongst loci for a particular genotype (Kinghorn, 1980 and Dickerson, 1972). However most economically important traits in established breed structures are controlled by additive gene action. This makes recombination loss in this study negligible.

An alternative low-cost breed improvement technique is grading up. First generation offspring from a cross of "exotic" breed sires crossed to native tropical pigs combine the advantage of adaptability and improved performance. Beyond this, however one would expect a decline in adaptive performance with an increase in inheritance from the "exotic" sires used in the grading program. Recombination of traits, though long and uncertain, if properly effected can be a breeding scheme of low cost to improve performance and increase adaptability.

The extensive overlapping of generations in the breeding program used in this study was probably intended to overcome the slow rate of progress when traits are recombined and selected for in discrete generations. This process is largely dependent on probability, i.e. chance of assembling the best genes in one animal. With the

animal having a small number of offspring, coupled with the many genes that control economically important traits, the probability of a perfect combination is quite small even with many generations of intense selection.

Heritability estimates reported here (Tables 4.13-4.14) are much higher than those reported elsewhere (Craft, 1958; Boylan et al., 1961; Enfield and Whatley, 1961 and Young et al., 1978). The difference can be attributed partly to the lower environmental effects observed in this study ( $P < .05$ , Tables 4.7-4.9) like season of farrow, year or live weight at slaughter. The method of heritability estimation in most studies reported daughter-dam regression, which would tend to include a higher environmental component of variance. A possible explanation is the larger number of sires introduced particularly in the later generations, causing a larger within-sires and between-dams component of variance (Tables 4.14 and 4.15). By removing the effect of the different factors (Tables 4.7 - 4.9), variances partitioned would reflect more truly the additive genetic effects on the traits. That the estimates did not consistently increase for all the traits in all 3 populations through the generations is probably an indication of low selection pressure or lack of significant progress from selection. In general the difference between sire and dam components of variance

were much larger for litter size than for backfat and loin eye area. This would suggest a greater maternal and non-additive genetic effect on litter size. Through the generations considered in the present study, dam component of variance was consistently greater than sire component. This difference was larger for Berkshire and Yorkshire parental breeds than for the Composite. The heritability estimates for the composite were generally lower than those for the parental Yorkshire and Berkshire breeds. This might imply that the population developed from the Yorkshire x Berkshire crossbred foundation had reduced enough genetic divergence to change the proportion of genetic variance.

The low heritability estimates reported here for litter size compared to those for loin eye area and backfat thickness is consistent with other studies (Craft, 1958, Spur, 1969 and Pumpfrey et al., 1975). Litter size with low heritability estimate indicates that progress from selection will likely be slow. Through the generations, the similarity of these estimates in all three populations might indicate that the cross of Berkshire x Yorkshire was between co-adapted genotypes and therefore did not create extensive new combinations of genes varying widely in effect from those of parental Berkshires and Yorkshires.

Loin eye area and backfat thickness heritability estimates for all the breeds were moderate to high in all the six generations. That much of the backfat and loin eye area heritability estimates were slightly removed from true literature estimates (Enfield and Whatley, 1961; Bereskin and Lush, 1965 and Young et al., 1978) reflect an inconsistency on which Feldman and Lewontin (1975) based their objection to the concept of heritability. Flock (1970), for example, found that heritabilities estimated from various sib correlations were all considerably larger than estimates earlier reported by Bereskin and Lush (1965). The latter study involved daughter-dam regression or relatives one generation removed whilst the former, like the present study, used half-sib estimates of variance. Estimates based on comparison selection gain to selection differential is realized heritability (Falconer, 1981); in this form it predicts gains from selecting in a breeding program with a two-way selection experiment (high and low lines for example) designed to standardize environmental effects. Hetzer and Harvey (1967) estimated realized heritabilities for backfat thickness through 10 generations of selection for high and low backfat in Yorkshires. For the first five generations their estimates compared to sib-correlation estimates were similar in both directions. Alsing et al. (1980), in comparing regression of daughter-litter size on dams found



a much smaller heritability estimate than regression on another litter of the same dam. The results obtained here could partly be explained by environmental correlation arising from maternal contribution to adjacent litters. Intangible environmental influences in this study possibly acted to increase similarity between animals. Limited space and feeding of relatives like siblings in a litter can lead to competition and therefore increase the variance between these animals. Jonsson (1959) reported that group feeding of litters resulted in five times as much variance as single-fed litter mates.

