SIRE BY MATING SYSTEM INTERACTION

IN SWINE

by

Keith Lawton Roache

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Department of Animal Science,
McGill University,
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INTRODUCTION

"It is not surprising that in their impatience to transform the animal populations under their control, experimenters and practical husbandmen, may have consciously or unconsciously tended to minimize the fact that they were pitting their short-term efforts against a phylogenetic history extending for many generations," Lerner (1954).

Recently, the literature on genetics in large farm animals has reflected some of this impatience. The Symposia on Germ Plasm Resources (1961) and on Renewable Animal Resources (1963) may be cited as examples. The Symposium on Germ Plasm Resources (1961) discussed the problem of whether there were sources of useful germ plasm not present in our more popular modern breeds of livestock, which could be introduced from less numerous breeds developed in specified areas of the world. The Symposium on Renewable Animal Resources (1963) envisaged the problem as one of crossing the more popular breeds of livestock, e.g. breeds of swine, with the hope of developing new and superior breeds from the crossbreds produced.

The apparent ineffectiveness of mass selection, attributed by Dickerson (1951) to weak selection response (i.e. low heritabilities coupled with negative genetic correlations) and by Fredeen (1958) to inconsistent and incoherent selection, has been a potent cause for this impatience and, nurtured by results with hybrid corn, cross breeding has increased in popularity among swine producers of North America.

There is, however, one possible problem with the "new breed" philosophy. If the heterosis obtained in crossing is a product of genetic diversity, then the process of producing new breeds from hybrid foundations might eventually be detrimental to maximum levels of crossbred productivity. If on the other hand, crossing of existing breeds is utilized to alleviate the alleged impasse to mass selection, caused by plateaus, different peaks of desirability or overdominance, then the advantages of this system rest on the differences in gene frequencies in the different breeds crossed. The more popular breeds of swine in North America seem to have been founded on large enough samples so that "useful" genes were not lost through random drift or chance, yet there seems to be real genetic breed differences for some traits, e.g. litter size at birth and at weaning, (Lush and Molln, 1942).

Research and experience indicate the merits of crossbreeding in commercial swine production. Fredeen (1957) has noted the lack of evidence to indicate the nature and source of so called heterotic effects produced in swine crosses. If further improvement in swine is dependent on the development of lines or breeds which excel in crossbred performance, then such evidence is needed to indicate the type of selection most effective in achieving this end.

In particular, the questions of immediate concern are:

(1) Are our current methods of selection effective in enhancing crossbred performance?

(2) Can the performance of the crossbred be predicted with reasonable accuracy?

The genetic progress that can be made in improving crossbred performance by selection within pure lines, is dependent on the covariance of sire effects in crossbred and purebred populations, the selection intensity in the purebred and phenotypic variance of the selection criteria in the purebred.

The threefold purpose of this study was as follows:

(1) To investigate the importance of heterosis for growth and carcass traits in crosses between Landrace and Yorkshire breeds of swine. The crosses involved being single cross, backcross and crisscross as defined by Winters _et_ _al_. (1935).

(2) To investigate the importance of sire by mating system interaction in representatives of these two breeds.

(3) To attempt to predict crossbred performance using the method developed by Carmon _et_ _al_. (1956).

REVIEW OF LITERATURE

Heterosis in Swine Breeding

Shull (1914) proposed the word heterosis to describe his observations in work with corn, that hybridity itself had a stimulating effect on the physiological activities of the organism. His intention was to describe a visible manifestation of a phenomena, rather than an attempt to explain the genetic and/or physiological processes involved in its expression, however, several attempts to define heterosis on a basis of gene action have resulted in wide discrepancies (Whaley, 1944; Crow, 1948) with regard to the real meaning of the word.

Shull (1952) attempted to clarify the situation by stating that the heterosis concept was the interpretation of increased vigor, size, fruitfulness, speed of development, resistance to disease and insect pests or to climatic rigors of any kind manifested by crossbred organisms as compared with corresponding inbreds, as the specific results of unlikeness in the constitutions of uniting parental gametes. Lush (1948) defines heterosis as the general term for the fact that crosses between moderately unrelated populations, or inbred lines, often produce offspring which on the average, are more vigorous, rapidly growing, more disease resistant than the average of the populations crossed. Buzzati - Traverso (1952) gives a brief definition of heterosis as: "That type and amount of heterozygosity that gives the population or individual the best adaptive value with respect to the conditions in which the organism lives."

Some workers, (Caroll and Roberts, 1942) prefer to restrict the definition of heterosis to cases in which the hybrid excel the larger or more vigorous parent. Others (Bruce, 1910; Lush <u>et</u> <u>al</u>., 1939) consider that heterosis is manifested in instances where the crosses excel the average of the two parental breeds. However, as Lush (1948) has pointed out much of the discrepancy between the two arguments is resolved when the facts with respect to the single characteristics have to be combined into facts with respect to net merit, as is necessary when practical use of heterosis is to be made.

Among the earliest reports on the results of crossing breeds of swine were those of Shaw and MacEwan (1936). These workers reported on the weaning weights of 91 purebred pigs and 700 crossbreds produced by various combinations of five breeds. The average weight of all purebreds was 35.7 pounds, compared with 39.4 pounds for all crossbreds. In feeding trials 77 purebred pigs gained an average of 1.15 pounds/day and required 440 pounds feed /100 pound gain, whilst 325 crossbreds gained 1.24 pounds/day and required 429 pounds feed/100 pounds gain. Winters <u>et</u> <u>al</u>.(1935), (Table 2), reported on a crossbreeding experiment in which three types of crossbreds were produced single cross, three breed cross and backcross. All the crossbreds were superior to the purebreds. Single cross and backcross groups were approximately equal in superiority to the purebreds. Three breed crosses had the greatest advantage. Litters from crossbred sows averaged from two-thirds to two pigs larger at weaning and were from 63 to 96 pounds heavier at weaning. Crossbred pigs reached market weight 17 to 22 days earlier than purebreds.

Lush *et al*. (1939) compared the pure and crossbred progeny from 36 double mated Duroc Jersey and Poland China sows, as well as backcross and three breed crossbred litter mates and concluded that there was a small but general superiority of crossbred pigs over purebred as efficient producers of pork. The differences in birth weight were small and inconsistent, but crossbreds showed rather definite indications of being more vigorous at birth than purebreds. Crossbreds had a lower (15.4 per cent) pre-weaning mortality. In a general summary of most of the crossbreeding work up to 1938 Lush *et al*. (1939) state, "However nearly all those who have studied this question have found advantages, (not always statistically significant ones), for the crossbred pigs and therefore in general crossbred pigs tend to be somewhat more vigorous and thrifty than would be expected from the average of the two parent breeds. Because of this added vigor, the crossbreds generally show a lower death rate up to weaning time and consequently, larger and heavier litters weaned. Also they generally gain weight a little more rapidly on a little less feed. For the same reasons the crossbred gilts or sows when used for breeding purposes can be expected to wean slightly heavier litters than purebreds, but these things should not be expected to happen every time a cross is made, any more than slightly loaded dice would be expected to turn up a winning combination every time they were thrown".

Carroll and Roberts (1942) in an attempt to evaluate the utility of crossbreeding, reviewed experiments covering over 50,000 animals from different countries. They found that the average value of the crossbreds for litter size, birth weight, weaning weight and economy of feed utilization was intermediate between the values for the two pure breeds. The average percentage survival of the crossbred pigs was equal to that of the higher surviving purebred. The average daily gain of all the crossbred pigs was .006 pounds above the figure for the more rapid gaining purebred.

Carroll and Roberts (1942) argued that if crossbreeding was to be judged beneficial, the performance of the crossbreds should exceed the better of the two parental strains of purebred. Crossbreds were therefore compared to the best performing purebred separately, for each of the six traits studied. In this way, the crossbreds were compared to one parent for some traits and to the other parent for other traits. Thus, crossbreds were compared to a composite purebred that did not exist.

Robison (1948) in a series of experiments involving four experimental stations,reported decided advantages in using crossbred sows for the production of market pigs. He suggested a breeding plan for the production of market pigs whereby purebred boars of three or more breeds are rotated on successive generations of sows selected from the herd. He, however, adds that any merit crossbreeding has for the production of market hogs, is the result of purebreeding that has preceeded it. Thus the producers of crossbreds must depend on the breeders of purebreds for any genetic improvement in the development of the swine industry. These results may be subject to bias as comparisons were made with only one of the purebred parental breeds.

Table 1 taken from Craft (1958) summarises the results obtained from the various crossbreeding groups as compared with purebreds in the Regional Swine Breeding Laboratory.

TABLE 1

SUMMARY OF LITTERS PRODUCED IN THE REGIONAL SWINE BREEDING LABORATORY (1937-1956 INCLUSIVE)[a].

	Purebreds excl. of inbreds	Crossbred breeding groups			
		Sows inbred	Sows linecrosses or outbred	Sows crossbred	Sires crossbred
No. litters farrowed	4435	1323	1384	2190	117
Av. no. pigs farrowed per litter	8.33	8.28	8.74	9.51	9.52
Percentage pigs weaned	70.2	74.6	79.8	77.2	79.3
Percentage of litters weaned	94.8	97.4	98.1	97.8	98.3

[a] Summarized from Craft (1958).

These results show an advantage for all crossbreeding groups for percentage pigs weaned and percentage of litters weaned.

Sierk (1948) compared crossbreds with the average of the parental stock for three measures of vigor; weaning weight, rate of gain, efficiency of feed utilization. Gilt litters from nine different inbred Poland China lines and their crosses, Minnesota No.1, Minnesota No.2, and the three breed crosses were studied. The best inbred linecrosses showed approximately 15 per cent advantage when compared with non-inbred lines and non-inbred breed crosses. Inbred linecrosses were less variable than inbred lines in weaning weight, 154 day weight and rate of gain. Gregory and Dickerson (1952) reported on heterosis in eleven breeding groups. The groups represented were two inbred lines of Poland Chinas, one of Hampshires, one non-inbred line of Duroc, their six crosses, and Poland China linecross gilts mated to Duroc boars. In full-fed linecrosses and topcrosses, hybrid vigor expressed itself in greater feed consumption (seven and two per cent respectively) and in more rapid and more economical gains (30 and 13 per cent faster gain and nine and seven per cent less feed per unit gain respectively). Linecrosses between breeds gave much more rapid and more economical gains than linecrosses within breeds. Topcrosses yielded carcasses that were superior in lean meat content to the parental groups. When restricted to the same level of feed intake as the full-fed inbred lines, the linecross and topcross pigs gained faster (13 and 26 per cent respectively) and more economically (nine and 19 per cent respectively) with no differences in ability to digest the rations and small differences in carcass composition. Compared with the mean of the two parent lines, at the same level of feed intake the topcross pigs gained ten per cent more rapidly, required ten per cent less feed and showed a marked superiority in lean meat content of carcass per unit of liveweight. These results were interpreted to mean that hybrid vigor produced a greater stimulus for growth of muscle and bone and that a more efficient metabolic system permitted the expression of this stimulus even without increasing rate of food consumption.

Fredeen (1957) has reviewed extensively, results obtained in crossbreeding pigs. Table 2 presents data in which the performance of the crossbreds has been compared with that of contemporary purebreds from the two or more parental breeds. Results from crosses involving inbred lines were not included.

TABLE 2. PERFORMANCE OF SINGLE CROSS, BACKCROSS, AND THREE-BREED CROSS PROGENY COMPARED WITH THE AVERAGE PERFORMANCE OF THE PARENTAL PUREBREDS. PERCENTAGE ADVANTAGE SHOWN IN BRACKETS[a]

	Double Matings	Single Crosses			Back Crosses			3-Breed Crosses
No. crossbred litters	188 pigs	45	58	10	16	18	836	24
Av. no. living								
pigs at birth	. . .	9.2 (11)	10.0 (-2)	8.0 (-15)	8.1 (-2)	10.6 (15)	8.9 (3)	9.9 (20)
at weaning	. . .	6.0 (6)	7.7 (8)	5.6 (1)	6.2 (12)	9.0 (31)		7.7 (36)
at 154 days	. . .	. . .	. . .	. . .	. . .	. . .	7.2 (10)	. . .
% survival to								
weaning	73 (15)	72 (-2)	77 (8)	70 (11)	74 (0)	85 (11)	. . .	76 (2)
to 154 days	. . .	. . .	. . .	. . .	. . .	. . .	81 (6)	. . .
Av. wt. (lb.)								
at birth	. . .	2.60 (2)	2.45 (2)	3.12 (-3)	2.91 (15)	2.91 (2)	. . .	2.59 (0)
at weaning	38.1 (11)	33.0 (18)	42.8 (10)	49.2 (8)	36.0 (24)	37.7 (-6)	. . .	33.0 (18)
at 154 days	. . .	. . .	. . .	. . .	. . .	. . .	136 (1)	. . .
Litter wt. (lb.)								
at birth	. . .	24.0 (13)	24.5 (1)	25.0 (-20)	23.7 (12)	30.9 (18)	. . .	25.6 (21)
at weaning	. . .	196 (25)	329 (20)	276 (5)	225 (39)	339 (23)	. . .	254 (61)
Feed lot performance								
Av. daily gain (lb.)	1.39 (6)	. . .	1.34 (8)	. . .	. . .	. . .	. . .	. . .
Feed (lb.) per 100 lb. gain	335 (8)	(3)	370 (4)	. . .	(3)	. . .	. . .	(4)
Purebred controls	174 pigs littermates	76 litters from 4 breeds	38 Yorks 36 Chester Whites	16 Poland China 10 Landrace	76 litters from 4 breeds	17 Poland China 3 Duroc	3003 Litters from 4 breeds	76 litters from 4 breeds
Source	Lush et al. 1939	Winters et al. 1935	Hutton & Russell 1939	Lush et al. 1939	Winters et al. 1935	Lush et al. 1939	Bradford et al. 1953	Winters et al. 1935

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[a] Taken from Fredeen (1957).

From this review Fredeen (1957) points out that statistically significant differences between purebreds and crossbreds have seldom been observed in individual experiments. This was due to the fact that variation in performance traits measured was so large that the number of animals required to show statistical significance was prohibitively large for any one experiment. Besides, few experiments could be compared directly due to management, experimental design and breed differences. However, generally heterosis appeared to be greatest for traits expressed in early life, up to weaning. The advantages of crossbreds in feed-lot performance were small and were also very small for the metric traits which measured carcass composition. Seale (1959) also presents data showing some advantage for crossbred pigs in growth rate and slight advantages in carcass quality. His feport showed that crossbreeding results obtained with Canadian data were essentially similar to results reported for breed crosses in other countries.

TABLE 3

AVERAGE PERFORMANCE OF SINGLE CROSS PROGENY COMPARED WITH PUREBRED "CONTROLS". PERCENTAGE ADVANTAGE SHOWN IN BRACKETS.[a]

Station	Lacombe	Scott	Alberta	Manitoba	Macdonald College
No.cross pigs	221	92	129	274	
Breeding*	L-Y (recip.)	L-Y	L-Y	B-Y Y-T,M-Y	Ld-Y
Market age	159(4)	161(9)	168(8)	183(4)	
Wt. (lb.) 154 days					168(11)
Daily gain (lb.)			1.55(7)	1.32(6)	
Feed (lb.) cwt. gain			393(3)		382(9)
Controls no.	190	64	105	496	

*L - Lacombe, Y - Yorkshire, T - Tamworth, B - Berkshire, M - Minnesota 1, Ld. - Landrace.

[a] Taken from Seale (1959).

TABLE 4

AVERAGE PERFORMANCE OF BACKCROSS COMPARED WITH PUREBRED "CONTROLS". PERCENTAGE ADVANTAGE SHOWN IN BRACKETS[a].

Station	Lacombe	Alberta	Manitoba	Macdonald College
No.cross pigs	40	176	116	74
Breeding*	L-LY Y-LY	Y-LY	Y-YT	Ld-Ld-Y Y-Ld-Y
Market age	168 (7)	160 (5)	190 (1)	
Wt.(lb.) 154 days				170 (12)
Feed (lb.)/cwt. gain				379 (10)
Controls no.	86	112	124	

* L - Lacombe, Y - Yorkshire, T - Tamworth, Ld. - Landrace.

[a] Taken from Seale (1959).

TABLE 5

AVERAGE PERFORMANCE OF SINGLE CROSS, BACKCROSS AND THREE BREED CROSS PROGENY COMPARED WITH PUREBRED "CONTROLS". PERCENTAGE ADVANTAGE SHOWN IN BRACKETS[a].

	Carcass Quality		
	Single Cross	Backcross	3 Breed Crosses
No. Pigs	664	305	158
A.R. Score	73 (1)	80 (13)	65 (-1)
Per cent A Grade	53 (.3)	72 (17)	44 (-9)

[a] Summarised from Seale (1959).

Gregory and Dickerson (1952) present results which indicate a heterotic effect on carcass traits. The tendency for crossbreds to have fatter carcass has been noted by Hetzer _et_ _al_. (1951) in data involving line crosses.

The utility of inbreeding and subsequent crossing must be evaluated as to whether the gains made in cross performance are sufficient to compensate for the decline in performance due to inbreeding. Bradford _et_ _al_. (1958a) and Dickerson _et_ _al_. (1954) reported on the ineffectiveness of selection to offset inbreeding decline. Fredeen (1956) suggested that the scientific evidence reviewed indicated a situation less gloomy than the one advanced by Dickerson _et_ _al_. (1954). The answer to the relative merit of crossing inbred lines might be partially arrived at by comparing inbred line crosses with purebred controls. One such study was that of Bradford _et_ _al_. (1958b) in which inbred and linecross boars were compared with outbred boars in two-sire farm herds. Results obtained showed that linecrossing resulted in a recovery of vigor lost during inbreeding, but showed no average advantage for the linecrosses over outbred controls. These workers concluded that the advantages of crossbreeding could be realised as fully by crossing non-inbred lines of different breeds as by crossing inbreds of different breeds. Comparison of linecrosses within breeds with linecrosses between breeds revealed a greater advantage of the latter for rate and economy of gain (Gregory and Dickerson, 1952).

The fact that crossbreds are able to withstand more rigorous environmental conditions than purebreds (Lush et al. 1939); the differences between strain crossing and breed crossing in some crossbreeding experiments (Bradford et al. 1958b; Gregory and Dickerson 1952); the feasibility of crossing already existing breeds to develop new and better breeds - a question indirectly implied in Carroll and Robert's (1942) "composite" purebred; the realization that net merit for total performance does not necessarily vary linearly with each component of net merit Lush (1948) all pose the question as to the type of gene action in heterosis.

Fredeen (1957) considers the problem to be one of the relative contributions of the known genetic mechanisms. Among these would be simple intra-allelelic dominance where the heterozygote possessed a greater variety of favourable dominant genes than existed in either parent.