Population (breed) differences in heritability are dependent in part on breeding histories. The Berkshire foundation stock was begun with higher initial homozygosity than the Yorkshire (England, D. C., personal communication). It was expected Berkshires would have lower variation in earlier generations resulting in lower heritability estimates.

The estimates of heritability in generations considered in this study were inconsistent. With selection for litter size from one generation to the next, it is expected that variance between sibs for this trait would decrease leading to a proportionate decrease in heritability (Pirchner, 1983). That the decrease was not consistent might be explained from two aspects. The first and probably most important for the present study was the

low and flexible selection pressure (to accommodate different performance traits) applied in the breeding program. Of less significance particularly for loin eye area and backfat thickness is the proximity of a trait to Darwinian fitness; so that selection would bring no significant improvement, the closer to Darwinian fitness a trait is (Fisher, 1930). With high heritability estimates, backfat and loin eye area can be effectively selected for. Results of Danish pig testing over 30 years have reported considerable progress in both backfat thickness and loin eye area but not for litter size (Stau 1978).

The phenotypic and possible genetic correlation between backfat thickness, litter size and loin eye area have been investigated using three pigs per litter in this study (Tables 4.11 and 4.12). Two traits of an individual may be correlated via a common environment or set of genes. Where heritability estimates of each trait is small, the correlation will be influenced predominantly by non-genetic effects. The trait under selection in this study was litter size, and to a small extent backfat thickness, in all the three breeds.

The phenotypic correlation between backfat and loin eye area in Berkshire, though not consistent, was mostly negative in later generations. This trend agrees with correlations reported by other studies (Roy et al., 1968,

Bruner and Swiger 1968 and McKay and Rahnfield, 1986.) in which phenotypic correlations varied from -15.00 to 0.40. This trend is observed for both Yorkshire and Composite, though for the latter, the relationship was only significant in generation 1 and 2. By removing the year, seasonal and sex effects, the trend in this relationship was still maintained; this would indicate that there is a genetic basis to the relationship. The small sample size in the different generations makes random genetic drift a more acceptable explanation for the strong negative association. An environmental effect through high level quality feeding might be a more logical cause of the relationship between backfat and loin eye area. Another line of thought might be that improved level of feeding permits higher average (additive) gene effect in both traits. Dickerson and Grimes (1947) and Dickerson (1951) reported that Duroc swine on a high plane of nutrition had, on average, thinner backfat and thicker muscling. Where selection in a breeding program is to emphasize backfat thickness, an optimum, rather than low depth is more profitable. An upward or downward direction reduces fitness, with a resulting reduction in growth rate (Morris, 1974). Low backfat thickness has been reported to aggravate Porcine Stress Syndrome (caused by autosomal recessive genes at a single locus) and decrease carcass

quality by making it soft, pale and watery, a condition known as Pale Soft Exudative (Krider et al., 1982).

The evidence in the literature on the association between litter size and either loin eye area or backfat thickness is confusing and inconsistent like those presented here. United States Department of Agriculture (1981) reported a tendency for litter size to increase when backfat thickness decreased in Duroc swine selected for low backfat thickness. The same study however showed an increase in litter size as backfat increased in Yorkshire selected for high and low backfat thickness. Fahmy and Bernard (1972) showed small and inconsistent trends in litter size when loin eye area was selected for over ten generations. Young (1977) reported a positive genetic correlation between growth rate and litter size; this is consistent with the generalization that fast-growing pigs tend to be less mature at a standard weight of 220 pounds, and therefore would be larger at maturity, ultimately producing larger litters. Taking this reasoning further, pigs with higher growth rate have been reported (McMeekan, 1940, and Dickerson, 1951), to have thicker backfat and larger loin eye area; so that litter size association with growth rate possibly correlates indirectly with backfat thickness and loin eye area. Hetzer and Miller (1972) however reported a negative genetic correlation between growth rate (post-weaning) and

backfat thickness in Yorkshire selected over eleven generations for high and low backfat thickness.

The primary trait, litter size, in this study increased for the Composite in generations 0.5, 2, 1.5 and 3 over generation 1 (the base population), but this increase did not translate into a consistent directional change in either loin eye area or backfat thickness, the secondary traits (Table 4.9). Selection was for large litter size, but the low selection differentials reported here (Table 4.14) suggest that little progress was made in this trait, which makes the relationships with loin eye area and backfat thickness reported in Tables 4.11 and 4.12 to be of little relevance in drawing conclusions on the strength and direction of the phenotypic correlations.