The dominance hypothesis (Bruce 1910) depends on the observation that there is a positive correlation between recessiveness and detrimental effect, some of the detrimental recessives brought into the hybrid zygote by one parent are rendered ineffective by dominant alleles from the other parent. The result is an increase in vigor of the hybrid as compared to the parent stock. Objections to this hypothesis were raised on the basis that it would result in a skewed distribution in the F_2, and that it should be possible to recover individuals homozygous for the dominant favourable genes concerned. These objections were largely removed by Jones (1917) and Collins (1921) who showed that with linkage and with a large number of factors the possibility of recovering homozygous dominants was extremely remote. In more recent times the theory of intra-allelic gene interaction has extended to include overdominance (East, 1936; Hull, 1946).

Non-allelic gene interaction in the form of epistasis and polygenic balance could also be important in heterosis. Sang (1956) has pointed out that the utilization of hybrid vigor in farm animals, must embody a different approach to that in plants. The primary reason for this is the difficulty of maintaining inbred lines, and the uncertainty of the type of gene action involved. The approach in animal breeding problems has been to rely on mass selection where heritability estimates are high for the traits concerned (Lush, 1948). Such traits seldom display hybrid vigor. Since the type of gene action involved not only influences the level of heterosis, but also response to selection, it will be discussed under the general heading of forces which cause selection to be ineffective.

Forces which cause Selection to be Ineffective.

At the onset of this discussion it may be worthwhile to recall Wright's (1935) statement. "It is the harmonious adjustment of all characteristics of the organism as a whole that is the object of selection, not the separate metrical characteristics." Any investigation of the response to selection must take into consideration whether the selection criteria is one metrical character or net merit. Net merit is a weighted measure of several characteristics each of which may be quantitative in nature. Mather (1941) suggests that adaptability is a result of an establishment of an equilibrium between genotypes and environment. This equilibrium being brought about by the evolution of polygenic combinations or complexes under the influence of natural selection. Changes in the polygenic complexes of a given population without changing the environment would result in a rupture of the established equilibrium with a tendency for the population to regain this equilibrium. This theory credits the environment as a powerful force in selection methods, and linkage as a force of conservation in maintaining these polygenic complexes. Lerner (1954) has reviewed the work on selection in poultry, pigs and to a lesser extent, in cattle. He observed that the indications from the literature were that heterozygosity reduced the variability around the adaptive mean value of a character in cross fertilized species. The degree of adaptedness therefore would be a function of heterozygosity. Natural selection would tend toward the establishment of a certain level of obligate heterozygosity, deviations from which would be discriminated against in most environments. This concept of an integrated genetic system - arrived at by previous evolutionary history, in a dynamic equilibrium was called Genetic Homeostasis by Lerner (1954). Based on the implications of this system Lerner (1954), states that the optimum genotype for fitness from the standpoint of natural selection does not coincide with the optimum genotype from the standpoint of artificial selection for extreme values of a given character. A correlated response in the direction of reduction of fitness would be a direct consequence of selection for extreme morphological phenotype. He further presents a model which shows how the operation of genetic homestasis, even in traits under additive genetic control leads to the establishment of a plateau below the maximum possible expression of a selected trait and requires continuous selection to prevent a relapse. Lush (1948) discusses the situations which modify the rate at which selection may change a population. The first condition is overdominance. The second is epistasis in which selection for a gene in one combination is balanced by selection against that gene when in other combinations. The third is the presence of negative genetic correlations. The fourth is the existance of genotype-environment interaction. If most of the phenotypic variability of a population upon which selection is practiced is due to one or more of these causes, a breeder may select intensively for a long period of time without making any improvement.

Overdominance

The literature is somewhat confusing on the use of the word overdominance. There are publications where overdominance is used as a synonym for heterosis. Jones (1957) considers the term to be restricted to intra-allelic gene interaction. In this sense overdominance would be one possible genetic explanation of heterosis. Since Shull's (1914) definition of heterosis made very little attempt to explain the genetic mechanism responsible for heterosis, and in the light of recent work by Sprague et al. (1959) it would appear that the more logical discussion of overdominance would be in the context of Jones'(1957) definition. Hull (1946) suggested the word overdominance to account for instances where the heterozygote has a selective advantage over both kinds of homozygotes. Crow (1948) supported the theory of overdominance by showing that under complete dominance and no epistasis, average superiority of maximum hybrid over the population at equilibrium gene frequency, would be the product of the mutation rate and number of loci involved or less than five per cent. This is based on the consideration that the effect of a detrimental gene on the selective value of the population is equal to the mutation rate to that gene and is independent of the selective disadvantage which that factor causes. Whereas in overdominance, the loss of fitness of the population is of the order of the magnitude of the selection coefficients. Hence, potential hybrid advantage under some degree of overdominance, at even a small proportion of loci, could be many times greater than five per cent.

Crow (1952) pursuing the overdominance hypothesis, pointed out that in order to have overdominance it was not necessary that the immediate gene products of the heterozygote exceed in quantity or variety, those of either homozygote. At the level of the immediate gene product or any intermediate state, the effect of the heterozygote may be intermediate between the two homozygotes and still result in a greater final result. Any kind of situation in which something is produced for which an intermediate amount is optimum, could be such that the heterozygote is nearer the optimum than either homozygote. One form of gene action that might account for overdominance is that in which two alleles differ qualitatively, or each does something the other fails to do. Irwin's (1947) work with blood group antigens in man and cattle may be cited as an example. In almost all instances the heterozygote has all the antigenic properties of both homozygotes. Overdominance may also be evidenced in cases where on the scale of desirability the heterozygote is preferred to either homozygote. Conceivably, overdominance is a function of the type of environment under which selection is practiced. If changes in the environment necessitate sudden changes in the direction of selection, e.g. changes in selection for "meat type" instead of lard type pigs, then the level of overdominance is related to the selective advantages of heterozygous loci.

The importance of overdominance in large farm animals is still largely a matter of speculation. The validity of Crow's (1948) calculations regarding overdominance has been questioned by Robinson *et al*. (1956) due to the fact that Crow (1948) assumed identical gene frequency for all populations. Recently Bowman (1960) has attempted to measure the extent of overdominance by use of two regressions calculated in terms of genotypic values for two alleles, at a single locus in a recurrent selection breeding scheme.

These regressions involve the relationship between the performance of a sire's testcross progeny and the performance of (1) his full sisters and (2) his pure strain progeny. It is pointed out that a negative regression can only be obtained when overdominance is present, though a positive or zero regression does not necessarily imply the absence of overdominance. The recurrent selection technique (Comstock et al. 1949) represents an attempt to obtain a measure of specific combining ability. Specific combining ability may be due to dominance or to a combination of dominance and epistasis. Overdominance can make the difference in specific combining ability considerably larger than dominance can.

Indirect evidence for the existence of overdominance include the fact that many undesired homozygous recessives remain in a population at too high a frequency to be explained by recurrent mutation alone, (Lush 1948). The ineffectiveness of selection in offsetting the decline in performance from mild inbreeding (Dickerson et al. 1954) has also been cited as indirect evidence. Bradford et al.(1958a) report that in swine an increase of ten per cent in litter inbreeding coefficient was accompanied by a decrease of approximately .20 pigs farrowed per litter, .45 pigs raised per litter, six pounds in individual pig weight at five months and 75 pounds in total litter weight at five months, even though considerable selection was practiced for individual weight of sires. Crow (1948) has maintained that without overdominance long continued selection in any form would have carried favourable alleles to a high frequency in equilibrium with reverse mutation where heterozygosity would be rare and heterosis small. Sprague *et al*. (1959) reported that evidence in their work with corn supported the dominance theory of heterosis, not the overdominance theory. The possibility of epistasis was also discussed.

Epistasis

The primary consideration here is that selection under general epistatic conditions results in changes in the mean which are to a large extent temporary. This is because under these conditions selection changes only the way the genes are combined not their frequency (Lush 1948). Hence some selection is necessary to maintain the merit of an improved population as a relaxation of selection would result in the population reverting to its original mean value.

Wright (1932) has dealt with the problem of selection under epistatic conditions when several genes are involved and different levels of optimum phenotype exist. Genetic variability is pictured in two dimensions, with contour lines showing many intermediate peaks of adaptability as a third dimension. Under these conditions selection for a given gene pool tends to move the population up the nearest slope to its peak, which may or may not be the highest. As soon as the genetic mean of the population is directly under the peak selection fails to move the mean any further, all the variance being epistatic. Increasing selection intensity fixes the population more firmly in the peak. Further response from selection requires a relaxation with a consequent descent of the population from the peak and an opportunity for random drift or segregation, to provide the means of moving the population to new peaks. Under these conditions inter-group competition in isolated subgroups becomes a potent force in evolution.

Comstock, (1960) in his discussion of problems associated with swine breeding, theorises that many breeds possessing the same genes may approach different adaptive peaks. Breed differences unalterable by positive selection would rest in gene frequency differences rather than actual gene differences. Negative selection followed by positive selection could transport a breed to a new and higher peak. However, the rapidity in changes in management and selection in swine production in the past decade leaves some question as to whether these peaks are imminent or distant.

The importance of epistasis in animal and plant breeding is not known. Jinks (1955) through an analysis of diallel crosses has reported the following findings:-

(1) Wherever overdominance was found non-allelic interaction was present also.

(2) Re-analysis of the data, after omitting all crosses showing significant non-allelic interaction led to a drop in the apparent degree of overdominance.

(3) Specific combining ability was always associated with the presence of non-allelic interaction while general com-

bining ability was the outcome of uncomplicated dominance.

Negative Genetic Correlations

Genetic correlations are correlations between the effects of sets of genes which influence two characteristics on the same animal. These correlations are primarily due to genes with manifold or pleiotropic effects. They may also arise due to linkage. Linkage would be a cause only when the coupling and repulsion phases are not in the proportion they would be if mating was completely at random. This would be the case in a population originating from a recent cross of two different lines. This effect of linkage would be of comparatively short duration decreasing rapidly as soon as random mating was resumed. The effect of selection as a cause of genetic correlations, depends primarily upon the extent to which selection varies in isolated sub-groups of the population. Negative genetic correlations may arise when a gene or sets of genes affect two traits differently, i.e. one favourably, the other unfavourably, simultaneous or consecutive selection for both these traits would result in little net selection pressure on the gene. The frequency of the gene or genes will remain at an intermediate level where it could contribute much to the variance of each characteristic. Lush (1948) observes that this effect of selection causes a negative genetic correlation which will be especially acute if the favourable effect is dominant for both characteristics. This amounts to overdominance for net merit, without overdominance necessarily existing for any of the separate primary components of net merit. Fredeen (1953) reported genetic correlations (Table 6) for Canadian Yorkshire swine. There were negative correlations between length and most of the carcass traits studied. Selection based on length alone should theoretically produce carcasses with less fat and smaller percentage ham. However, as Fredeen (1953) pointed out the data were on pigs slaughtered at a reasonably constant liveweight. Since constant weight is a function of all component parts of the carcass, restriction of the data to a constant weight basis automatically introduced some negative correlations. Hazel _et_ _al_. (1943) analyzed the gross correlations of the growth rate of swine in three 56 day periods from birth to 168 days. They found that the genetic variance accounted for 15 per cent, 28 per cent, and 17 per cent of the observed variance in each of three periods. The genetic correlations were all positive and larger than corresponding environmental correlations, indicating that genes with persistent effects were responsible for much of the genetic variation. Hence, heredity had a less important but more consistent influence upon growth rate than environmental sources.

Dickerson (1947) has postulated a negative genetic correlation between milking ability in sows and rate of fat deposition and feed requirements per pound gain. In a subsequent paper Dickerson and Grimes (1947) computed the regression of progeny on sire and dam separately, (Table 7).

TABLE 6

GENETIC CORRELATIONS AMONG TRAITS BASED ON 564 DEGREES OF FREEDOM[a]

	Length	Shoulder Fat	Back Fat	Loin Fat	Percent Ham	Percent Shoulder	Loin Area	Belly Score	Total Score	Feed
Age at 200 lb. livewt.	-0.153	0.128	-0.046	-0.009	0.093	0.090	0.101	0.006	-0.130	0.373
Length of carcass		-.172	- .267	-.110	-.225	-.017	-.166	.009	.455	.018
Thickness of shoulder fat			.653	.667	-.402	-.209	-.161	-.234	-.564	.034
Back fat				.740	-.360	-.503	-.077	-.217	-.377	-.011
Loin fat					-.307	-.493	-.190	-.009	-.449	.003
Percent ham						.194	.273	.087	.239	-.086
Percent shoulder							.167	-.058	-.034	-.044
Loin area								.312	.480	-.128
Belly score									.608	-.116
Total score										-.064

[a] Taken from Fredeen (1953).

TABLE 7

REGRESSION OF OFFSPRING ON PARENT, WITHIN LINE AND YEAR OF PARENT AND OFFSPRING[a]

		Regression of offspring on:			
Variable	D/F	Sire (s)	Dam (d)	Mean of Parents	Rsd.
Wt. at birth	69	-.19 ± .07	-.06 ± .09	-.23 ± .13	-.26*
Wt. at 72 days	69	.02 ± .09	.08 ± .09	.09 ± .12	.08
Feeding period	69	.23 ± .08	.33 ± .10	.47 ± .12	.15
Daily gain	69	.22 ± .07	.29 ± .09	.43 ± .10	.15
Feed/gain	62	.23 ± .08	.01 ± .11	.26 ± .12	.17

* Indicates $P \leq .05$.

[a] Taken from Dickerson and Grimes (1947).

The values for the regression on sire (.23) were considerably larger than those for regression on dam (.01) for feed requirements relative to daily gain. The regression of offspring on dam would include the dam's transmitted as well as her direct nutritional influence on her pigs, whereas the regression of offspring on sire would measure only the transmitted influence. Dickerson and Grimes (1947) interpret the difference in the size of these regressions as further evidence (Dickerson 1947) that dams which transmit more economical gaining ability provide poorer nutrition during the suckling period, thus neutralizing their transmitted influence. Comparison of the regression on dam for feed requirements per unit gain and rate of gain (.01 vs..29) led Dickerson and Grimes

(1947) to hypothesise that lower feed requirements was caused partly by genes which did not increase rate of gain but which reduced milking ability. This would be so if these genes reduced the animal's rate of metabolism, impaired lactation and concurrently lowered the requirements for maintenance, leading to increased fat deposition. The negative heritability of birthweight poses the question of a negative correlation between intrauterine environment of the pig and the transmission by the dam of genes for size at birth.

Bradford _et_ _al_. (1958c) found a negative association between the additively genetic effects in the pig and the maternal effects in different breeding lines for weaning weight and 154 day weight. This was based on the performance of five lines as inbreds, in two, three and four line-crosses and in topcrosses. The validity of this observation is limited because the number of lines involved were small and in the analysis these two effects were assumed to be independent. Vogt _et_ _al_. (1963) studied the genetic correlations between growth rate and (1) feed efficiency, (2) litter size and (3) weaning weight. Values obtained were -.22, .06, .47 respectively. None of the estimates were statistically significant. King (1957) reported the following genetic correlations between carcass traits, (Table 8).

TABLE 8

ESTIMATED GENETIC CORRELATIONS BETWEEN CARCASS TRAITS[a]

	Length of body	Thickness of backfat Shoulder	Thickness of backfat Mid-back	Thickness of backfat Rump	Depth of eye muscle
Carcass weight	-0.73	0.39	0.95	0.35	0.04
Length of body		-0.50	-0.51	-0.24	-0.16
Thickness of backfat:-					
Shoulder			0.77	0.62	-0.13
Midback				0.65	-0.26
Rump					-0.48

[a] Summarised from King (1957).

The large negative correlation between length and carcass weight would indicate that for a given liveweight, pigs that were shorter and fatter, would produce a heavier carcass. Hence dressing percentage was due largely to an increased rate of fat deposition. Genetic correlations between different measures of backfat were large and positive .62, .65, .77, and negative -.2 to -.5 between measures of backfat and eye muscle depth. These correlations based on 239 degrees of freedom were estimated from line components of variance and covariance from inbred lines. Each line represented by a sire and his daughters. Hence they are subject to large sampling errors, values lower than .5 should be regarded as non-significant.

Genotype - Environment Interaction

Animal breeders are aware of the interdependence of genetic and environmental factors in the final form of the phenotype. Research workers in animal genetics attempt statistical separation of genetic and environmental variation. Generally, the genetic variance is that due to variance in the strictly additive sense, any departures from additivity are classed or grouped as environmental. In this sense, the environmental component of variance serves as a "catch all" term for variations not directly attributable to the additive effects of the genotype. As such, the environmental component might include epistatic effects, dominance effects and the joint effects of genotype and environment along with any truly environmental effects. Dickerson (1962) has presented rather lucidly the general line of thought behind methods of obtaining separate measures of genetic and environmental effects. He states, "In the broad sense there are no 'independent' genetic and environmental variations in animal performance. Any phenotypic expression of the genotype requires a relatively specific sequence of environments and any environmental influence is measurable only as it changes the expression of reasonably well integrated (e.g. viable) genotypes. However, differences in phenotypes among a series of genotypes can remain relatively constant under several differing environments, so long as the ranges of both meet requirements for survival; in this sense one can speak of separate average 'genetic' and 'environmental' contributions to variations in performance, and of additional variation due to the joint effects of genotypes and environment, not predictable from their separate average effects." He lists five environmental factors which may modify genetic differences producing interaction thus:

(1) External physical influences
(2) Background genotype
(3) Maternal effect
(4) Social climate
(5) Economic factors.

The consequence and the importance of genotype - environment interaction is reflected in the arguments of Hammond (1947) and Falconer (1960) as regards the optimum environment for selection. Hammond (1947) considers that the most rapid genetic advance will be achieved when selection is practised in the environment most favourable for the expression of the selected character. Most of the progress obtained by selection in the most favourable environment will tend to be maintained if the selected population is transferred to a less favourable environment. Falconer (1960) takes the view that selection should be carried on in the environment under which the population or breed is designed to live. This theory assumes a high degree of genotype-environment interaction.

Genotype-environment interaction has largely been estimated by analysing for and testing the significance of sire x environment interaction in a variance component analysis. Falconer (1960) has considered the problem of performance under two environments as a case of two different correlated characters. The genetic similarity between the two characters is expressed as the genetic correlation between them. From a knowledge of the genetic correlation and of the heritability of each character it should be possible to predict how much of the improvement made by selection in one environment would be carried over when the improved breed is transferred to another environment. In terms of response to selection, Falconer's (1960) formula may be expressed as follows:

$$\frac{CR_L}{R_L} = \frac{i_H}{i_L} \times \frac{h_H}{h_L} \times r_A$$

Where CR_L = correlated response

R_L = direct response

i_H = intensity of selection for correlated character

i_L = intensity of selection for character selected

h_H = heritability of correlated character

h_L = heritability of character selected

r_A = genetic correlation between the two characters.

Falconer (1960) applied the above theoretical considerations to results obtained in selection for three to six week growth in mice on high or low feeding regimes. He found that over the first four generations of selection observed, responses were in agreement with the theory of selection for correlated characters. However, after four generations the two characters (growth on high plane, growth on low plane) yielded widely discrepant estimates of the genetic correlation. After 13 generations of selection, growth on high plane was increased equally by selection on low plane as by selection on high plane, but growth on low plane was increased only by selection on low plane.

The importance of genotype - environment interaction in dairy cattle has been investigated by Robertson et al. (1960). They ascertained management levels on the basis of heifer milk yield and mean yield of contemporaries. Mean yield of the contemporaries were 7020, 8,570 lbs., 10,250 lbs. for low, medium and high levels respectively. They found that total variability and genetic variability increased with herd level. The fraction of genetic variance remained relatively constant over all herd levels. This finding was further supported by Legates (1962) who studied the heritability of fat yields in herds with different production levels. He concluded that the fraction which the additive genetic variance comprised of the total variance was not related to the environmental level. Van Vleck (1963) divided first and second lactation records into four groups depending on the level of their adjusted herd mate average relative to the D.H.I.A. season average. The high level was greater than 1,000 lbs. of milk above the season average whereas the low level was more than 1,000 lbs. of milk below the season average. The data was analysed to investigate the importance of genotype - environment interaction. Results indicated that genetic variability for milk production was different from one environmental level to the other increasing with the higher levels. The genetic variability expressed as a fraction of the total variability was smaller in lower levels of environment than in the higher. There was, however, no difference in the ranking of sires in different environments. Dickerson (1962) found important but largely unpredictable shifts in ranking of genetic stocks for egg production among poultry farm environments.

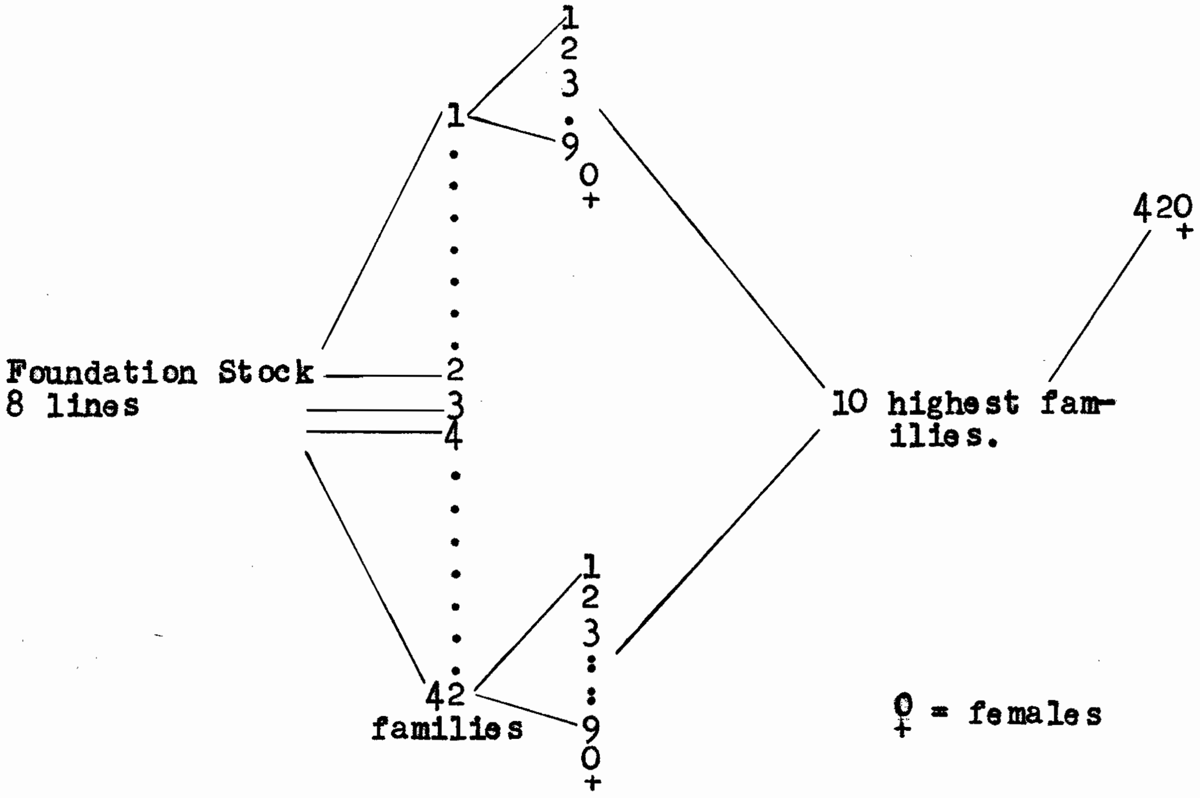
In swine, King (1963) reported no significant gentotype-environment interaction for growth rate, feed conversion and carcass measurements. However, the 140 pigs used in this study represented progeny of three inbred boars of three breeds mated to Large White sows. Salmela _et_ _al_. (1963) studied the reaction of single cross pigs - all produced by Minnesota No. 1 sows out of either Minnesota No. 1, No. 3, or No. 2A boars, to three levels of feed intake, full fed, 85% full fed and full fed 20% roughage diluted ration. There was a highly significant breeding x treatment interaction for rate of gain and age at 200 lbs. There was also significant interactions for ham weight, loin eye area and carcass length. These results substantiated earlier conclusions (Salmela _et_ _al_. 1960), that comparative performance of two or more types of breeding in a particular trial should not be depended upon as final evidence of the relative values of different breeds or crosses.

Kristjansson (1957) reported significant sire and treatment interaction for loin eye area for pigs out of four sires subjected to two management and feeding regimes. Plank and Berg (1963) investigated the effects of plane of nutrition on purebred Yorkshire, Lacombe x Yorkshire, and Landrace x Yorkshire pigs . Genotype x plane of nutrition interactions were significant for average daily gain, carcass length and total Record of Performance score. Thus genotype-environmental interaction seems to be important in swine breeding. Dickerson (1962) has suggested that one of the most probable causes of genotype-environment interaction, is a shift of emphasis in selection intensity between traits as the environment changes. The swine industry is noted for rather dramatic changes in consumer preferences for certain carcass traits.

Comparison of Crossbred and Purebred Selection Schemes.

Evidence for the actual response to selection of large farm animals is scarce. The major reason for this seems to be the difficulty of obtaining adequate controls, and the separation of improvement achieved into genetic and environmental components. Hull (1945) proposed recurrent selection to an inbred tester line to test for specific combining ability in corn. Comstock _et al_. (1949) suggested a modification of recurrent selection, i.e. (reciprocal recurrent selection) to obtain maximum utilization of general and specific combining ability. These methods were proposed as being especially efficient in exploiting maximum heterosis in traits influenced largely by overdominance. An answer to the problem of the relative effectiveness of purebred and crossbred selection schemes, therefore, may be arrived at by comparing Individual and Family Selection with Reciprocal Recurrent Selection.

To date, experiments to test the effectiveness of these two methods have been largely confined to laboratory animals. Bell _et al_. (1955) reported on two selection experiments with _Drosophila melanogaster_. Four methods of selection were used namely: Recurrent Selection, Reciprocal Recurrent Selection, Individual and Family Selection within closed populations, and Inbreeding and Hybridization. All the flies used in this experiment were derived from eight laboratory stocks. In the Closed Population method these stocks were mated to produce 42 families. Nine females from each of the 42 families were tested for fecundity and egg size. Forty-two daughters with the highest performance index were selected from the ten highest families and along with their mates produced the next 42 families for the next cycle of selection. Thus graphically:



In the Recurrent Selection breeding system 42 males from the original segregating population in the Closed Population method, were each mated to four inbred tester females. The seven males with the highest combining ability were chosen to sire the next generation of the segregating population. Selection was accomplished by discarding the progenies from the 35 less desirable males.

In Reciprocal Recurrent Selection the eight foundation stocks were combined by groups of four into two unrelated segregating populations. The breeding scheme was essentially the same as that for Recurrent Selection except that each segregating population would serve as the tester line in alternate generations.

In this experiment selection was on a Performance Index. This was defined as: Performance Index = 4 days egg production + 10 (total of five egg lengths). This first experiment was carried on for 16 generations, at the end of which, the inbred lines were combined into single crosses for comparison with the other methods in terminal performance tests. In the second experiment of the series, foundation stock used consisted of the Closed Population for the first experiment and selected non-inbred laboratory stock of two non-inbred lines. The only major change in selection technique involved Reciprocal Recurrent Selection where 20 sires for each line were test crossed in each generation. Four sires out of the twenty tested in each line were selected to provide five sons each for the next generation of testing. Selection within each method was based solely on fecundity over a three day period between five and seven days of age. Egg size was measured but only for the purpose of studying drift in an unselected trait. This experiment was carried on for 39 generations. Figures 1 and 2 represent results obtained in experiments 1 and 2 respectively.

Results from these experiments suggest that Individual and Family Selection within a closed population is superior to the other methods tested for improving quantitative traits determined by additive genes. Whilst the Closed Population method was initially more effective than the other methods in improving a highly heterotic trait

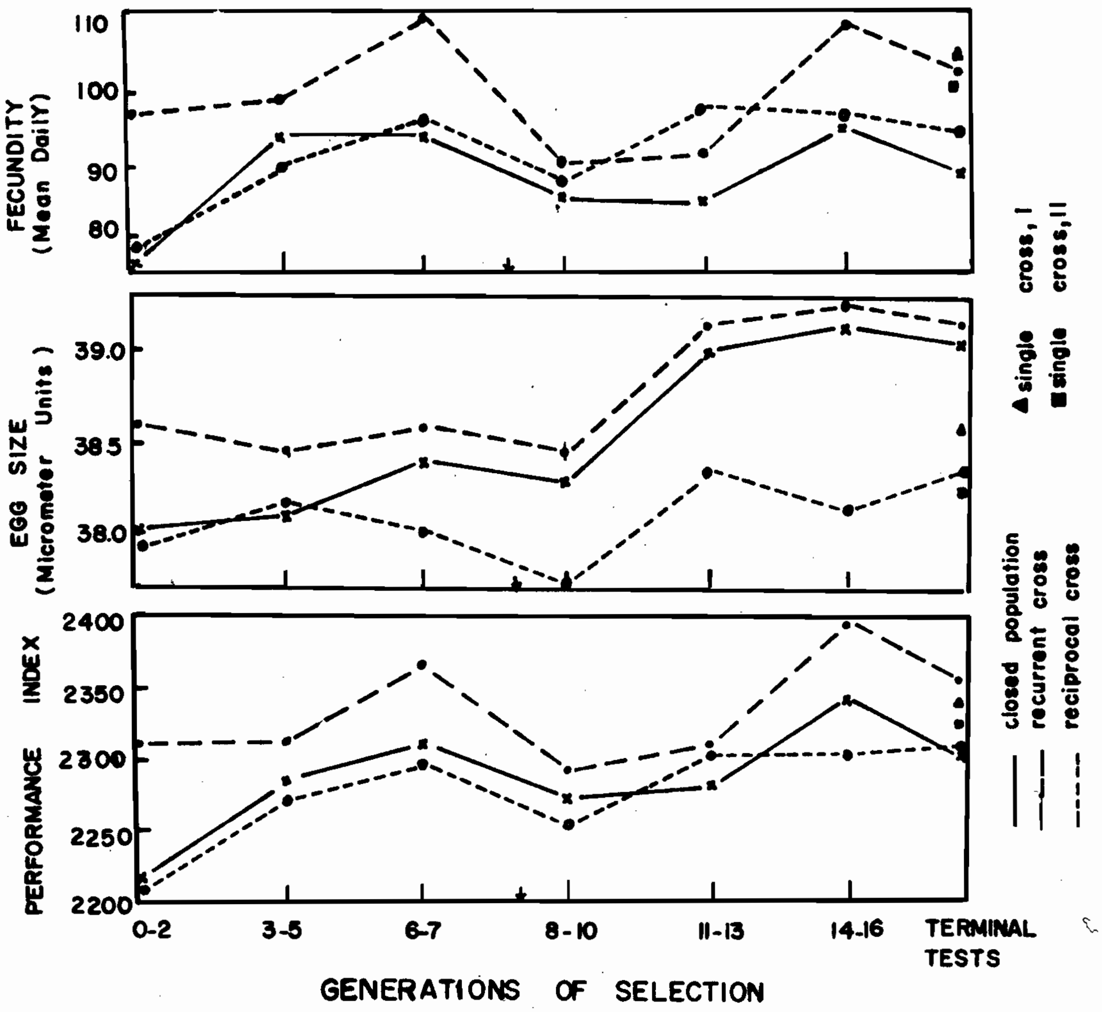


FIGURE 1. Comparison of three methods of selection over 16 generations, plus a terminal test including single cross hybrids, (Experiment I).

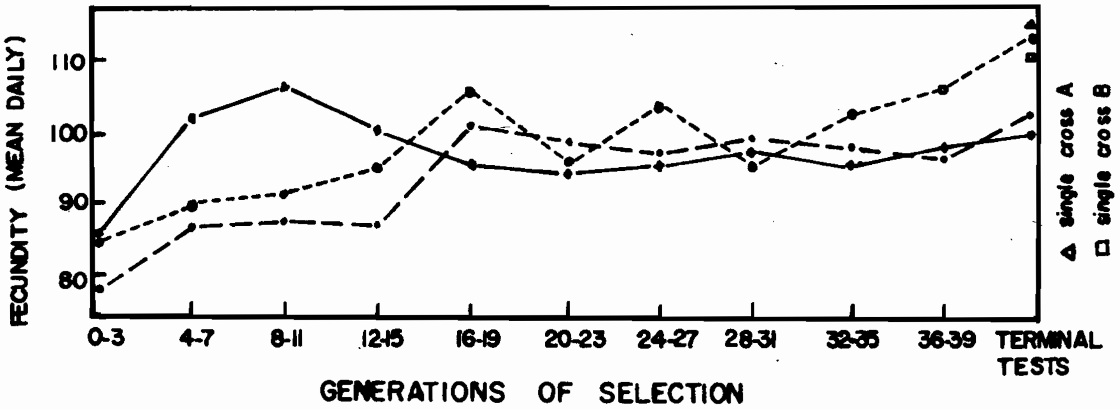


FIGURE 2. Comparison of three methods of selection, plus a terminal test including single cross hybrids, (Experiment II).

(fecundity) in newly formed populations; in the long run, both Reciprocal Recurrent Selection and Recurrent Selection are superior to the Closed Population method for maximum performance in heterotic traits. As indicated in the graphs, the Closed Population plateaued in fecundity after about 12 generations. However, comparison of the Reciprocal Recurrent Selection method with the results obtained from single crosses of inbred strains showed that maximum heterosis was not realised in the former method since these single crosses performed at an equal or higher level than the cross populations derived from the Reciprocal Recurrent method.

Accepting the concept that both Reciprocal Selection and Recurrent Cross Selection are basically selection toward eventual homozygosity within the segregating populations, Bell et al. (1955), suggest that both these types of selection should be accompanied by inbreeding for maximum heterosis. The rate of approach to homozygosity would depend on whether natural selection was acting opposite to or concurrent with artificial selection (Lerner 1954). Kojima and Kelleher (1963) report a higher efficiency of Reciprocal Recurrent Selection than in full sib Family Selection for egg production; however, in this case the additive variance for egg production was low in the base population. Bell and Moore (1958) found Individual Family Selection superior to Reciprocal Recurrent Selection and single cross hybrids for improvement of the highly heritable trait, body weight in Tribolium castaneum.

Griesbach (1962) found that Reciprocal Recurrent Selection was ineffective for increasing heterosis in body weight in poultry.

It is hazardous to attempt to extrapolate results from laboratory animals to large farm animals. Reciprocal recurrent selection schemes require large numbers, further, they greatly increase the generation interval. For these reasons their application to large farm animals would be expensive and time consuming. The indirect evidence - i.e. specific combining ability has been found to be small for pigs (Henderson 1949, Hetzer et al. 1961). On the other hand Dickerson (1949) takes the view that selection has plateaued for some characters in swine variability and has suggested the use of Reciprocal Recurrent Selection for achieving higher levels. Plateaued populations are theoretically expected to be homozygous for the superior allele at loci where the gene action is additive. Fredeen (1958) ascribes the lack of response to selection, to the fact that selection has not actually been applied. Smith (1963) found a small but positive genetic change in backfat thickness in Landrace pigs.

The type of gene action involved in heterosis is by no means clear. If epistasis is important then the method of selection should be on a family basis so as to attempt to preserve those gene combinations that "nick" well with the other families or lines. If overdominance is important then selection should be based on the individual's performance in crosses. If negative genetic correlations exist between traits being selected for, then as Robertson (1955) has pointed out, heritability estimates are useless in predicting response to selection. If dominance is important individual selection should offer the most effective method of improving cross performance.

Predicting Crossbred Performance.

Time and money spent in investigating results of crossbreeding experiments could be reduced if there was some satisfactory method of predicting performance of crosses. Jenkins (1934) presented data on the efficiency of four methods of predicting crossbred performance in corn. Carmon et al. (1956) have presented equations for predicting performance in a rotational breeding scheme. Prediction was based on single cross and parental line performance. The assumptions made in the development of these equations were as follows: (1) diploid behaviour at meiosis (2) two alleles per locus (3) no epistasis (4) parent lines or breeds do not change in gene frequency and (5) sires and dams are random members of their respective populations.

The method of Carmon et al. (1956) may be explained as follows. Considering one locus, let the genotypes, their phenotypic values and frequencies be represented thus:

Genotype	Frequency	Average Phenotype	Y
AA	p^2	$Z + 2x$	$2x$
Aa	$2p(1-p)$	$Z + x + hx$	$x + hx$
aa	$(1-p)^2$	Z	0

where x is half the difference in average phonotypic value between AA and aa, h is equal to the level of dominance and p is the population frequency of the gene A. The use of h makes this general for all levels of dominance. Computations can be simplified by subtracting Z from each of the phenotypic values. The coded phenotypic values are listed under Y.