Success in a selection program for  $n$  independent traits is, among other factors, dependent on  $1/\sqrt{n}$  intensity of selection on each trait (Dickerson, 1969; and DeNise et al., 1983). The fewer the traits selected for, the more progress per trait one can expect. With one trait emphasized over many generations of selection, significant improvement can be expected. Genetic correlation between traits offers the opportunity for breeders to emphasize fewer or de-emphasize more traits in the breeding program. The correlations reported here between backfat, loin eye area and litter size were quite erratic; a much more conclusive study would select for

high and low backfat on loin eye area, or litter size and then evaluate for each line the correlated response in the non-selected trait.

Realized heritabilities reported here (Table 4.16) along with selection response underlie the complexity of litter size. The realized heritability estimates are consistent with those reported by other workers (Dickerson et al., 1974 and Pumpfrey et al., 1975). The litter size, due to its complexity, is dependent upon ovulation rate, fertilization rate and prenatal viability of embryos (Johnson and Zimmerman, 1986). In the present study, increased ovulation and prenatal viability of embryos due to dam's and embryo's heterosis may account for the larger litters observed for the Composite in earlier generations. Initiated from a crossbred foundation one would expect it to have a higher proportion of heterozygote loci than either Yorkshire or Berkshire. With progressive *inter se* mating in subsequent generations, it is expected that the proportion of homozygote loci would increase, and in the process lose the advantage conferred by heterozygosis (heterosis). Embryo survival may be influenced in a significant way by both vigor of the embryo and the ability of the sow to provide nutrients; heterosis increases both these physical characteristics (Skarman, 1965; and Hacker et al., 1970). For Berkshire and Yorkshire sows, it is possible that the rate of inbreeding

in subsequent generations was much higher than that computed (Table 4.3). It is also possible that the environmental factors removed in this study through adjusting for seasonal and year effect encompass more complex items, most of which are intangible. Precision of calculations to evaluate genetic and environmental parameters in a small population are possibly reduced by random population drift. Random drift would change gene frequency that would be reflected in changes of the generation mean. The results reported here should be considered on a limited basis and not generalized as the number of animals used in the generations might not be representative of the breeds. Experiments designed to estimate genetic improvement by selection would use an unselected population as a control group with the assumption that environmental differences affect both population equally, eliminating environmental fluctuations from assessment of the rate of genetic response. These experiments, like two-way or divergent selections are still subject to genetic drift. In a two-way selection experiment (high and low lines), it is expected that the standard deviation between lines is doubled causing the response to double.

Table 5.1: Heritability estimates reported in this study:

Gen	Trait	Berkshire			Yorkshire			Composite		
		BF	LEA	LS	BF	LEA	LS	BF	LEA	LS
1		0.49	0.62	0.13	0.54	0.71	0.29	0.66	0.72	0.17
0.5		0.47	0.61	0.15	0.61	0.78	0.27	0.65	0.69	0.16
1.5		0.66	0.65	0.31	0.40	0.41	0.20	0.31	0.40	0.15
2		0.51	0.83	0.17	0.68	0.36	0.13	0.44	0.36	0.13
2.5		0.60	0.54	0.23	0.78	0.39	0.25	0.51	0.53	0.25
3		0.47	0.59	0.32	0.43	0.63	0.16	0.37	0.48	0.17



## 6. Summary and Conclusions

Records on a total of 456 litters were used to assess response to a primary and two secondary traits, 140 of these were from Berkshire dams; 159 litters were from Yorkshire dams and 148 were from Composite dams. The data were collected over an eleven year period, 1962-73, in which selection was based on a flexible value system and were analyzed after adjusting for different variables, for the association of generation with litter size, loin eye area and backfat thickness. Analysis within three discrete and three overlapping generations was done to determine the phenotypic correlation between litter size, the primary trait, backfat thickness and loin eye area.

The results of these analyses support the following conclusions:

1. Composite dams in earlier generations, had significantly larger litters than both Yorkshire and Berkshire dams. There is a significant decline in litter size of Composite dams in later generations, possibly a result of loss of heterozygote advantage. The differences among generations in litter size within Berkshire and Yorkshire dams were small; suggesting a failure to

improve this trait in these breeds by selection.