The expected mean phenotypic value for a single locus in a line or breed in which genotypic values are in Hardy-Weinberg equilibrium is

$$\bar{Y} = 2p^2x + 2p(1-p)\ (x + hx)$$

which reduces to

$$\bar{Y} = 2x\left[p + hp\ (1-p)\right]$$

The average performance of n lines or breeds is

$$\bar{N}_n = 2x\left[\ \bar{p} + h\left\{\bar{p}\ (1-\bar{p}) - \sigma p^2\right\}\ \right]$$

Where $\bar{p} = \sum_{i=1}^{n} \frac{p_i}{n}$ and $\sigma_p^2 = \sum_{i=1}^{n} \frac{(p_i - \bar{p})^2}{n}$

The expected phenotypic mean for n $\left(\frac{n-1}{2}\right)$ single crosses among n lines is

$$S_n = 2x\left[\bar{p} + h\left\{\bar{p}\ (1-\bar{p}) + \frac{\sigma p^2}{n-1}\right\}\right]$$

For 2 lines this becomes

$$S_2 = 2x\left[\bar{p} + h\left\{\bar{p}\ (1-p) + \sigma p^2\right\}\right]$$

For a two line rotational breeding program the expected mean that is approached when the number of generations increase is

$$R_2 = 2x\left[\bar{p} + h\left\{\bar{p}\,(1-\bar{p}) + \frac{\sigma_p^2}{2^2 - 1}\right\}\right]$$

For a two line rotation the prediction equations may be derived from the expressions for phenotypic means as follows: substituting $\bar{N}_2$ for $\bar{N}_n$

$$S_2 - \bar{N}_2 = 4\ hx\ \sigma p^2$$

$$S_2 - R_2 = \frac{4}{3}\ hx\ \sigma p^2$$

Hence $$R_2 = S_2 - \left(\frac{S_2 - \bar{N}_2}{3}\right)$$

With no epistasis the expressions for one locus may be summed over all loci to obtain expressions reflecting the effect of the entire genotype. Thus the mean performance of a two line rotational breeding programme is predicted by the average performance of the single cross minus one third of the difference between the average of the single cross and the average of the mean performance in the two parental lines.

Carmon (1960)reports highly significant correlations between observed and predicted results in rotational breeding involving four lines in mice.

Enfield and Rempel (1962) calculated the expected improvement in crossbreds as the product of the average selection in purebreds times the ratio of four times the covariance of sire effects divided by the phenotypic variance in the purebred. Estimates of this ratio for weaning weight, average daily gain and backfat probe in swine were -.17, .42, .07 respectively.

These two methods (Carmon et al., 1956 and Enfield and Rempel, 1962) seem to offer some promise for predicting crossbred performance.

The scientific evidence reviewed tends to indicate that selection within purebred lines of swine should still be effective in improving swine productivity. Until the nature of gene action in heterosis is clarified and the predictability of crossbred performance established, any radical deviation from selection based on the assumption of additive genetic inheritance does not seem warranted.

SOURCE OF DATA

The data used in this study extend over the period 1958-62 and were obtained from the Macdonald College swine herd. Growth and carcass measurements were available for 1227 pigs in 239 litters. These litters represented purebred Yorkshire, purebred Landrace, single cross, backcross and crisscross between the two breeds.

In 1957, Macdonald College initiated a crossbreeding project involving Yorkshire and Landrace breeds with one of its aims being to determine the utility or advantage of using crossbred sows for producing market hogs. A report of the factors affecting sow productivity up to weaning was prepared by Holness (1963).

The general breeding plan was as follows: Starting in late 1957, two Yorkshire boars and two Landrace boars were mated to the original College population of Yorkshire females to produce purebred and crossbred offspring. In the period 1958-1962, 28 Landrace gilts in groups of four litter mates were purchased. Four such groups were purchased in 1958 and one group in each of the years 1959 - 1961. There were two purchases of Yorkshire gilts, one group of four in 1960, the other in 1961. All boars were purchased from private breeders' herds. Of the nine purebred Yorkshire boars used, three were from Ontario, four from Quebec and two were from Prince Edward Island. None of these boars were related. Landrace boars were from Ontario (seven), New Brunswick (one) and Quebec (five). Boars and gilts brought in, were selected where possible out of dams scoring higher than 70 on the Advanced Registry (1954) score.

For purposes of analysis the data were divided into seasons on a half yearly basis, from 1959 - 1962. Pigs born in the period March 1st to the end of August were classified as spring farrowed and those bron in the period September to February as fall farrowed. The periods of most intensive farrowing were March to May and September to November. However, due to the incidence of transmissible gastroenteritis in early 1958, there were no litters represented in this data until the middle of April, with the final litter for the year being farrowed in November. It was therefore decided to treat the data collected in this year as one season, as the distribution of farrowings was different compared with the other years. The classification by seasons was as follows:

Season	Date of Farrowing
1	1958
2	Spring 1959
3	Fall 1959
4	Spring 1960
5	Fall 1960
6	Spring 1961
7	Fall 1961
8	Spring 1962
9	Fall 1962

The distribution of litters by season and mating type is given in Table 9. It may be observed that of the four mating types in season 1, only two are represented in season 2. Whereas the other mating types once started show some continuity for subsequent seasons.

The litter distribution of sire progenies on a seasonal basis are illustrated in Table 10. If season 1 is omitted then it would appear that the general breeding practice was to have some overlap in sire progenies within breeds, with each sire having litters in at least two seasons. This is better illustrated with the Yorkshire sires than with the Landrace. Deviations from this general practice are to be expected in data where the incidence of disease, fluctuations in sire performance and in availability of sires play a part.

In each breeding season approximately half of the gilts of each breeding group were selected randomly and mated to sires of one breed whilst the other half was mated to sires of the other breed. The breed of sire was reversed for subsequent litters. Random mating was practiced within breeding groups - except in the case of full sib gilts where an attempt was made to mate them either to different sires of the same or of a different breed. Inbreeding was avoided as much as possible. Up to 1960, all litters were either first or second litters. In 1961, and 1962 some of the sows were kept for more than two litters.

General management practice was to offer piglets pre-

TABLE 9

DISTRIBUTION OF LITTERS BY SEASON AND MATING TYPE.

Mating Type	Season									Total
	1	2	3	4	5	6	7	8	9	
Purebred Landrace		7	5	4	4	3	4	2	3	32
Landrace x Yorkshire	9	3	8	4	6	5	1	2	1	39
Landrace x(Yorkshire x Landrace)				4	8	5	1	1		19
Landrace x(Landrace x Yorkshire)	10			1	5	2	2	1		21
Landrace x(Yorkshire x (Landrace x Yorkshire))						1		2	2	5
Purebred Yorkshire	8	5	2	6	3	4	7	3	4	42
Yorkshire x Landrace		7	6	5	3	2	2	4	1	30
Yorkshire (Yorkshire x Landrace				5	7	3	4	2		21
Yorkshire (Landrace x Yorkshire)	10			2	1	3	3	1	1	21
Yorkshire x (Landrace x (Yorkshire x Landrace))						2	3	4		9
Total	37	22	21	31	37	30	27	22	12	

TABLE 10

LITTER DISTRIBUTION OF SIRE PROGENIES BY SEASONS.

Sires	Seasons									
Yorkshire	1	2	3	4	5	6	7	8	9	Total
3	12									12
4	6									6
5		5	6	6						17
6		7	2	10						19
7				2	7	4	1			14
8					7	8	7			22
9						2				2
20							11	12	2	25
21								2	4	6
Landrace										
13	12									12
14	6									6
15	1									1
16		2	4	2						8
17		4	4	6						14
18		4	5	3						12
19				2	6					8
30					9	8				17
31					7					7
32					1					1
33						8	6	4		18
34							2	4	5	11
35									1	1
										239

starter rations commencing at ten days of age. Litters were weaned at 21 days of age and provided with rations prepared according to the Quebec Feed Board (1957) nutrient recommendations for bacon type pigs. At a liveweight of approximately 50 to 60 pounds, animals were fed Grower rations containing approximately 16 per cent crude protein and 75 per cent total digestible nutrients. At liveweights of from 110 to 125 pounds, Finisher rations containing approximately 14 per cent crude protein and 70 per cent total digestible nutrients were provided.

Animals were slaughtered within a week after exceeding 190 pounds liveweight. Following slaughter and cooling in the Canada Packers' plant in Montreal, the right side of each pig was cut according to the Canada Department of Agriculture Record of Performance (R.O.P.) Requirements for Swine (1954). The left side was cut into Montreal commercial trimmed wholesale cuts, as shown in Figure 3. The relative location of the different cuts are demonstrated in Figure 3. The commercial trimmed ham was cut obliquely about two and one-half inches in front of the aitch bone, and the hind leg severed at the hock joint. There was very little trimming done on this cut, the extent of the trimming was such as was necessary to present the ham in an acceptable condition for curing.

The trimmed shoulder known locally as the Montreal shoulder, extended from the atlas joint to about the third thoracic vertebra, the leg was removed at a location very

Left Side of Carcass

Trimmed Ham

Trimmed Shoulder

Trimmed Loin and Belly

Figure 3. Relative Location of Wholesale Carcass Cuts.

close to the shoulder joint. Excessive fat was removed until the colour of the lean was faintly discernible through the layer of fat.

The trimmed belly, represents the condition of the belly prior to curing for the production of belly bacon, i.e. with spare ribs removed and some excess fat trimmed. The relative position of this cut to the loin is shown in the lower section of Figure 3. Weights of these cuts were recorded to the nearest tenth of a pound.

Traits used in this study were, weight at 56 and 154 days, age at marketing, area of the _m_. _longissimus_ _dorsi_ (loin area), weight of the trimmed commercial ham, shoulder, loin and belly cuts expressed as a percentage of carcass weight; the total weight of the commercial trimmed cuts of ham, loin and shoulder expressed as a percentage of carcass weight, (hereafter called per cent three primal cuts), and carcass weight.

These percentages were calculated as twice the weight of each cut expressed as a percentage of total carcass weight. Robison _et_ _al_. (1960) working with swine carcasses cut on the basis outlined in the Fifth Reciprocal Meats Conference Proceedings (1952), found that right sides were heavier although not yielding a significantly higher percentage of lean cuts than left sides. From this they suggested that the difference in weights between the two sides was due to errors in cutting in the fatty portion of the carcass. The correlations of lean cuts from each side (expressed as a percentage of that side) with total per cent lean cuts were similar to the correlations of lean cuts from a side (expressed as a percentage of total carcass weight) with total per cent lean cuts. They concluded that twice the weight of the lean cuts from one side expressed as a per cent of total carcass weight would give the most accurate estimate of yield of lean cuts. Bowman _et al_. (1962) observed that where per cent of fat and lean are desired from half-carcass analyses, carcass weight divided by two would be a more appropriate weight than weight of the separated half. This is substantially in agreement with the findings of Robison _et al_. (1960).

The carcass yields used in this study were based on commercial cuts. Differences in yield could be brought about by changes in the amount of trimming based on market trends and on individual differences due to butchers. Since there is no way of critically assessing them, these differences have to be treated as random for this data.

METHOD OF ANALYSIS

Least squares appears to be the most appropriate method of estimating population parameters from this sample. Disproportionate subclass frequencies cause the different classes of effects to be non-orthogonal. Thus it is necessary to consider all effects simultaneously in order to avoid confounding of effects which can occur under non-orthogonal conditions.

Of the several estimation procedures available, least squares is the "best" in that the sum of squares of the differences between the observed values and the least squares estimates is a minimum, and of all unbiased estimates which are linear functions of the sample data, the least squares estimates have the smallest sampling variance.

In its simplest form the method of least squares can be considered a problem of fitting a straight line

$$y = mx + b$$

to a set of experimentally observed points (x_1, y_1), $(x_2\ y_2)$,.............., $(x_n\ y_n)$. Corresponding to each of the observed values of x we consider two values of y, namely the observed value y_o and the value y_e predicted by the straight line

$$mx_o + b.$$

The method of least squares says "take as the line $y = mx + b$, of best fit that one for which the sum of squares of the deviations $(y_o - y_e)$ is a minimum."

$$f(m, b) = d_1^2 + d_2^2 + \ldots\ldots\ldots\ldots + d_n^2$$

where $d_i = y_{io} - mx_{io} - b$.

To do this we solve the equations

$$\frac{\delta f}{\delta m} = o \quad \frac{\delta f}{\delta b} = o$$

simultaneously to provide least squares estimates of m and b.

This principle of least squares may be extended to more complex problems. A linear model is written to indicate the effects to be estimated and the least squares normal equations which are derived from partial differentiation are easy to write. One equation must be written for each constant to be estimated and each equation must include all elements associated with the particular constant in the model. Harvey (1960) has outlined the mathematical procedures for solving a number of basic models and they form the basis for the models used in this analysis.

Harvey's (1960) method may be outlined using the following model:

$$Y_{ijkl} = u + a_i + b_j + c_k + e_{ijkl}$$

where Y_{ijkl} denotes a measurement on the l^{th} litter born in the i^{th} season of the j^{th} mating type in the k^{th} litter sequence.

$i = 1, 2 \ldots\ldots\ldots p$

$j = 1, 2 \ldots\ldots\ldots q$

$k = 1, = \ldots\ldots\ldots t$

u = population mean

a_i = effect common to all litters born in the i^{th} season

b_j = effect common to all litters of the j^{th} mating type

c_k = effect common to all litters of the k^{th} litter sequence

e_{ijkl} = random error, normally independently distributed $(0, \sigma_e^2)$.

Interactions are assumed to be absent. All effects are considered fixed.

The least squares equations for this analysis are presented in tabular form. The first equation pertains to the estimation of u. The left-hand members (L.H.M.) of the equations , i.e. equations to the left of the equal sign, giving the number of observations in the various subclasses, the right hand members (R.H.M.) giving the sum of the observed values.

The second set of equations give the equations pertaining to the p seasons. The third set of equations give the equations pertaining to the q mating types. The fourth set of equations give the equations pertaining to the t litter sequences.

$$\begin{array}{llc|ccccc}
 & & \hat{u} & \hat{a}_i & \hat{b}_j & \hat{c}_k & & \\
u & : & n_{\cdot\cdot\cdot} & n_{i\cdot\cdot} & n_{\cdot j\cdot} & n_{\cdot\cdot k} & = & Y_{\cdot\cdot\cdot} \\
\cline{4-6}
a_i & : & n_{i\cdot\cdot} & n_{i\cdot\cdot} & n_{ij\cdot} & n_{i\cdot k} & = & Y_{i\cdot\cdot} \\
b_j & : & n_{\cdot j\cdot} & n_{ij\cdot} & n_{\cdot j\cdot} & n_{\cdot jk} & = & Y_{\cdot j\cdot} \\
c_k & : & n_{\cdot\cdot k} & n_{i\cdot k} & n_{\cdot jk} & n_{\cdot\cdot k} & = & Y_{\cdot\cdot k}
\end{array}$$

A dot in the subscript indicates that summation has been made over that subscript.

The restrictions to permit calculation of least squares estimates were $\sum_j \hat{b}_j = \sum_k \hat{c}_k = 0$.

It is also necessary to let $\overline{\sum_{i = 1,p} a_i} = 0$ or eliminate the equation pertaining to the mean.

If $u + a_i = a_i^1$ then the new set of equations previous to imposing the restrictions will be identical to those in the above table with the row and column, pertaining to the mean deleted (i.e., equations below and right of the broken lines).

In matrix notation this can be written as follows:

$$\begin{pmatrix} A & B & C \\ B^1 & D & E \\ C^1 & E^1 & F \end{pmatrix} \begin{pmatrix} a^1 \\ b^1 \\ c^1 \end{pmatrix} \begin{matrix} = Y_1 \\ = Y_2 \\ = Y_3 \end{matrix}$$

Where A = diagonal $n_{i..}$ matrix

B = $n_{ij.}$ matrix

C = $n_{i.k}$ matrix

D = diagonal $n_{.j.}$ matrix

E = $n_{.jk}$ matrix

F = diagonal $n_{..k}$ matrix

B^1, C^1 and E^1 are the transpose of B, C and E respectively. a^1, b^1, c^1 are vectors of effects to be estimated and Y_1, Y_2 and Y_3 are the appropriate right hand member vectors of the sums of the observations for the equations.

The first set of equations is absorbed into the second and third set as follows:

$$\begin{matrix} (D - B^1 A^{-1} B) & (E - B^1 A^{-1} C) & b^1 = Y_2 - B^1 A^{-1} Y_1 \\ (E - C^1 A^{-1} B) & (F - C^1 A^{-1} C) & c^1 = Y_3 = C^1 A^{-1} Y_1 \end{matrix}$$

The restrictions $\sum_j \hat{b}_j = \sum_k \hat{c}_k = 0$ were imposed after the absorption of the $u + a_1$ set of equations by subtracting the b_q th and the c_t th rows and columns from the 1, 2......

$q - 1$ and $1, 2 \ldots\ldots t - 1$ rows and columns respectively and deleting the bq^{th} and ct^{th} rows and columns.

If the resulting equations are represented as follows:

$$(G) \quad (b^1) = (Z)$$

where b^1 represents the vector of effects to be estimated then

$$b^1 = G^{-1} Z$$

$$bq^{th} \text{ effect} = 0 - \sum_{1, q-1} b_j$$

$$c_t^{th} \text{ effect} = 0 - \sum_{1, t-1} C_{\text{[illegible]}}$$

The error sum of squares was computed from

$$\text{Error} = \sum_i \sum_j \sum_k \sum_l Y^2_{ijkl} - \left(\sum_i \frac{Y^2_i}{ni} - \sum_m b^1_m \cdot Z_m \cdot \right)$$

where $m = q - 1 + t - 1$. The sums of squares for the fixed effects of mating type and litter sequence are obtained as:

$$\text{S. Sqs.} = V^1 W^{-1} V$$

where V^1 and V are row and column vectors of the particular least square estimates (i.e., $b_j = 1, 2 \ldots\ldots\ldots\ldots q-1$) and W^{-1} is the inverse of the matrix on the diagonal of G^{-1} pertaining to the effect concerned (i.e., for mating type the segment corresponding to the $D - B^1 B^{-1} B$ matrix with the q^{th} row and column deleted).

The sum of squares for the absorbed effects is calculated from the adjusted subclass totals.

$$\text{Sum of Squares Seasons} = \sum_i \frac{Y'^2_i}{n_i} - \frac{\sum Y'^2_{\cdot\cdot\cdot}}{n_{\cdot\cdot\cdot}}$$

In the instance where interaction was tested, the same method of analysis was used and the appropriate reduction sums of squares were calculated according to Henderson's method 3 (1953) e.g. Sire x Mating System = R(sire x mating type of dam subclasses, season, litter sequence) - R(sire, mating type of dam, season, litter sequence).

The computational work was done on a 7040 I.B.M. computer.

ANALYSIS OF DATA AND RESULTS

Treatment of the Observations

Mating Types

In order to facilitate electronic computation it was necessary to allot code numbers to the different mating types. A coding system was developed whereby the purebred of each breed was listed first with the various crosses following in order. The breed of sire was listed first in each cross. The coding system is presented below.

Code	Mating Type
1	Purebred Landrace
2	Landrace x Yorkshire
3	Landrace x (Yorkshire x Landrace)
4	Landrace x (Landrace x Yorkshire)
5	Landrace x (Yorkshire x (Landrace x Yorkshire))
6	Purebred Yorkshire
7	Yorkshire x Landrace
8	Yorkshire x (Yorkshire x Landrace)
9	Yorkshire x (Landrace x Yorkshire)
10	Yorkshire x (Landrace x (Yorkshire x Landrace))

For convenience these numbers will be used in most of the tables presented hereafter.

Sex Effects

A preliminary analysis revealed that sex had a highly significant effect on all traits except 56 day weight.

Hetzer et al (1961) reported highly significant effects of sex on yield of lean cuts, yield of trimmed belly, yield of fat cuts,and average backfat thickness. Fredeen (1953) noted sex differences in favour of females for carcass traits, however, barrows reached market weight faster than gilts. Plank and Berg (1963) point out that the differences between gilts and barrows in growth rate and carcass traits was dependent on the method of feeding involved. This differential response of the sexes to different nutritional regimes could have important effects where average correction factors for sex are used for data collected under different nutritional regimes.

Least squares estimates (Table 11) of sex on the traits were obtained on a within litter basis. Whilst sex effects were obtained for each mating type independently, it would appear from the least squares estimates that sex effects on each trait were similar for all mating groups. The data were corrected on a basis of equal sex distribution. The corrected data were then summarized and averaged by litters. The average number of pigs per litter for which growth and carcass data were available was 5.9, 5.1, 5.3, 5.4 and 3.4 for 1958, 1959, 1960, 1961 and 1962 litters respectively. The main reason for the lower number of pigs in 1962 was a shift from feeding test groups of six to four pigs.

Litter Averages

Tables 12 and 13 show the means of raw data for the

TABLE 11

LEAST SQUARES ESTIMATES OF SEX DIFFERENCES WITHIN LITTERS BY MATING TYPES. (Males +, Females -)

Mating Type	56 day Wt. (lbs.)	154 day Wt. (lbs.)	Age at Marketing (days)	Carcass Wt. (lbs.)	Loin Area (ins.)^2	Per cent Ham	Per cent Shoulder	Per cent Loin	Per cent Belly	Per cent 3 Primal Cuts
1	.4	-8.0	5.0	0.0	.20	.4	.4	.3	-.2	1.1
2	-.6	-8.0	5.0	0.0	.21	.3	.4	.3	-.2	1.0
3	-.5	-8.0	0.0	0.0	.17	.2	.1	.2	-.2	.6
4	.2	-3.0	1.0	0.0	.17	.2	-.1	.4	-.1	.5
5	-2.3	-9.0	6.0	-2.0	.00	.8	.4	.3	-.1	1.4
6	.3	-7.0	6.0	0.0	.27	.4	.2	.5	-.1	1.1
7	-.9	-9.0	3.0	-1.0	.10	.2	.3	.3	-.2	.8
8	.1	-8.0	5.0	0.0	.15	.4	.5	.3	-.2	1.2
9	-.4	-6.0	5.0	0.0	.24	.6	.5	.5	-.3	1.5
10	-.3	-8.0	5.0	-1.0	.25	.3	.4	.3	-.5	1.0

TABLE 12

SEASONAL AVERAGES FOR GROWTH TRAITS.

Season	No. of Litters	56 day Wt.(lbs.)	154 day Wt.(lbs.)	Age at Marketing (days)
1	37	31.2	161	177
2	22	29.8	154	186
3	21	29.8	162	175
4	31	32.1	168	170
5	37	30.1	156	180
6	30	34.9	150	187
7	27	27.5	157	179
8	22	28.2	163	174
9	12	34.0	168	176
Spring farrowed		31.3	159	179
Fall farrowed		30.3	161	177

TABLE 13

SEASONAL AVERAGES FOR CARCASS TRAITS

Season	No. of Litters	Carcass Wt. (lbs.)	Loin Area (ins.)^2	Per cent Ham	Per cent Shoulder	Per cent Loin	Per cent Belly	Per cent 3 Primal Cuts
1	37	148	4.01	20.9	17.0	15.7	13.4	53.7
2	22	146	4.11	21.3	17.8	16.6	12.1	55.8
3	21	149	3.91	21.1	17.0	15.5	12.4	53.7
4.	31	146	3.86	21.3	18.2	15.7	12.4	55.3
5	37	143	4.11	21.9	17.5	15.9	12.4	55.5
6	30	148	4.07	21.3	17.8	15.6	12.3	54.7
7	27	147	4.15	21.3	17.8	15.9	12.6	55.2
8	22	146	3.90	21.2	18.1	15.2	12.9	54.6
9	12	146	3.89	20.0	17.1	15.0	13.1	52.2
Spring farrowed		147	3.99	21.3	18.0	15.8	12.4	55.1
Fall farrowed		147	4.02	21.1	17.3	15.6	12.6	54.1

traits studied on a seasonal basis. In general there were small differences between the means for carcass measurements over the different seasons, the measurements for growth, expecially 154 day weight, showed some differences. Differences between spring farrowed and fall farrowed litters were also small. However, there may be some bias here as replacement gilts were most frequantly selected from spring litters. Selection was on a basis of 154 day weight. Data on these gilts were not included in this study, hence the estimates for growth rate may be biased downward for spring litters. Also these gilts would produce their first litters in the spring of the succeeding year. Hence litter sequence effects would be partially confounded with season effects.

The averages by mating types are presented in Tables 14 and 15. There was only two pounds difference in carcass weight between the heaviest and lightest mating groups. This was largely due to management procedure, i.e. slaughtering pigs within a week after they acquired a liveweight of 190 pounds. This difference would also be confounded with dressing percentage differences, but it was not feasible to correct for dressing percentage, as pigs shipped to slaughter were not always treated uniformly as regards time of slaughter after shipping. Since the regression of age at marketing on carcass weight was not significantly different from zero, it was considered unnecessary to adjust age at market weight for carcass weight.

TABLE 14

AVERAGES BY MATING TYPE FOR GROWTH TRAITS.

Mating Type	No. of Litters	56 day Wt.(lbs.)	154 day Wt.(lbs.)	Age at Marketing (days)
1	32	30.7	156	180
2	39	30.0	159	179
3	19	33.4	161	184
4	21	32.5	161	177
5	5	34.5	170	169
6	42	27.8	145	187
7	30	31.8	168	172
8	21	27.0	158	178
9	21	31.7	160	177
10	9	28.5	167	172

TABLE 15

AVERAGES BY MATING TYPE FOR CARCASS TRAITS

Mating Type	No. of litters	Carcass Wt. (lbs.)	Loin Area (ins.)^2	Per cent Ham	Per cent Shoulder	Per cent Loin	Per cent Belly	Per cent 3 Primal Cuts
1	32	147	3.98	21.5	16.7	15.5	12.7	53.8
2	39	148	4.07	20.8	17.1	15.5	12.8	53.5
3	19	148	3.94	21.5	17.4	15.4	12.8	54.4
4	21	147	4.11	21.2	17.1	15.7	13.1	54.1
5	5	146	4.14	21.5	18.6	15.4	12.8	55.5
6	42	147	3.97	20.6	17.8	15.6	12.6	54.1
7	30	147	3.82	21.0	17.4	15.6	12.8	54.1
8	21	146	3.85	21.0	17.8	15.3	12.5	54.3
9	21	148	4.10	20.5	17.4	15.7	12.8	53.7
10	9	147	3.98	21.3	18.3	15.3	12.6	55.0

Gross Analysis Involving Major Sources of Variation for Growth and Carcass Traits.

The mathematical model used was:

$$Y_{ijkl} = u + a_i + b_j + c_k + e_{ijkl}$$

where: Y_{ijkl} denotes a measurement on the l^{th} litter born in the i^{th} season of the j^{th} mating type in the k^{th} litter sequence.

u = mean

a_i = effect common to all litters born in the i^{th} season.

b_j = effect common to all litters of the j^{th} mating type.

c_k = effect common to all litters of the k^{th} litter sequence.

e_{ijkl} = random error randomly independently distributed, i.e. N.I.D $(0,\sigma_e^{\,2})$.

All effects were considered fixed.

Least squares estimates are presented in Table 16. The estimates suggest a significant effect of season and mating type on all traits. Both season 6 and mating type 6 had the largest effects on growth traits. The importance of seasonal effects on growth (Tables 16 and 17) is not surprising, the data were collected over a five year period and changes in environment (particularly climate and feed quality) undoubtedly occurred. Genetic changes may also have contributed to seasonal differences; nine of the sires produced litters in one season only and, unless they were all

TABLE 16

LEAST SQUARES ESTIMATES OF THE EFFECTS OF SEASON OF BIRTH, MATING TYPE AND LITTER SEQUENCE ON GROWTH AND CARCASS TRAITS.

Source	56 day Wt. (lbs.)	154 day Wt. (lbs.)	Age at Marketing (days)	Carcass Wt. (lbs.)	Loin Area $(ins.)^2$	Per cent Ham	Per cent Shoulder	Per cent Loin	Per cent Belly	Per cent 3 Primal cuts
Season										
1	.33	1.4	-1.2	1.2	.005	-.20	-.58	-.02	.77	-.80
2	-1.05	-5.7	7.8	-.7	.111	.18	.25	.89	-.50	1.29
3	-1.08	2.3	-3.1	2.4	-.089	-.03	-.63	-.14	-.19	-.79
4	1.32	7.7	-8.3	-.8	-.138	.15	.59	.03	-.20	.78
5	-.78	-4.0	1.8	-3.5	.108	.77	-.07	.25	-.19	.94
6	4.07	-9.9	8.9	1.3	.067	.12	.18	-.12	-.33	.18
7	-3.33	-2.4	.4	.6	.150	.12	.26	.27	-.05	.65
8	-2.65	2.9	-4.2	-.2	-.103	.06	.50	-.48	.26	.06
9	3.17	7.6	-2.1	-.3	-.111	-1.17	-.50	-.67	.44	-2.32
Mating Type										
1	.41	-4.2	1.6	.4	-.037	.38	-.89	-.14	.14	-.66
2	-1.00	-1.9	1.2	.8	.087	-.34	-.26	-.08	.07	-.67
3	1.70	2.2	5.1	1.8	-.073	.03	-.29	-.20	.31	-.45
4	1.43	.5	-.1	.2	.113	.08	-.21	.17	.12	.02
5	2.66	6.5	-6.8	-1.7	.228	.92	1.04	.40	-.14	2.37
6	-2.95	-15.2	9.0	-.1	-.041	-.46	.26	-.06	-.18	-.29
7	1.57	6.6	-4.4	-.5	-.165	-.07	-.23	-.02	.20	-.27
8	-3.48	-1.4	.5	-.3	-.179	-.32	.09	-.26	-.11	-.50
9	.39	-1.1	-.5	.5	.101	-.48	.04	.20	-.19	-.24
10	-.75	8.0	-5.5	-1.1	-.034	.25	.45	-.05	-.22	.69
Litter Sequence										
1	-.87	.6	-1.4	1.2	.031	-.19	-.17	-.32	.26	-.68
2	1.17	2.5	-.3	.0	-.089	-.14	.02	-.04	-.03	-.16
3	-.30	-3.0	1.6	-1.2	.058	.33	.15	.36	-.23	.84

TABLE 17

ANALYSIS OF VARIANCE FOR GROWTH TRAITS (GROSS ANALYSIS)

		Mean Squares		
Source	df	56 day Wt.	154 day Wt.	Age at Marketing
Season	8	150.27**	899.14**	829.85**
Mating Type	9	88.75**	1114.62**	445.34**
Litter Sequence	2	84.70	220.95	62.07
Error	219	29.80	201.06	178.68

**Highly significant at the .01 level of probability.

TABLE 18

ANALYSIS VARIANCE FOR CARCASS TRAITS (GROSS ANALYSIS).

		Mean Squares						
Source	df	Carcass Wt.	Loin Area	Per cent Ham	Per cent Shoulder	Per cent Loin	Per cent Belly	Per cent 3 Primal cuts
Season	8	88.05**	.3196**	5.001**	5.542**	4.040**	4.692**	24.523**
Mating Type	9	11.58	.2492**	2.575**	3.732**	.467	.690	5.082*
Litter Sequence	2	48.46*	.3454*	1.729*	.966	3.384**	2.329*	15.753**
Error	219	15.42	.0788	.512	.799	.453	.638	2.377

*Significant at the .05 level of probability.

**Highly significant at the .01 level of probability.

of average genetic merit, this pattern of use would contribute to seasonal differences. Season was also important as a source of variance for carcass traits (Tables 16 and 18). These may reflect genetic differences or, alternatively, may have resulted from non-random changes in the method of trimming. Litters were weaned at 21 days, thus environmental effects other than maternal effects would likely be a more important source of variation than in litters weaned at later ages. Boaz and Elsley (1962) have compared the performance of early weaned pigs (i.e. pigs weaned at ten pounds weight) with pigs weaned at 56 days and observed no differences in growth rate due to method of rearing.

Mating type had a highly significant effect on all growth traits and on loin area, per cent ham, per cent shoulder, and per cent three primal cuts. For reasons previously outlined mating type had no effect on carcass weight. Per cent belly and per cent loin were not significantly affected by the different mating types. Phenotypically the differences in Landrace and Yorkshire breeds have been attributed to the Landrace having "fuller" hams and "lighter" shoulders. As these mating types represent various combinations of these two breeds it could be the effect of mating types on these three carcass traits are primarily due to real breed differences in per cent ham and per cent shoulder. This is partially confirmed by the least squares estimates (Table 16) where mating type 1 (purebred Landrace) is higher in per cent ham and lower in per cent shoulder than mating type 6 (purebred Yorkshire).

The main feature of the analysis as disclosed by the least squares estimates (Table 16) is the inferiority of the purebred Yorkshire in this sample compared with all other breeding groups for growth rate. This may have been conditioned by a litter sequence by mating type interaction since most of the 24 litters of litter sequence three were purebred Yorkshires. To examine this possibility the analysis was repeated using the model heretofore mentioned but omitting the third litter sequence.

In the analysis restricted to first and second litters purebred Yorkshires retained their low rank for growth traits (Tables 19, 20, and 21). This could mean that selection was effective in improving litter performance as sows allowed to have a third litter would be from a selected population. Unlike the previous analysis, sequence was a significant source of variation for 56 day weight. There was also a change in the level of significance for litter sequence effects on loin area and per cent three primal cuts. This litter sequence effect for 56 day weight might have been caused by age of dam effects within litter sequence as found for growth data by Hetzer _et_ _al_. (1961). However, Holness (1963) using part of the data used in this study concluded that weight of sow was a more important factor than age of sow within litter sequence for total litter birthweight. The importance of the litter sequence effect was not reported. These results applied to all pigs alive at birth; the present

TABLE 19

LEAST SQUARES ESTIMATES OF THE EFFECTS OF SEASON OF BIRTH, MATING TYPE AND LITTER SEQUENCE ON GROWTH AND CARCASS TRAITS FOR FIRST AND SECOND LITTERS.

Source	56day Wt. (lbs.)	154day Wt. (lbs.)	Age at Marketing(days)	Carcass Wt. (lbs.)	Loin Area (ins.)^2	Per cent Ham	Per cent Shoulder	Per cent Loin	Per cent Belly	Per cent 3 Primal Cuts
Season										
1	.33	1.2	-.9	1.0	.021	-.11	-.48	.03	.74	-.56
2	-1.05	-5.7	7.9	-.9	.116	.19	.28	.90	-.51	1.35
3	-1.03	2.0	-2.7	2.3	-.083	.02	-.62	-.13	-.22	-.72
4	1.36	7.7	-8.2	-.7	-.131	.20	.63	.06	-.19	.90
5	-.73	-4.2	2.2	-3.3	.117	.85	-.05	.28	-.18	1.08
6	4.06	-10.5	9.4	1.2	.080	.30	.30	-.06	-.28	.55
7	-3.17	-1.5	.3	1.1	.182	.17	.39	.35	-.09	.90
8	-3.24	-1.6	-.7	-.9	-.102	.18	.14	-.52	-.08	-.21
9	3.47	12.5	-7.1	-.0	-.200	-1.80	-.59	-.90	.81	-3.27
Mating Type										
1	.69	-4.1	1.3	.4	-.034	.43	-.90	-.09	.09	.57
2	-1.39	-2.2	1.2	.8	.090	-.36	-.28	-.09	.10	-.72
3	1.55	1.8	5.7	1.1	-.080	-.03	-.39	-.31	.16	-.72
4	1.38	.4	-.1	.3	.106	.05	-.26	.14	.13	-.09
5	2.73	6.0	-6.0	-1.5	.266	1.14	1.20	.51	-.18	2.87
6	-3.17	-16.3	10.2	.4	-.048	-.40	.21	-.09	-.13	-.30
7	1.57	6.7	-4.6	-.4	-.163	-.05	-.20	.03	.23	-.22
8	-3.60	-1.5	.3	-.7	-.170	-.34	.21	-.21	-.11	-.35
9	.80	-.4	-1.2	.6	.076	-.62	-.15	.15	-.21	-.63
10	-.57	9.5	-6.8	-1.0	-.042	.19	.56	-.04	-.08	.73
Litter Sequence										
1	-1.04	-1.2	-.3	.6	.061	- .016	-.109	-.139	.122	-.265
2	1.04	1.2	.3	-.6	-.061	.016	.109	.139	-.122	.265

TABLE 20

ANALYSIS OF VARIANCE FOR GROWTH TRAITS (INVOLVING LITTER SEQUENCE 1 AND 2).

		Mean Squares		
Source	df	56 day Wt.	154 day Wt.	Age at Marketing
Season	8	123.14**	875.17**	793.41**
Mating Type	9	90.47**	1112.70**	497.03**
Litter Sequence	1	168.80*	213.17	13.74
Error	196	31.19	205.10	178.68

* Significant at the .05 level of probability.

**Highly significant at the .01 level of probability.

TABLE 21

ANALYSIS OF VARIANCE FOR CARCASS TRAITS

(INVOLVING LITTER SEQUENCE 1 AND 2).