2. Effect of generation on loin eye area though generally positive was not significant for the Berkshire, Yorkshire and Composite pigs.
3. Backfat did not change significantly with generation in the Composite, Yorkshire or Berkshire animals. That this trait along with loin eye area was not significantly affected in the Composite as litter size changed significantly between generations suggests the absence of, but does not preclude, phenotypic correlation.
4. The phenotypic correlations were very inconsistent. However, the trends indicate that phenotypic correlation between loin eye area and backfat thickness in the Berkshire, Yorkshire and Composite pigs is large and negative. By removing year and seasonal effects for phenotypic correlation to

reflect genetic correlation more closely, estimated correlation values remained mostly negative, though lower levels of significance.

5. Extensive overlapping of generations led to lower selection pressure which reduced the response below that expected from selection per unit of time for large litters. This was reflected in the low estimates of heritability and selection differential.
6. Recombination successfully combines loin eye area, backfat thickness and litter size in the Composite without significant decline over Berkshire and Yorkshire parental breeds. The heritability estimates of backfat thickness and loin eye area are high; recombination supported by strong emphasis on these traits would probably significantly increase the average value of these in generations.
7. Variances between progenies from different dams and sires for litter size, loin eye area and backfat

thickness were not significantly affected by the flexible selection system. Low selection pressure in overlapping generations might be responsible.

Recommendation: Determining genetic correlation amongst economic traits has a high potential benefit: A more conclusive study to determine genetic correlation between backfat, loin eye area and litter size should involve six lines; covariation of these traits amongst the lines would provide the basis for determining genetic correlation between traits directly selected for and the correlated traits not under selection.

## Bibliography

- Alsing, I., J. Krippel and F. Pirchner. 1980. Maternal effects on the heritability of traits of pigs. Z. Tierz. Zuchtunysbiol. 97, 241.
- Barr, A. J., J. H. Goodnight, J. P. Sall, W. H. Blacr and D. M. Chilko. 1987. SAS USERS GUIDE. 1987ed. SAS Institute, Inc., Cary, N.C.
- Bauman, R. H., J. E. Kadlec and P. A. Powlen. 1966. Some factors affecting death loss in baby pigs. Lafayette, Indiana. 9 p. Purdue Univ. Ag. Expt. Station Bulletin no. 810.
- Becker, W. A. 1984. Manual of procedures in quantitative genetics. 2d ed. Pullman, Washington State University.
- Bellaty, P. T. 1987. Genetic Components of genetic influence on traits of purebred and crossbred populations of swine of Berkshire and Yorkshire Origin. Ph.D thesis, Corvallis, Oregon State University. 92 pp.
- Bereskin, B., C. E. Shelby, K. E. Rowe, W. E. Urban, Jr., C. T. Blunn, A. B. Chapman, V. A. Garwood, L. N. Hazel, J. F. Lasley, W. T. Magee, J. W. McCarthy and J. A. Whatley, Jr. 1968. Inbreeding and swine productivity traits. J. Anim. Sci. 27:339.
- Bereskin, B. 1986. A genetic analysis of breed conversion and associated trait in swine. J. Anim. Sci. 62:910.
- Berruecos, J. M., E. U. Dillard and O. W. Robison. 1970. Selection for low backfat thickness in swine. J. Anim. Sci. 30:844.
- Bichard, M., A. H. R. Pease, P. H. Swales and K. Ozkutuk. 1973. Selection in a population with overlapping generations. Anim. Prod. 17:215.
- Bowman, J. C. 1984. An introduction to Animal breeding. 2nd ed. Edward Arnold. Baltimore.
- Boylan, W. J., W. E. Rempel and R. E. Comstock. 1961. Heritability of litter size in swine. J. Anim. Sci. 20:566.