		Mean Squares						
Source	df	Carcass Wt.	Loin Area	Per cent Ham	Per cent Shoulder	Per cent Loin	Per cent Belly	Per cent 3 Primal Cuts
Season	8	80.85**	.3271**	5.511**	4.821**	3.722**	4.402**	24.522**
Mating Type	9	7.54	.2329**	2.530**	3.664**	.470	.449	6.286**
Litter Sequence	1	55.85*	.5845**	.044	1.835	3.003**	2.308	10.912*
Error	196	10.81	.0752	.489	.770	.442	.612	2.260

* Significant at the .05 level of probability.
**Highly significant at the .01 level of probability.

data are restricted to all pigs sent to slaughter. Holness (1963) also indicated that litter size (numbers) was larger for sows having their second litter. The least squares estimates (Table 19) support the contention that sows having their second litters were better dams producing heavier pigs at 56 days than their first litter counterparts. Bowman et al. (1961) reported that age of sow, breeding weight and litter order were highly correlated and were mutually dependent in their effect on litter performance. The effect of litter sequence on per cent loin and per cent three primal cuts may be a reflection of the effect on carcass weight. The least square estimates (Table 19) indicate that second litter pigs were heavier at 154 days, hence the lighter carcass weight presumably points to a lower dressing percentage. The above consideration does not seem to provide an adequate answer for the highly significant effect on loin eye area.

In view of these results it was decided to do all subsequent analyses including only litter sequence one and two, as on this basis all mating groups were represented.

Comparison of Mating Systems.

Purebred with Crossbred Litters.

The mathematical model used in this analysis was as follows:

$$Y_{ijklo} = u + a_i + b_j + c_k + d_{jk} + g_l + e_{ijklo}$$

where: Y_{ijklo} designates a measurement on the 0^{th} litter of a mating between a male of the j^{th} breed and a female of the k^{th} breed of the l^{th} litter sequence born in the i^{th} season.

u = mean

a_i = effect common to all litters born in the i^{th} season

b_j = effect common to all litters out of the j^{th} breed of sire

c_k = effect common to all litters out of the k^{th} breed of dam

d_{jk} = effect common to all litters sired by the j^{th} breed of sire, out of the k^{th} breed of dam, i.e. effect of mating system

g_l = effect common to all litters of the l^{th} litter sequence

e_{ijklo} = random error N.I.D $(0\ \sigma_e^2)$

All effects were considered fixed.

From the analyses of variance (Tables 22 and 23) breed of dam had a highly significant effect on all growth traits, whereas breed of sire had no significant effect. Mating system had highly significant effects on 154 day weight and age at marketing.

The least squares estimates (Table 24) as well as the analysis of variance (Tables 22, 23) indicate a relationship whereby because of its initial major importance as a source of variation in 56 day weight, maternal effect maintains its importance as a source of variation for subsequent growth rate. Although breed of sire was not an important source of variation for growth, mating system was important at 154 days and at age at marketing. It seems

TABLE 22

ANALYSIS OF VARIANCE FOR GROWTH TRAITS (PUREBREDS VERSUS CROSSBREDS).

		Mean Squares		
Source	df	56 day Wt.	154 day Wt.	Age at Marketing
Season	8	150.86**	709.58**	235.48
Breed of Sire	1	2.22	45.84	42.10
Breed of Dam	1	404.66**	3246.73**	1993.04**
Mating System	1	55.04	4587.33**	1618.88**
Litter Sequence	1	220.20**	489.68	174.13
Error	112	31.85	214.52	164.09

**Highly significant at the .01 level of probability.

TABLE 23

ANALYSIS OF VARIANCE FOR CARCASS TRAITS

(PUREBREDS VERSUS CROSSBREDS).

		Mean Squares						
Source	df	Carcass Wt.	Loin Area	Per cent Ham	Per cent Shoulder	Per cent Loin	Per cent Belly	Per cent 3 Primal Cuts
Season	8	47.36**	.1659*	2.799**	3.847**	2.673**	3.612**	18.390**
Breed of Sire	1	7.90	.5010**	2.438*	10.495**	.172	.0834	4.18
Breed of Dam	1	6.18	.3974*	6.317**	4.821*	.005	.641	.188
Mating System	1	1.60	.0002	1.038	.535	.098	.686	.019
Litter Sequence	1	32.37	.3610*	.002	1.309	.428	.298	3.671
Error	112	10.32	.0666	.461	.834	.509	.600	2.362

* Significant at .05 level of probability.
**Highly significant at .01 level of probability.

TABLE 24

LEAST SQUARES ESTIMATES OF THE EFFECTS OF MATING SYSTEM, BREED OF SIRE, BREED OF DAM, ON GROWTH AND CARCASS TRAITS FOR PUREBRED AND CROSSBRED LITTERS.

Source	56 day Wt. (lbs.)	154 day Wt. (lbs.)	Age at Marketing (days)	Carcass Wt. (lbs.)	Loin Area (ins.)^2	Per cent Ham	Per cent Shoulder	Per cent Loin	Per cent Belly	Per cent 3 Primal Cuts
Purebreds	-.69	-6.3	3.7	.1	.002	.10	-.07	-.03	-.08	-.01
Crossbreds	.69	6.3	-3.7	-.1	-.002	-.10	.07	.03	.08	.01
Landrace Sires	.14	.6	-.6	.3	.065	.14	-.30	-.04	.03	-.19
Yorkshire Sires	-.14	-.6	.6	-.3	-.065	-.14	.30	.04	-.03	.19
Landrace Dams	2.04	5.8	-4.5	-.3	-.064	.26	-.22	.01	.08	.04
Yorkshire Dams	-2.04	-5.8	4.5	.3	.064	-.26	.22	-.01	-.08	-.04

that the early environment (i.e. before 21 days) is a potent force in determining subsequent growth rate with the individual's gentoype becoming important at some time between the ages of 56 and 154 days. In fostering experiments in swine Cox and Willham (1962) found that postnatal factors including mothering ability and pen environment were maximum at 42 days representing 26 per cent of the total variance. Pre-natal effects and individual genetic differences among litters rose from six per cent to thirteen per cent between 21 and 154 days.

Results obtained by MacDonald _et al_. (1959) suggest that relationships between weights at different ages differ according to breeding plan. Two of the mating types he studied were purebred Yorkshire and Landrace x Yorkshire crossbred from the Macdonald College swine herd. A birthweight of one pound above average resulted in a positive increase above average of 3.4 and 3.9 pounds at 21 days; 6.4 and 9.0 pounds at 56 days; 18.4 and 28.8 pounds at 154 days for purebred and crossbred pigs respectively.

The analysis involving carcass measurements (Table 23) shows that both breed of dam and breed of sire were important sources of variation for loin area, per cent ham, and per cent shoulder. The least squares estimates (Table 24) indicate real breed differences between Landrace and Yorkshire for per cent ham and per cent shoulder with the crossbreds being intermediate.

Purebred with Backcross Litters

The major purpose of this analysis was to investigate the importance of mating system as such, hence all crossbred dams were grouped together irrespective of the order of parentage, i.e. no attempt was made to investigate the importance of mating type of dam within the four crossbred group of dams.

The mathematical model used was as follows:

$$Y_{ijkl} = u + a_i + b_j + c_k + e_{ijkl}$$

Where: Y_{ijkl} denotes a measurement on the l^{th} litter of the k^{th} litter sequence born in the i^{th} season and of the j^{th} mating system.

u = mean

a_i = effect common to all litters born in the i^{th} season.

b_j = effect common to all litters of the j^{th} mating system, i.e. purebred or backcross.

c_k = effect common to all litters of the k^{th} litter sequence.

e_{ijkl} = random error N.I.D. $(0, \sigma_e)$.

All effects were considered fixed. Results obtained (Tables 25, 26) indicated that there was no difference between mating systems for carcass traits and for 56 day weight, but highly significant and significant differences for 154 day weight and age at marketing respectively. The least squares estimates of the effects of crossbred dams on litter

TABLE 25

ANALYSIS OF VARIANCE GROWTH TRAITS

(PUREBREDS VERSUS BACKCROSS)

		Mean Squares		
Source	df	56 day Wt.	154 day Wt.	Age at Marketing
Season	8	75.06*	704.25**	422.21*
Mating System	1	45.72	3415.81**	1211.52**
Litter Sequence	1	.79	165.92	455.55
Error	125	30.15	213.06	192.060

* Significant at .05 level of probability.

**Highly significant at .01 level of probability.

TABLE 26

ANALYSIS OF VARIANCE CARCASS TRAITS

(PUREBREDS VERSUS BACKCROSS)

		Mean Squares						
Source	df	Carcass Wt.	Loin Area	Per cent Ham	Per cent Shoulder	Per cent Loin	Per cent Belly	Per cent 3 Primal Cuts
Season	8	38.10**	.2228**	3.819**	5.244**	2.080**	2.897**	17.391**
Mating System	1	.77	.1016	.210	.001	.165	.111	.000
Litter Sequence	1	34.80	.2609	.083	1.795	2.405*	2.094*	9.677*
Error	125	11.02	.0791	.661	.834	.380	.516	2.166

* Significant at .05 level of probability.

**Highly significant at .01 level of probability.

weight at 56 and 154 days were .70 and 5.6 pounds respectively. These estimates are comparable to the estimates for purebreds versus crossbreds in the previous analysis (Table 24). The estimate in this analysis for 56 day weight is smaller than the estimate for Landrace dams (Table 24).

Heterosis.

The mean performance for the mating types corrected for litter sequence and seasonal differences are given in Tables 27 and 28. These means were calculated omitting season 1 as it was felt that there was not enough continuity in distribution of mating types between this and the other seasons for proper comparisons. The first point illustrated by Table 28, is that there was no heterotic response in any of the carcass traits studied. This is in keeping with the findings of the previous analyses (Tables 22, 23, 25, 26) where mating system had no effect on carcass traits. There was, however, some expression of heterosis in growth traits. These results are substantially in agreement with the findings of Fredeen (1957).

Crossbreds exceeded the average of the purebreds by four per cent for 56 day weight, six per cent for 154 day weight and reached market weight nine days earlier than purebreds. The performance of the crossbreds was inferior to the performance of the better performing purebred (Landrace) for 56 day weight and superior to the Landrace for 154 day weight and age at marketing. Weight at 56 days for

TABLE 27

MEAN PERFORMANCE FOR MATING TYPES CORRECTED FOR LITTER SEQUENCE AND SEASONAL DIFFERENCES (GROWTH TRAITS).

Mating Type	56 day Wt.(lbs.)	154 day Wt.(lbs.)	Age at Marketing (days)
Purebreds	30.0	154	183
Crossbreds	31.2	164	174
Purebred Landrace	32.8	160	178
Landrace x Yorkshire	30.1	159	178
Purebred Yorkshire	26.4	146	189
Yorkshire x Landrace	32.5	169	169
Landrace Backcross	33.1	165	177
Yorkshire Backcross	30.7	162	173

TABLE 28

MEAN PERFORMANCE FOR MATING TYPES CORRECTED FOR LITTER SEQUENCE AND SEASONAL DIFFERENCES (CARCASS TRAITS).

Mating Types	Carcass Wt. (lbs.)	Loin Area (ins.)^2	Per cent Ham	Per cent Shoulder	Per cent Loin	Per cent Belly	Per cent 3 Primal Cuts
Purebreds	148	3.97	20.9	17.4	15.5	12.6	53.9
Crossbreds	147	3.97	20.9	17.3	15.6	12.9	53.9
Purebred Landrace	147	3.98	21.2	16.8	15.5	12.7	53.5
Landrace x Yorkshire	147	4.07	20.7	17.4	15.5	12.5	53.8
Purebred Yorkshire	148	3.95	20.6	17.9	15.4	12.4	53.9
Yorkshire x Landrace	147	3.86	21.0	17.2	15.7	13.0	54.1
Landrace Backcross	150	4.10	20.7	17.2	15.5	13.0	53.5
Yorkshire Backcross	147	3.86	20.5	17.9	15.5	12.8	54.0

the crossbreds seems to be largely due to the superior mothering ability of the Landrace. The results for 154 day weight and age at marketing suggest some non additivity in the nature of the heterotic response obtained. There are distinct breed differences between the Yorkshire and Landrace for growth traits and slight differences for per cent ham and per cent shoulder.

The Yorkshire backcross groups ranked between the average of the purebreds and crossbreds for 56 day and 154 day weight, whereas the Landrace backcross was superior to the performance of the crossbreds for 56 day and 154 day weight although taking a longer time to reach market weight. The indications are that the Landrace backcrosses were heavier than crossbreds at time of slaughtering, having a heavier carcass weight, (Table 28). The measure of age at marketing is of limited utility as it is dependent on the day of the week when the pig reached 190 pounds. For example, a pig 190 pounds, two days after the regular date of shipping would be kept for five days before being sent to market, as pigs were shipped only once per week. Some of this difference between pigs within litters would be eliminated on a litter basis.

Both the Landrace and Yorkshire backcross groups excelled the performance of the corresponding purebred lines. This was partially implied in the analysis comparing purebred with backcross litters. This seems feasible for the comparison Yorkshire backcross with Yorkshire purebred due to the low level of growth performance in the purebreds. However, the situation where the Landrace backcross excel the purebred Landrace requires explanation. Whether the fact that these backcross litters were produced in fewer seasons and are a smaller total group as compared to purebreds, would affect these results is not known. On the other hand, the backcross groups may be reflecting the advantage of having crossbred dams.

These comparisons (Table 27) show a difference in the growth performance of the Landrace x Yorkshire and Yorkshire x Landrace crosses, the latter being 2.4 pounds heavier at 56 days, ten pounds heavier at 154 days and arriving at market weight nine days earlier. The Yorkshire x Landrace crosses were superior to the Landrace in weight at 154 days and marketing age, the Landrace x Yorkshire crosses were not. Gaines and Hazel (1957) reported on crosses of Landrace and Poland China pigs, the crosses were superior to the purebreds in growth rate at 56 and 154 days. However, Poland China x Landrace crosses were far superior to Landrace x Poland China crosses.

The above findings raised the question of a differential performance of these reciprocal single crosses as dams.

Comparison of the Performance of Landrace x Yorkshire and Yorkshire x Landrace females.

The mathematical model used in the analysis designed to answer this question was as follows:

$$Y_{ijklo} = u + a_i + b_j + c_k + g_l + e_{ijklo}$$

Where: Y_{ijklo} denotes a measurement on the 0^{th} litter of the l^{th} litter sequence in the i^{th} season and sired by the j^{th} breed of sire out of the k^{th} breed of dam.

u = mean

a_i = effect common to all litters born in the i^{th} season

b_j = effect common to all litters out of the j^{th} breed of sire

c_k = effect common to all litters out of the k^{th} mating type of dam i.e., Landrace x Yorkshire or Yorkshire x Landrace

g_l = effect common to all litters of the l^{th} litter sequence

e_{ijklo} = random error $(0, \sigma_e{}^2)$.

The analysis involving purebreds and crossbreds, Table 24 , showed that Landrace dams were superior to Yorkshires for producing fast growing litters. The analysis involving purebreds and backcross litters indicated advantages for crossbred sows. The present analysis indicates no significant difference in the performance of the two reciprocal crosses as dams, (Tables 29, 30, 31). Yorkshire x Landrace dams had heavier litters at 154 days but the difference between both types of dam for 56 day weight are small (Table 29). These results are in agreement with those of Gaines and Hazel (1957) in that there was no difference in the maternal effect between the reciprocal single crosses.

TABLE 29

LEAST SQUARES ESTIMATES OF THE EFFECTS OF BREED OF SIRE AND MATING TYPE OF DAM IN LANDRACE YORKSHIRE RECIPROCAL CROSSES FOR GROWTH AND CARCASS TRAITS.

	56 Day Wt. (lbs.)	154 Day Wt. (lbs.)	Age at Marketing (days)	Carcass Wt. (lbs.)	Loin Area (ins.)^2	Per Cent Ham	Per Cent Shoulder	Per Cent Loin	Per Cent Belly	Per Cent 3 Primal Cuts
Landrace Sires	2.7	2.1	0.7	0.2	0.041	0.24	-0.22	-0.04	0.15	-0.01
Yorkshire Sires	-2.7	-2.1	-0.7	-0.2	-0.041	-0.24	0.22	0.04	-0.15	0.01
Yorkshire x Landrace Dams	-0.5	1.9	1.4	-0.3	-0.082	0.04	-0.01	-0.14	.00	-0.10
Landrace x Yorkshire Dams	0.5	-1.9	-1.4	0.3	0.082	-0.04	0.01	0.14	.00	0.10

TABLE 30

ANALYSIS OF VARIANCE FOR GROWTH TRAITS (RECIPROCAL CROSS DAMS).

		Mean Squares		
Source	df	56 Day Wt.	154 Day Wt.	Age at Marketing
Season	4	20.08	340.54	587.10
Breed of Sire	1	376.28**	331.42	23.50
Mating Type of Dam	1	10.78	168.82	87.56
Litter Sequence	1	44.04	33.43	567.15
Error	48	23.99	169.29	257.34

**Highly significant at the .01 level of probability.

TABLE 31

ANALYSIS OF VARIANCE FOR CARCASS TRAITS

(RECIPROCAL CROSS DAMS)

		Mean Squares						
Source	df	Carcass Wt.	Loin Area	Per Cent Ham	Per Cent Shoulder	Per Cent Loin	Per Cent Belly	Per Cent 3 Primal Cuts
Season	4	40.24*	.1543	2.094*	1.371	.365	.447	2.017
Breed of Sire	1	2.79	.0829	2.985*	2.419	.094	1.116	.008
Mating Type of Dam	1	4.32	.3100	.081	.002	.889	.000	.489
Litter Sequence	1	2.27	.0041	.401	.246	3.171**	1.425	8.103
Error	48	13.52	.0781	.624	.638	.354	.482	2.369

*Significant at .05 level of probability.
**Highly significant at .01 level of probability.

The breed of sire had a highly significant effect on 56 day weight but not on later stages of growth. In view of previous results, this was not expected. It must be pointed out that this analysis was confined to the last five seasons as there were no Yorkshire x Landrace females in the herd before this period. For the first time in any of these analyses, season had no significant effect on any of the growth traits. It would appear that with maternal and seasonal effects being unimportant, breed of sire effects were able to express themselves. The reason why these effects were not carried through for later growth stages is obscure. Breed of sire significantly affected per cent ham, but no other carcass trait. Here, as with 56 day weight, the Landrace was the favoured breed. Seasonal differences had a significant effect on carcass weight and per cent ham. It may be that heavier (fatter?) carcasses had fatter hams. The highly significant effect of litter sequence on per cent loin is difficult to explain, in view of the fact that season had no significant effect on this trait. Yet, it must be remembered that litter sequence effect was important in the Gross Analysis (Tables 18, 20) for per cent loin. This effect was not significant in the comparisons of mating systems. Possibly, this effect is confined to the backcross groups.

The breed of sire effects on 56 day weight suggest a sire by mating system interaction, i.e. - whether the effects of a sire differed when he was used in a purebred as compared to a crossbred mating system.

This might help to explain the situation where a three-quarter (theoretically) bred Landrace has a slight advantage over a purebred Landrace for 154 day weight and age at marketing. Admittedly purebreeding does not mean homzygosity - expecially in data of this sort where the purebred populations are outbred, yet breed differences including sires within breed differences for growth rate appear to exist. It could be that purebred Landrace sires used in the later seasons were superior to their predecessors in both crossbred and purebred performance, and hence some of this enhanced performance of the backcross might be due to the fact that they were from a more highly selected population and produced during a shorter period of the experiment. An investigation of sire by mating system interaction was attempted to arrive at an answer to this problem.

Sire by Mating System Interaction

Least squares analysis was used to obtain the appropriate sums of squares according to Henderson method 3 (1953).

The models used to calculate the sums of squares were:

1. $Y_{ijklno} = u + a_i + b_{ij} + c_k + d_l + f_n + e_{ijklno}$

2. $Y_{ijklno} = u + a_i + b_{ij}\ c_k + d_l + f_n + e_{ijklno}$

Where: Y_{ijklno} denotes the O^{th} litter produced by the j^{th} sire of the i^{th} breed when mated to a dam of the k^{th} mating type in the l^{th} season and the n^{th} litter sequence.

u = mean

a_i = effect of the i^{th} breed of sire

b_{ij} = effect of the j^{th} sire of the i^{th} breed

c_k = effect of the k^{th} mating type of dam (i.e. purebred Landrace, purebred Yorkshire, crossbred)

$b_{ij}c_k$ = effect of the j^{th} sire of the i^{th} breed and the k^{th} mating type of dam subclass

d_l = effect of the l^{th} season

f_n = effect of the n^{th} litter sequence

e_{ijklno} = random error N.I.D. $(0, \sigma_e^2)$.

Sires within breeds were considered as random variables and interactions other than sire x mating system were ignored. In order to minimize the confounding of sire and season effects, the data used was confined to litters in which there was some overlap between sire progenies. A total of 164 litters out of nine Landrace and seven Yorkshire boars were used in this analysis. The sire by mating system interaction sums of squares were obtained by difference of the reduction sums of squares. The error used to test the interaction was derived from the second model.

Sire by mating system interaction was not significant for any of the traits except per cent ham (Tables 32, 33). This is surprising in view of the fact that the interaction was not significant for per cent 3 primal cuts, although the least squares estimates (Table 24) indicate breed differences for per cent ham and per cent shoulder. These percentage

TABLE 32

SIRE BY MATING SYSTEM INTERACTION. (GROWTH TRAITS)

		Mean Squares		
Source	df	56 Day Wt.	154 Day Wt.	Age at Marketing
Interaction	26	47.23	256.04	191.52
Error	112	32.03	202.87	211.07

TABLE 33

SIRE BY MATING SYSTEM INTERACTION. (CARCASS TRAITS)

		Mean Squares						
Source	df	Carcass Wt.	Loin Area	Per Cent Ham	Per Cent Shoulder	Per Cent Loin	Per Cent Belly	Per Cent 3 Primal Cuts
Interaction	26	6.36	.0710	.967**	.772	.303	.513	1.721
Error	112	12.15	.0632	.429	.706	.419	.484	2.001

**Highly significant at the .01 level of probability.

cuts are based on commercial cuts, in the case of commercial trimmed hams, the weight of the trimmed ham may not be a very accurate measure of lean content of the ham as a large portion of fat is left on this cut.

There was a highly significant difference in all carcass traits - except per cent three primal cuts in which the difference was significant, attributed to sire effects (Table 35). There was no sifnificant effect of sire on 56 day weight, 154 day weight or age at marketing (Table 34). Mating type of dam had a highly significant effect on 154 day weight and a significant effect on age at marketing, but no significant effect on carcass traits.

The rating of each sire based on the mean plus the least squares estimate of his effect on 154 day weight, per cent three primal cuts, and per cent ham are given in Tables 36, 37, and 38, respectively. The overall rating is based on estimates obtained from the first set of analyses considering only main effects. The ratings for the different mating systems were derived from the set of analyses including the sires by mating system interaction effects. It may be noted that with a few exceptions the sires tend to retain the same order of merit for three primal cuts regardless of mating system. Most of the deviations in ratings may be attributed to the limited number of observations available to rate some sires. With per cent ham the individual rankings are quite different to those of per cent three primal cuts. The rating of sires by different mating systems for

154 day weight is quite variable. However, it should be pointed out that in this particular sample, boars did not have a significant effect on 154 day weight. As might be expected mating system had a highly significant effect on 154 day weight. While not considered in this particular analysis, it is apparent from Table 36 - as previously pointed out, that the Landrace, Yorkshire reciprocal crosses differ with regard to 154 day weight.

TABLE 34

ANALYSIS OF VARIANCE FOR GROWTH TRAITS (SIRE WITHIN BREED EFFECTS).

		Mean Squares		
Source	df	56 day wt.	154 day wt.	Age at Marketing
Sire	14	29.81	180.61	318.88
Mating Type of Dam	2	25.06	1668.19**	702.32*
Season	7	98.48**	463.65*	602.80
Litter Sequence	1	339.36**	913.50*	95.49
Error	138	34.90	212.89	207.39

* Significant at .05 level of probability.
**Highly significant at .01 level of probability.

TABLE 35

ANALYSIS OF VARIANCE FOR CARCASS TRAITS

(SIRE WITHIN BREED EFFECTS).

Source	df	Carcass Wt.	Loin Area	Per Cent Ham	Per Cent Shoulder	Per Cent Loin	Per Cent Belly	Per Cent 3 Primal Cuts
Sire	14	20.30	.2008**	1.270**	2.250**	1.185**	1.766**	4.289*
Mating Type of Dam	2	1.13	.0154	.687	.214	.357	.438	.678
Season	7	66.39**	.2716**	2.020**	2.488**	2.955**	.522	10.490**
Litter Sequence	1	2.28	.0259	.003	.844	1.758*	.800	4.953
Error	138	11.06	.0647	.531	.719	.397	.490	1.952

* Significant at .05 level of probability.
**Highly significant at .01 level of probability.

TABLE 36

RATING OF SIRES ON THE BASIS OF MATING SYSTEM FOR 154 DAY WEIGHT

(MEAN + SIRE EFFECT).

Sire No.	Overall Rating No. of Litters	Overall Rating 154 Day Wt.(lbs.)	Purebred No. of Litters	Purebred 154 Day Wt.(lbs.)	Crossbred No. of Litters	Crossbred 154 Day Wt.(lbs.)	Backcross No. of Litters	Backcross 154 Day Wt.(lbs.)
Landrace								
31	7	171	2	184	1	169	4	164
18	12	166	5	169	6	166	1	165
32	1	164					1	165
17	14	163	7	160	4	164	3	163
19	8	161	1	171	3	158	4	164
33	12	159	3	159	3	150	6	165
30	14	156	2	142	4	159	8	158
16	8	156	4	152	4	160		
34	5	153	3	143	1	145	1	173
Yorkshire								
9	2	165			1	163	1	171
6	19	163	6	152	8	175	5	162
7	12	159	3	155	2	169	7	157
8	18	159	7	149	3	177	8	158
21	4	158	1	123	2	169	1	165
20	11	158	3	153	4	162	4	166
5	17	157	5	141	10	169	2	157

TABLE 37

RATING OF SIRES ON THE BASIS OF MATING SYSTEM FOR PER CENT 3 PRIMAL CUTS

(MEAN + SIRE EFFECT).

Sire No.	Overall Rating No. of Litters	Overall Rating Per Cent 3 Primal Cuts	Purebred No. of Litters	Purebred Per Cent 3 Primal Cuts	Crossbred No. of Litters	Crossbred Per Cent 3 Primal Cuts	Backcross No. of Litters	Backcross Per Cent 3 Primal Cuts
Landrace								
17	14	54.3	7	54.8	4	54.0	3	54.5
33	12	54.2	3	55.2	3	54.4	6	54.0
19	8	54.1	1	55.3	3	53.6	4	54.4
32	1	54.0					1	54.1
30	14	53.6	2	55.2	4	53.3	8	54.4
16	8	53.4	4	54.3	4	52.9		
31	7	52.9	2	53.2	1	54.4	4	52.7
18	12	52.6	5	52.8	6	53.1	1	52.4
34	5	51.6	3	50.1	1	54.3	1	51.3
Yorkshire								
21	4	54.5	1	51.7	2	54.8	1	54.3
20	11	54.4	3	54.5	4	55.3	4	54.1
7	12	54.2	3	54.9	2	53.9	7	54.2
5	17	53.9	5	54.8	10	53.8	2	54.0
9	2	53.6			1	53.1	1	54.5
6	19	53.5	6	54.0	8	53.7	5	53.6
8	18	53.2	7	53.5	3	54.0	8	53.3

TABLE 38

RATING OF SIRES ON THE BASIS OF MATING SYSTEM FOR PER CENT HAM (MEAN + SIRE EFFECT).

	Overall Rating		Purebred		Crossbred		Backcross	
Sire No.	No. of Litters	Per Cent Ham	No. of Litters	Per Cent Ham	No. of Litters	Per Cent Ham	No. of Litters	Per Cent Ham
Landrace								
16	8	21.7	4	22.2	4	20.7		
17	14	21.5	7	21.5	4	20.8	3	21.3
33	12	21.4	3	22.5	3	20.6	6	21.1
31	7	21.1	2	21.0	1	21.5	4	20.8
18	12	21.1	5	21.1	6	20.8	1	19.7
32	1	21.1					1	20.8
19	8	21.0	1	20.7	3	20.0	4	21.4
30	14	20.9	2	20.2	4	20.3	8	20.9
34	9	20.1	3	20.7	1	21.2	1	19.3
Yorkshire								
5	17	21.3	5	21.3	10	20.9	2	20.6
9	2	21.0			1	20.9	1	20.6
7	12	20.9	3	20.8	2	20.9	7	20.5
6	19	20.7	6	20.4	8	20.6	5	20.3
20	11	20.6	3	19.9	4	21.6	4	21.1
8	18	20.5	7	20.4	3	20.8	8	20.2
21	4	20.4	1	20.5	2	21.4	2	20.5

Predicting Crossbred Performance

All the analyses so far have indicated that mating system is a highly significant source of variation for 154 day weight and significant for age at marketing. Also there is a difference in growth rate among single crosses, as well as among backcrosses. This raises the question of how predictable are the results in crossbreeding data of this kind. Carmon's (1956) method essentially implies that the average performance of backcrosses in a two breed rotational system should be equal to the average performance of the single crosses minus 1/3 of the heterosis obtained in the single cross. Table 39, presents the observed and predicted results using Carmon's method for the three growth traits corrected for seasonal and litter sequence effects. Generally the accuracy of prediction is high, more so for 56 day weight. It is doubtful whether this method would have been sensitive to particular single cross differences as it is based on the average of both types of single cross. A more severe test of the accuracy of this prediction method may be attempted when more data become available for the criss-cross groups.

TABLE 39

OBSERVED AND PREDICTED VALUES FOR GROWTH TRAITS

	Observed	Predicted
56 day wt. (lbs.)	31.9	30.9
154 day wt. (lbs.)	164	161
Age at Marketing (days)	175	170

DISCUSSION

Preliminary Considerations

Population genetics as applied to large farm animals is beset with the problem of the expense and time involved in collecting large bodies of data, to ensure adequate statistical proof of genetic theories. Admittedly, the alternative is to work with small animals where maintenance costs are low and generation turnover rapid enough to ensure large numbers within a relatively short period of time. However, the question not yet fully answered is whether the assumptions made in attempting to extrapolate information obtained from experiments with laboratory animals to large farm animals are sufficiently less erroneous than attempting to use the limited data available on the latter group of animals by applying appropriate statistical procedures. Both methods are subject to error, nevertheless if results are interpreted in their true context they may be helpful in indicating trends if not answers.

The data used in this study were unique in that it allowed for comparisons between the two parental breeds and their crosses, all raised in the same herd. Also no sires were selected from within the purebreds for replacements. Hence the two purebred populations were essentially outbred. The weaning age was 21 days. This early weaning practice was developed by the Macdonald College Nutrition Department and still is quite uncommon in farm practice.

Gross Analysis Involving Major Sources of Variation for First and Second Litters.

As previously mentioned, the fact that seasonal effects played an important part in the measures used is not surprising. A priori one would expect the early weaning procedure to increase the environmental (seasonal) component by elimination of a maternal component that would have been completely confounded with dam and hence breed of dam and/or mating type. In other words, of the total variance in the population, that due to the dam (i.e. breed or mating type), should have been reduced to a smaller (but none the less more valid assessment of genetic worth) component than would have been the case with later weaning. However, the significance of litter sequence effects on 56 day weight would indicate that the early weaning procedure was not quite as efficient a method of removing maternal effects as expected.

The significant effect of litter sequence on yield of primal cuts, as well as the highly significant effects on per cent loin, implies an association between litter sequence and carcass weight. This could arise if pigs out of the second litters were heavier at marketing than first litter pigs. The least squares estimates do not indicate large differences between litter sequences for 154 day weight. Perhaps, there are also dressing percentage differences between first and second litters. McMeekan (1940) has shown that controlling the early nutrition of the pig and hence the growth rate, results in significant effects on the lean and fat yields of the carcass. In the present analyses age of dam effects are confounded with litter sequence effects. This should not invalidate comparisons between mating types as both litter sequences are represented in each mating type.

The most important finding in this analysis is the inferiority of the Yorkshire purebred litters for growth rate and a relatively unimpressive performance in carcass yields as compared with the other mating types. The purebred populations in this study are outbred populations. The ancestral history of the purebred Yorkshires in the College herd is three years longer than that of the Landrace.

The results obtained in this study are indicative of real breed differences between the samples of the two breeds for growth rate. The annual reports of the Canadian Record of Performance for swine in 1961 and 1962, have shown an advantage of four days for age at slaughtering for Landrace as compared with Yorkshires. This is about one third of the difference found in this study. This would indicate that the breed differences in this study are enlarged by some situation peculiar to Macdonald College. A perusal of the data revealed that for Yorkshire sired litters, four boars produced 66 per cent of the litters. For Landrace, the four most productive boars produced 52 per cent of the Landrace sired litters. The breed differences obtained in this study could have been exaggerated if the most productive Yorkshire boars used were genetically below breed average and the Landrace genetically above breed average. Hence as far as these results are concerned, it can only be inferred that due to chance Macdonald College obtained a superior sample of Landrace as compared with Yorkshire boars.

The crisscross groups show impressive growth performance but this is limited to the smaller numbers in those groups. For carcass traits, the pattern is obscure, although one of the crisscross groups excels all other mating types for yield of three primal cuts.

Comparison of Mating Systems

In both comparisons purebreds with crossbreds, and purebreds with backcross, mating system had a highly significant effect on 154 day weight but no effect on 56 day weight. This is in contrast to most reports on crossbreeding results where hybrid vigor usually expresses itself at an early age, Fredeen (1957) Lush _et_ _al_. 1939. The highly significant breed of dam effects on all growth traits reemphasizes the importance of maintaining control lines of parental breeds in any investigation of heterosis. As far as the single crosses are concerned, the breed of dam effects support the hypothesis of a maternal effect on 56 day weight sufficiently important to obscure mating system effect at that age and which carried over into subsequent growth rate. Mating system was not an important source of variation before 154 days for the comparison purebred with backcross litters. Mating type of dam effects would be confounded with mating system effects in the analysis but if the former were important one would have expected mating system to be important at 56 days. The similarity of the mating system effects in both comparisons of mating systems implies that the individuals genotype becomes important for growth rate at some period between 56 and 154 days, previous to which maternal and other environmental effects were of major importance. Evidence to support this type of a relationship may be found in the work of Cox and Willham (1962) where prenatal effects and individual genetic differences among litters rose from six to thirteen per cent of the total variance between 21 and 154 days. Hazel _et al_. (1943) found that the genetic variance accounted for 15, 28, and 17 per cent of the total variance for growth rate in three 56 day periods from birth to 168 days.

Mating system had no significant effects on carcass traits. However, for the comparison of purebreds and crossbreds, breed of sire had highly significant effects on loin area, and per cent shoulder and a significant effect on per cent ham. Breed of dam effects were significant for loin area and per cent shoulder and highly significant for per cent ham. These results indicate breed differences for carcass traits which tended to cancel out in the crossbreds.

Heterosis

The comparisons of the means of the different mating types have to be evaluated in terms of the analyses involving mating system comparisons. As such, the hybrid vigor obtained was significant at 154 days age and at age at marketing, although this does not imply that hybrid vigor was absent before 154 days. The important finding in this aspect of the work is that the crossbreds exceeded the average of the better performing purebred for these growth traits. This suggests some non-additivity in the heterotic response obtained. This is reflected in the single cross differences. These differences seem to be largely due to the superior maternal ability of the Landrace sows.

Differences in favour of the Landrace breed as dams have been previously noted by Gaines and Hazel (1957).

The question now arises as to the cause of this superior maternal ability. It could be that the Landrace females provided a more favourable in utero environment for the production of heavier and larger litters at birth, or that Landrace dams were superior milkers to Yorkshire. Holness (1963) found that the average birthweight of the purebred Yorkshire and Landrace x Yorkshire crossbred was lower than the Landrace purebred and Yorkshire x Landrace crossbred. Pigs out of Landrace dams had a mean birthweight of 3.1 pounds, pigs out of Yorkshire dams 2.4. This was irrespective of the breed of sire. Hence for this data breed of sire effect and genotype of the pig were unimportant for birthweight. It appears that the initial advantage in weight at birth provides these litters with an increasing advantage with age. Blunn et al. (1954) report average within litter correlations of .53 between birth and weaning weight, .40 between birth and 154 day weight, and .63 between 56 day and 154 day weight. Results reported by MacDonald et al. (1959) using a part of the data used in this study, suggest that these correlations vary with type of mating. These workers observed that for purebred Yorkshire pigs a birthweight of one pound above average resulted in a positive increase of 6.4 pounds at 56 days. If it is assumed that these results would apply equally well to purebred Landrace then 70 per cent of the difference in 56 day weight found in this study between Landrace and Yorkshires, could be explained on the basis of the birthweight advantage for Landrace reported by Holness (1963). It is therefore tempting to hypothesise that the single cross difference can be largely attributed to birthweight advantage of the litters out of Landrace females.

Maternal effects other than birthweight effects would be less prevalent in data on early weaned litters as compared to litters weaned at 42 days. These findings do not invalidate comparisons between the averages of the purebreds and crossbreds, but they caution against making any generalization in the nature of the gene action involved in the heterosis obtained. A precise assessment of heterosis in data of this sort can only be established by utilizing the double mating technique used by Lush _et al_. (1939).