- Briggs, H. M. 1969. Modern breeds of livestock. 3rd ed. The Macmillan Company, New York.
- Bruner, W. H. and L. A. Swiger. 1968. Effects of sex, season and breed on live and carcass traits at the Ohio Swine evaluation station. J. Anim. Sci. 27:383.
- Bulmer, M. G. 1971. The effect of selection on genetic variability. Am. Nat. 105:201.
- Cleveland, E. R., R. K. Johnson and P. J. Cunningham. 1988. Correlated responses of carcass and reproductive traits to selection for rate of lean growth in swine. J. Anim. Sci. 66:1371.
- Cox, D. F. 1964. Heritability of backfat thickness measured on the live pig at a constant age. J. Anim. Sci. 23:447.
- Craft, W. A. 1968. Fifty years of progress in swine breeding. J. Anim. Sci. 17:960.
- Cunningham, E. P. 1983. Modern developments in animal breeding. In Proc. 5th Wld Conf. Anim. Prod., Tokyo 1:35.
- DeNise, R. S., K. M. Irvin, L. A. Swiger and R. F. Plimpton. 1988. Selection for increased leanness of Yorkshire swine. IV. Indirect responses of the carcass, breeding efficiency and pre-weaning traits. J. Anim. Sci. 66:551.
- Dickerson, G. E. and J. C. Grimes. 1947. Efficiency of selection for efficiency of gain in Duroc swine. J. Anim. Sci. 6:256.
- Dickerson, G. E. 1951. Effectiveness of selection for economic characters in swine. J. Anim. Sci. 10:12.
- 1969a. Techniques for research in quantitative animal genetics. In: Techniques and Procedures in Animal Science Research. Amer. Soc. of Anim. Sci., Champaign, IL.
- 1969b. Experimental approaches in utilizing breed resources. An. Brg. Abstr. 37:191.
- 1972. Inbreeding and heterosis in animals. Proc. An. Br. and Gen. Symp. in honor of J. L. Lush. Virginia Polytech. Inst. 1972. pp 54-76.

- Drewry, K. J. 1973. Button your (swine) genes. Indiana Swine Days. Purdue Univ. W. Lafayette, In.
- Duncan, D. B. 1955. Multiple range and multiple F-tests. Biometrics. 11:1.
- 1975. T tests and intervals for comparisons by the data. Biometrics. 31:339.
- Emik, L. O. and C. E. Terril. 1949. Systematic procedures for calculating inbreeding coefficients. J. Hered. 40:51.
- Enfield, F. D. and J. W. Whatley. 1961. Heritability of carcass length, carcass backfat thickness and loin in swine. J. Anim. Sci. 20:631.
- England, D. C. 1952. Crossbreeding in swine. Ph.D. thesis. Minneapolis, University of Minnesota. 117 p.
- England, D. C. and L. M. Winters. 1953. The effects of genetic diversity and performance of inbred lines *per se* on hybrid vigor in swine. J. Anim. Sci. 12:836.
- England, D. C., L. M. Winters and L. E. Carpenter. 1954. The development of a breed of Miniature swine. Growth; 18:207.
- England, D. C. and V. M. Chapman. 1962. Relationship of ovulation rate and embryo survival to litter size in swine. Corvallis. 5 p. (Oregon Agricultural Experiment Station. Technical paper no. 1569.
- Fahmy, M. H. and C. S. Bernard. 1972. Reproductive performance of gilts from line selected for feed utilization and carcass score. Can. J. Anim. Sci. 52:267.
- Falconer, D. S. 1953. Selection of large and small size in mice. J. Genet., 51:470.
- 1981. Introduction to quantitative genetics, 2nd ed. Longman Inc., New York.
- Feldman, M. W. C. and Lewontin, R. C. 1975. The heritability hang up. Science. 190:1163.
- Fetuga, B. L., G. M. Babatunde and V. A. Oyenuga. 1976. Performance of the indigenous pigs of Nigeria under intensive management conditions. Nigerian Jour. of Anim. Prod. 3:148.

- Fisher, R. A. 1930. The genetical theory of Natural Selection. Oxford University Press, Oxford.
- Fisher, R. A. and F. Yates. 1963. Statistical tables. 4th ed. Oliver and Boyd, Edinburgh.
- Fitzugh, H. A. 1983. Commercial systems producing marketable products. In. Proc. 5th wld conf. Anim. Prod., Tokyo 1:35.
- Flock, D. K. 1970. Genetic parameters of German Landrace pigs estimated from different relationships. J. Anim. Sci. 30:839.
- Fredeen, H. T. and R. N. Planck. 1963. Litter size and post-weaning performance in swine. J. Anim. Sci. 43:135.
- Fredeen, H. T. and H. Mikami. 1986a. Mass selection in a pig population: direct selection for rapid growth and minimum fat. J. Anim. Sci. 62:1492.
- 1986b. Mass selection in a pig population: Correlated responses in carcass traits. J. Anim. Sci. 62:1502.
- Gray, R. C., L. F. Tribble, D. N. Day and J. F. Lasley. 1968. Results of five generations of selection for low backfat thickness in swine. J. Anim. Sci. 27:331.
- Godbey, E. G. and W. C. Grodley. 1961. Effects of inbreeding and other factors on weights, measurements and mortality of pigs. South Carolina Ag. Expt. Station. Technical Bulletin No. 1004. Clemson. 15 p.
- Gunst, R. F. and R. L. Mason. 1980. Regression analysis and its application. Marcel Dekker, Inc. New York.
- Hacker, D. E., W. E. Rempel, F. D. Enfeld and W. J. Boylan. 1970. Evaluation of two rotational crosses of swine on the basis of their crossbred progeny performance. J. Anim. Sci. 30:167.
- Hallam, D., J. A. Gartner and J. P. Hrabovsky. 1983. A quantitative framework for livestock development planning. Part 1. The planning context and an overview. Agric. Systems. 12:347.
- Harvey, W. R. 1975. Least squares analysis of data with unequal subclass numbers. U.S.D.A., A.R.S. 20-8. U.S. Government printing office, Washington, D.C.



- Hazel, L. M. and E. A. Kline. 1952. Mechanical measurements of fatness and carcass value on live hogs. *J. Anim. Sci.* 11:313.
- Hetzer, H. O. and W. R. Harvey. 1967. Selection for high and low fatness in swine. *J. Anim. Sci.* 26:214.
- Hetzer, H. O. and L. R. Miller. 1970. Influence of selection for high and low fatness on reproductive performance in swine. *J. Anim. Sci.* 30:481.
- Hill, W. G. and A. Robertson. 1968. The effects of inbreeding at Loci with heterozygote advantage. *Genetics* 60:615.
- Hill, W. G. 1972. Estimation of genetic change. II. Experimental evaluation of control populations. *Am. Breed Abstr.* 40:193.
- \_\_\_\_\_. 1977. Variation in response to selection. pp. 343-652 in *Proc. Int. Conf. Quantitative Genetics*, Iowa State University, Ames, Iowa, USA.
- \_\_\_\_\_. 1979. A note on effective population size with overlapping generations. *Genetics*, 92:317.
- Johnson, R. K. and D. R. Zimmerman. 1986. Selection for larger litters and earlier breeding gilts. *Nebraska Swine Rep.* EC86-219.
- Kachigan, S. K. 1986. *Statistical Analysis: An interdisciplinary introduction to univariate and multivariate methods.* Radius Press, New York.
- King, J. W. D. and R. C. Roberts. 1959. The effects of inbreeding on carcass traits. *Anim. Prod.* 1:123.
- Krider, J. L., J. H. Conrad and W. L. Carroll. 1982. *Swine Production.* 5th ed. McGraw-Hill, New York.
- Legault, C. 1971. Relationship between reproductive performance and fattening and carcass characters in the pig. *Annls. Genet. Sel. Anim.* 3:153.
- McMeekan, C. P. 1940. Growth and development in the pig, with special reference to carcass quality characters. *J. Agric. Sci.* 30:276.
- McKay, R. M. and G. W. Rahnfeld. 1986. Genetic correlation between boars, barrows and gilts for various carcass traits. *J. Anim. Sci.* 62:618.

- Malecot, G. 1948. Les mathematiques de l'heredite. Paris, Masson et cie. 63p.
- Morris, C. A. 1974. Genetic relationships of reproduction with growth and with carcass traits in British pigs. Anim. Prod. 20:31.
- National Swine Improvement Federation. 1981. Guidelines for swine improvement programs. Program AID 1157. USDA Extension Service.
- Noland, P. R., W. Gifford and C. J. Brown. 1964. Effects of inbreeding in a Poland China line of swine on certain productivity traits. Fayetteville. 19 p. Ark. Agric. Expt. Station. Bulletin no. 830.
- Olbrycht, T. M. 1943. Statistical basis of selection in animal husbandry. I. Studies on life performance of brood sows; An analysis of variance and covariance of progeny born and reared. J. Agri. Sci. 33:28.
- Pathiraja, N. 1987. Improvement of pig meat production in developing countries. 2. Selection schemes. Wld Anim. Rev. 61:1.
- Pirchner, P. 1983. Population genetics in animal breeding. 2nd ed. Plenum Press, New York.
- Polge, C. 1983. Plenary session 1. Summary and conclusion. In Proc. 5th Wld Conf. Anim Prod., Tokyo, 1:79.
- Pond, W. G., S. J. Roberts, J. A. Dunn and J. P. Willman. 1960. Late embryonic mortality and stillbirths in three breeds of swine. J. Anim. Sci. 19:881.
- Pumpfrey, R. A., P. J. Cunningham and D. R. Zimmerman. 1975. Heritabilities of swine reproductive and performance traits. J. Anim. Sci. 41:256(Abstr).
- Rahnefeld, G. W. and I. Barnett. 1976. Mass selection for post-weaning growth in swine IV. Selection response and control population stability. Can. J. Anim. Sci. 56:783.
- Reddy, V. B., J. F. Lasley and L. F. Tribble. 1959. Heritabilities and Heterosis of some economic traits in swine. Columbia. 27 p. Missouri Ag. Expt. Station.