The analysis involving the two single crosses as dams showed no significant differences in maternal ability of these two groups. This tends to support the hypothesis that maternal effects other than birthweight effects were not important for these data. A clearer indication of the cross differences might be had by computing on a within litter basis the genetic and phenotypic correlations between weights at different ages. The present data is much too restricted in number of sires used to attach any meaning to genetic correlations. Without them, the phenotypic correlations are of limited utility in interpreting the single cross differences.

Generally, there was some expression of heterosis in crosses of the two outbred populations. Results obtained substantiate earlier observations of Robison (1948) that cross-breeding response is dependent on the purebreeding that has preceeded it. There seems to be breed differences between the two breeds for growth and some carcass traits. There is also some advantage to be had by using crossbred sows. This advantage is less than that obtained in Yorkshire x Landrace crosses as compared with purebred Yorkshire. The single cross differences noted are useful in drawing attention to the fact that these observations apply to this data and should not be depended upon as final evidence of the relative values of these two breeds. To all appearances sires used were representative of the two breeds, however, it may be that in other herds the Yorkshire would outperform the Landrace.

Blatant statements as regards recommendations for the maximum utilization of heterosis based on these results are unwarranted. There are several other factors in efficient swine production than weight at 154 days.

Sire by Mating System Interaction

The results of this analysis showed that sire by mating system interaction was not important for growth traits and for most carcass traits. Based on the sire ratings it seems that the simplest approach to further improvement in growth and carcass lean meat yield is to establish what particular lines or breeds provide the best performance when crossed and carry on selection within the lines.

Predicting Crossbred Performance

The method of Carmon *et al.* (1956) may be used to evaluate the relative values of breeds or lines in crossbred performance. The accuracy and utility of the prediction seems to be related to the type of gene action involved in heterosis and also to the number of lines being evaluated. If additive effects are of major importance, then one might question the utility of this method for a two breed rotational system. Since one of the assumptions made in the development of these prediction equations was that there was no epistasis, it appears that this method would be particularly useful in instances where dominance was important in heterosis.

SUMMARY AND CONCLUSIONS

The objects of this study were (1) to obtain information regarding the importance of heterosis in crosses of Landrace and Yorkshire breeds of swine, (2) to investigate the importance of sire by mating system interaction, and (3) to apply the method of **Carmen** et al. (1956) to crossbred swine data.

The measurements used were average litter growth rate - as expressed by weight at 56 and 154 days and age at marketing, and average carcass lean cut yields. The major part of the analyses was carried out on data restricted to first and second litters of the various crosses.

Breed effects were considered separately to mating system effects. There was no heterosis for any of the carcass traits studied. Breed differences existed for some of the carcass traits studied. Statistical significance of heterotic effects were obtained for average litter weight at **154 days and age** at marketing. Breed of dam effects were important for all growth traits. These effects seem to be largely as a result of average birthweight differences between the two breeds. These results point out the bias that may be introduced in comparing the performance of crossbreds with only one of the parental lines. Litters out of crossbred sows were significantly heavier at 154 days than litters out of purebred sows. This advantage for backcross litters was less than that of the Yorkshire x Landrace single cross.

Sire by mating system interaction was unimportant for growth traits and all carcass traits, except per cent ham. This indicates that selection based on purebred selection methods should be effective in enhancing crossbred performance.

The theoretical testing procedure developed by Carmon et al. (1956) and later tested by Carmon (1960) in mice, shows some promise for predicting crossbred performance in farm animals. This method may be particularly useful in data involving more lines than in a two breed rotational system. The accuracy of this method as the number of lines and possible crosses increase must await further research.

When more data become available, further research is needed to determine the phenotypic and genetic correlations between various periods of growth on a within litter by mating type basis. There are some indications in this data that these correlations may vary according to mating type. A study based on the heritabilities within breeds of growth and carcass traits would throw some light on the breed differences obtained in this study. A critical evaluation of heterosis should be attempted by using the double mating technique and maintaining concurrently, control lines of both parental breeds.

CLAIMS TO ORIGINAL RESEARCH

1. This study represents the first as far as the author is aware, in which an attempt was made to separate breed effects from mating system effects in crossbred swine data.

2. It is also the first for Canadian swine in which the statistical significance of breed of sire, breed of dam, and mating system effects are investigated in a two breed rotational breeding system.

3. The breeding structure of the purebred populations provided a unique opportunity for an assessment of heterosis in that both purebred populations were outbred and maintained as control lines in the same herd.

4. The investigation of sire by mating system interaction represents original research and is the first instance in which an attempt has been made to rank sires on the basis of purebred and crossbred performance in data involving purebred as well as crossbred dams.

5. This work represents the first report, as far as the author is aware, in which the theoretical method of Carmon et al. (1956) for predicting crossbred performance has been applied to farm animals.

LITERATURE CITED

Anonymous, 1954. National bacon hog policy. Record of performance and advanced registry for purebred swine. Production Service, Can. Dept. of Agric., Ottawa.

Bell, A.E., Moore, C.H. and Warren, D.C. 1955. The evaluation of new methods for the improvement of quantitative characteristics. Cold Spring Harbour. Symp. Quant. Biol. 20: 197-212.

Bell, A.E. and Moore, C.H. 1958. Further comparison of reciprocal recurrent selection with conventional methods for the improvement of quantitative characters. Proc. 10th Intl. Cong. Gen. 11: 20 (Abst.).

Blunn, C.T., Warwick, E.J. and Wiley, J.R. 1954. Inter-relationships of swine weights at three ages. J. An. Sci. 13: 383-388.

Boaz, T.G., and Elsley, F.W.H. 1962. The growth and carcass quality of bacon pigs reared to different weights at 56 days old. An. Prod. 4: 13-24.

Bowman, G.H., Bowland, J.P. and Fredeen, H.T. 1961. An appraisal of certain sources of environmental variation in the productivity of Yorkshire sows. Can. J. An. Sci. 41: 220-229.

Bowman, G.H., Whatley, J.A. (Jr.) and Walters, L.E. 1962. Separation and measuring errors in swine carcasses. J. An. Sci. 21: 950-954.

Bowman, J.C. 1960. Recurrent selection. The detection of overdominance. Hered. 14: 197-205.

Bradford, G.E., Chapman, A.B., and Grummer, R.H. 1953. Performance of hogs of different breeds and from straightbred and crossbred dams on Wisconsin farms. J. An. Sci. 12: 582-590.

Bradford, G.E., Chapman, A.B., and Grummer, R.H. 1958a. Effects of inbreeding, selection, linecrossing and topcrossing in swine. I. Inbreeding and selection. J. An. Sci. 17: 426-441.

Bradford, G.E., Chapman, A.B. and Grummer, R.N. 1958b. Effects of inbreeding, selection, linecrossing and topcrossing in swine. II. Linecrossing and topcrossing. J. An. Sci. 17: 441-455.

Bradford, G.E., Chapman, A.B. and Grummer, R.H. 1958c. Effects of inbreeding, selection, linecrossing and topcrossing in swine. III. Predicting combining ability and general conclusions. J. An. Sci. 17: 456-467.

Bruce, A.B. 1910. The Mendelian theory of heredity and the augmentation of vigor. Science 32: 627-628.

Buzzati-Traverso, A.A. 1952. Heterosis in population genetics. Heterosis. Edited by J.W. Gowen. Ames, Iowa. Iowa State College Press.

Canadian Record of Performance for Swine. 1961. Annual Report. Can. Dept. of Agr.

Canadian Record of Performance for Swine. 1962. Annual Report. Can. Dept. of Agr.

Carmon, J.L. 1960. A comparison of several crossbreeding systems and the prediction of crossbred performance. Georg. Agr. Exp. Sta. Tech. Bull. 19.

Carmon, J.L., Stewart, H.A., Cockerham, C.C. and Comstock, R.E. 1956. Prediction equations for rotational crossbreeding. J. Am. Sci. 15: 930-936.

Carroll, W.E. and Roberts, E. 1942. Crossbreeding in swine. Ill. Agr. Exp. Sta. Bull. 489.

Collins, G.N. 1921. Dominance and the vigor of first generation hybrids. Amer. Nat. 55: 133-166.

Comstock, R.E., Robinson, H.F. and Harvey, P.H. 1949. A breeding procedure designed to make use of both general and specific combining ability. Agron. Jour. 41: 360-367.

Comstock, R.E. 1960. Problems and evidence in swine breeding. J. An. Sci. 19: 75-83.

Cox, D.F. and Willham, R.L. 1962. Systematic fostering experiments in swine. J. An. Sci. 21: 366-368.

Craft, W.A. 1958. Fifty years of progress in swine breeding. J. An. Sci. 17: 960-980.

Crow, J.F. 1948. Alternative hypothesis of hybrid vigor. Gen. 33: 477-487.

Crow, J.F. 1952. Dominance and overdominance. Heterosis. Edited by J.W. Gowen. Ames, Iowa. Iowa State College Press.

Dickerson, G.E. 1947. Composition of hog carcasses as influenced by heritable differences in rate and economy of gain. Iowa. Agr. Exp. Sta. Res. Bull. 354.

Dickerson, G.E. 1949. Importance of heterosis for total performance in animals. Proc. 8th Intl. Cong. of Genetics. Suppl. Vol. Heriditas. 1949. 560.

Dickerson, G.E. 1951. Effectiveness of selection for economic characters in swine. J. An. Sci. 10: 12-17.

Dickerson, G.E. 1962. Implications of genetic-environmental interaction in animal breeding. An. Prod. 4: 47-63.

Dickerson, G.E. and Grimes, J.C. 1947. Effectiveness of selection for efficiency of gain in Duroc swine. J. An. Sci. 6: 266-287.

Dickerson, G.E., Blunn, C.T., Chapman, A.B., Kottman, R.M., Krider, J.L., Warwick, E.J. and Whatley, J.A. 1954. Evaluation of selection in developing inbred lines of swine. Mo. Agr. Exp. Sta. Res. Bull. 551.

East, E.M. 1936. Heterosis. Gen. 21: 375-397.

Enfield, F.D. and Rempel, W.E. 1962. Covariance of sire effects in purebred and crossbred populations. J. An. Sci. 21: 971. (Abst.).

Falconer, D.S. 1960. Selection of mice for growth on high and low planes of nitrition. Genet. Res. Camb. 1: 91-113.

Fifth Annual Reciprocal Meats Conference Proceedings. 1952. Chicago, Illinois.

Fredeen, H.T. 1953. Genetic aspects of Canadian bacon production. Can. Dept. of Agr. Pub. 889.

Fredeen, H.T. 1956. Inbreeding and swine improvement. An. Breed. Abst. 24: 317-326.

Fredeen, H.T. 1957. Crossbreeding and swine production. An. Breed. Abst. 25: 339-347.

Fredeen, H.T. 1958. Selection and swine improvement. An. Breed. Abst. 26: 229-241.

Gaines, J.A. and Hazel, L.N. 1957. Differences in litter size and growth rate among purebred and crossbred swine.
J. An. Sci. 16: 1066 (Abst.).

Gregory, K.E. and Dickerson, G.E. 1952. Influence of heterosis and plane of nutrition on rate and economy of gains, digestion and carcass composition of pigs. Mo. Agr. Exp. Sta. Res. Bull. 493.

Griesbach, L. 1962. A test of the reciprocal recurrent selection technique with chicken broiler. Can. J. An. Sci 42: 145-157.

Hammond, J. 1947. Animal breeding in relation to nutrition and environmental conditions. Biol. Rev. 22: 195-213

Harvey, W.R. 1960. Least-squares analysis of data with unequal subclass numbers. U.S.D.A. Pub. ARS-20-8.

Hazel, L.N., Baker, M.L. and Reinmiller, C.F. 1943. Genetic and environmental correlations between the growth rates of pigs at different ages. J. An. Sci. 2: 118-128.

Henderson, C.R. 1949. Estimation of general, specific and maternal combining abilities in crosses among inbred lines of swine. J. An. Sci. 8: 606 (Abst.).

Henderson, C.R. 1953. Estimation of variance and covariance components. Biom. 9: 226-252.

Hetzer, H.D., Harkins, O.G. and Zeller, J.H. 1951. Performance of crosses between six inbred lines of swine. J. Amer. Soc. Agron. 26: 199-204.

Hetzer, H.O., Comstock, R.E., Zeller, J.H., Hiner, R.L. and Harvey, W.R. 1961. Combining abilities in crosses among six inbred lines of swine. U.S.D.A. Tech. Bull. 1237.

Hodgson, R.E. -(Editor) 1961. Germ plasm resources. Amer. Soc. for Adv. of Sci. Washington, D.C.

Holness, D.E. 1963. Factors affecting the reproductive performance of sows. Unpublished M.Sc. Thesis, Macdonald College Library, McGill University.

Hull, F.H. 1945. Recurrent selection for specific combining ability in corn. J. Amer. Soc. Agron. 37: 134-145.

Hull, F.H. 1946. Overdominance and corn breeding where hybrid seed is not feasible. J. Amer. Soc. Agron. 38: 1100-1103.

Hutton, R.E. and Russell, E.Z. 1939. Production of hogs suitable for Wiltshire sides. Circ. U.S.D.A. No. 532.

Irwin, M.R. 1947. Immunogenetics. Advances in Genetics. 1: 133-160. Academic Press. Inc., New York.

Jenkins, M.T. 1934. Methods of estimating the performance of double crosses in corn. J. Amer. Soc. Agron. 26: 199-204.

Jinks, L. 1955. A survey of the genetic basis of heterosis in a variety of dialled crosses. Hered. 9: 223-238.

Jones, D.F. 1917. Dominance of linked factors as a means of accounting for heterosis. Gen. 2: 466-497.

Jones, D.F. 1957. Gene action in heterosis. Gen. 42: 93-103.

King, J.W.B. 1957. The heritability of carcass traits in British bacon pigs. Proc. British. Soc. An. Prod. 49-69.

King, J.W.B. 1963. A genotype-environment interaction experiment with bacon pigs. An. Prod. 5: 283-288.

Kojima, K. and Kelleher, T.M. 1963. A comparison of purebred and crossbred selection schemes with two populations of _Drosophila_ _pseudo_-_obscura_. Gen. 48: 57-72.

Kristjansson, F.K. 1957. Observations on genotype-environment interaction in swine. Can. J. An. Sci. 37: 179-184.

Legates, J.E. 1962. Heritability of fat yields in herds with different production levels. J. Dairy Sci. 45: 990-992.

Lerner, I.M. 1954. Genetic homeostasis. London, England. Oliver and Boyd.

Lush, J.L. 1948. The genetics of populations (mimeographed). Ames, Iowa. Iowa State Univ. Dept. of An. Husbandry.

Lush, J.L., Shearer, P.S. and Culbertson, C.C. 1939. Crossbreeding hogs for pork production. Iowa Agr. Exp. Sta. Bull. 380.

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

MacDonald, M.A., Moxley, J.E. and Hamilton, L.H. 1959. Interrelationships between weights at different ages of Yorkshire, Landrace and Yorkshire-Landrace crossbred pigs. J. An. Sci. 18: 1468 (Abst.).

Mather, K. 1941. Variation and selection of polygenic characters. Gen. 42: 160-193.

McMeekan, C.P. 1940. Growth and development in the pig with special reference to carcass quality characters. J. Agr. Sci. 30: 276-569.

Plank, R.N. and Berg, R.T. 1963. Inheritance and plane of nutrition in swine. 1. Effects of season, plane of nutrition, sex and sire on feed lot performance and carcass characteristics. Can. J. An. Sci. 43: 72-84.

Quebec Provincial Feed Board. 1957. Feeders' Guide and Formulae for Meal Mixtures. 29th ed. 66 pp.

Renewable Animal Resources (Germ Plasm) 1963. Proc. Can. Soc. An. Prod.

Robertson, A. 1955. Selection in animals - Synthesis. Cold Spring Harbour. Symp. Quant. Biology. 21: 225-229.

Robertson, A., Occonor, L.K. and Edwards, J. 1960. Progeny testing dairy bulls at different management levels. An. Prod. 2: 141-152.

Robinson, H.F., Comstock, R.E., Khalil, A. and Harvey, P.H. 1956. Dominance versus overdominance in heterosis: Evidence from crosses between open-pollinated varieties of maize. Amer. Nat. 90: 127-131.

Robison, W.L. 1948. Crossbreeding for the production of market hogs. Ohio Agr. Exp. Sta. Bull. 675.

Robison, O.W., Cooksey, J.H. and Chapman, A.B. 1960. Estimation of carcass merit of swine from live animal measurements. J. An. Sci. 19: 1013-1022.

Salmela, A.B., Rempel, W.E. and Comstock, R.E. 1960. Reactions of three kinds of single cross pigs to three levels of feed intake. 1. Feed lot performance. J. An. Sci. 19: 84-88.

Salmela, A.B., Rempel, W.E. and Gates, G.E. 1963. Reactions of three kinds of single cross pigs to three levels of feed intake. II. Carcass Characteristics. J. An. Sci. 22: 886-889.

Sang, J.H. 1956. Hybrid vigor and animal production. An. Breed. Abst. 24: 1-5.

Seale, M.E. 1959. What is possible through crossbreeding of swine. Proc. Can. Soc. An. Prod. 15-23.

Shaw, A.M. and MacEwan, J.W.G. 1936. A study of certain breeding practices in pig production. Sci. Agr. 16: 322-330.

Shull, G.H. 1914. Duplicate genes for capsule form in Bursa bursa-pastoris. Zeitschr. indukt. Abstamm.-u. Vererbungsl. 12: 97-149.

Shull, G.H. 1952. Beginnings of the heterosis concept. Heterosis. Edited by J.W. Gowen. Ames, Iowa. Iowa State College Press.

Sierk, C.F. 1948. A study of heterosis in swine. J. An. Sci. 7: 515 (Abst.).

Smith, C. 1963. Genetic change of backfat thickness in Danish Landrace breed of pigs from 1952 to 1960. An. Prod. 5: 259-268.

Sprague, G.F., Russell, W.A. and Penny, L.H. 1959. Further studies on convergent improvement in corn. Gen. 44: 341-346.

Van Vleck, L.D. 1963. Genotype and environment in sire evaluation. J. Dairy Sci. 46: 983-987.

Vogt, D.W., Comstock, R.E. and Rempel, W.E. 1963. Genetic correlations between some economically important traits in swine. J. An. Sci. 22: 214-217.

Whaley, W.G. 1944. Heterosis. Bot. Rev. 10: 461-498.

Winters, L.M., Kiser, O.M., Jordon, P.S. and Peters, W.H. 1935. A six year study of crossbreeding swine. Minn. Agr. Exp. Sta. Bull. 320.

Wright, S. 1932. The roles of mutation, inbreeding, crossbreeding and selection in evolution. Proc. 6th Intl. Cong. of Genetics. 356-366.

Wright, S. 1935. Evolution in populations in approximate equilibrium. Gen. 30: 257-264.