- Rendel, J. M. and A. Robertson. 1959. Estimates of genetic gain in milk yield by selection in a closed herd of dairy cattle. *J. Genet.* 50:1.
- Robertson, A. and I. M. Lerner. 1949. The heritability of all-or-none traits: viability of poultry. *Genetics*, 34:395.
- Robertson, A. 1959. The sampling variance of the genetic correlation coefficient. *Biometrics* 15:469.
- Roy, G. L., W. J. Boylan and M. E. Seale. 1968. Estimates of genetic correlations among certain carcass and performance traits in swine. *Can. J. Anim. Sci.* 48:1.
- Rutledge, J. J., E. J. Eisen and J. E. Legates. 1973. An experimental evaluation of genetic correlation. *Genetics* 75:709.
- Rutzmoser, K. and F. Pirchner. 1979. Zurschatzing genetisther Parameter der Fleischleistung stationsgeprupter Mastbullen. II. *Z. Tierz. Zuchtungsbiol.* 96:151.
- Santa Gertrudis Breeders International. 1979. Santa Gertrudis: an American original. SGBI, Kingsville.
- Skarman, S. 1965. Crossbreeding experiments in swine. *Lautbrukshogskloons Annater.* 31:3.
- Snedecor, G. W. and W. G. Cochran. 1967. *Statistical Methods*. 6th ed. Iowa State Univ., Ames, Iowa.
- Spurr, D. T. 1969. Some genetic and environmental factors affecting performance and carcass measurements in swine Ph.D Thesis. Corvallis, Oregon State University. 119 p.
- Staun, H. 1978. Pig testing in Denmark. National Institute of Animal Science, Copenhagen.
- Stockhausen, C. W. F. and W. J. Boylan. 1968. Heritability and genetic correlation estimates in a new breed of swine. *Can. J. Anim. Sci.* 46:211.
- Strang, G. S. and C. Smith. 1979. A note on the heritability of litter traits in pigs. *Anim. Prod.* 28:403.

- Takahashi, J., S. S. Rojas, P. G. Castellani and F. C. Denis. 1988. Post-weaning growth of Brahman and Santa Gertrudis steers under feedlots in the subtropics. *A. Aust. J. Anim. Sci.* 1:149.
- U. S. Department of Agriculture. 1981. Guidelines for uniform swine improvement programs. Program aid 1157. Extension Service, Science and Education Administration.
- Warwick, E. J. and J. E. Legates. 1979. Breeding and improvement of farm animals, 7th ed. McGraw-Hill, New York.
- Winters, L. M., P. S. Jordan, R. E. Hodgson, O. M. Kiser and W. W. Green. 1944. Preliminary reports on crossing of inbred lines of swine. *J. Anim. Sci.* 33:923.
- Wright, S. 1922. Coefficients of inbreeding and relationship. *Amer. Nat.* 56:330.
- Yamada, Y. 1962. Genotype by environment interaction and genetic correlation of the same trait under different environments. *Jap. J. Genet.* 37:498.
- Young, L. D., R. K. Johnson and I. T. Omtveldt. 1977. An analysis of the dependency structure between a gilt's phenotypic prebreeding and reproductive traits and genetic correlations. *J. Anim. Sci.* 44:557.
- Young, L. D., R. A. Pumpfrey, P. J. Cunningham and D. R. Zimmermann. 1978. Heritabilities and genetic and phenotypic correlations for prebreeding traits, reproductive traits and principal components. *J. Anim. Sci.* 46:937.