

THE GENETIC ASPECTS OF LITTER PRODUCTIVITY
IN BRITISH PIGS

by

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I. SUMMARY

The object of this study was to investigate the relative importance of various sources of variation affecting litter productivity and, in particular, to obtain estimates for some of the genetic parameters of litter productivity traits. The data were obtained from the Pig Industry Development Authority and consisted of 38,000 Large White litters farrowed in 146 herds between October 1959 and September 1965. The analysis was carried out on the nine litter performance traits listed in the table on the next page.

The effects of the season and the year of farrowing on litter performance were very small relative to the effect of the herd of farrowing, which was particularly large on the litter and average pig weights at three weeks.

There was a small increase in the size of gilt litters as the age of the gilt at first farrowing increased. Litter size was at its lowest in gilt litters. It increased progressively with parity up to around the fourth litter and then declined gradually at higher parities.

Repeatability and heritability estimates of the traits were calculated and are listed in the table on the next page. The heritabilities were calculated by the daughter-dam regression method.

The phenotypic and genetic correlations between the traits were found to have similar values. Litter size and litter weight were positively correlated as were litter size and pre-weaning mortality.

Character	Repeatability	Heritability	Standard Error of Heritability
Number of pigs born alive	0.15	0.07	0.02
Number of pigs at 3 wks.	0.14	0.07	0.02
Litter wt. at 3 wks.	0.15	0.08	0.02
Average pig wt. at 3 wks.	0.17	0.07	0.02
Mortality from birth to 3 wks.	0.10	0.03	0.02
Number of pigs at 8 wks.	0.14	0.09	0.03
Litter wt. at 8 wks.	0.04	0.03	0.02
Average pig wt. at 8 wks.	0.04	0.11	0.02
Mortality from birth to 8 wks.	0.12	0.04	0.02

A maternal effect is known to exist in mice whereby animals reared in large litters tend to have small litters and vice versa. An examination of the data suggested that a similar effect probably does not exist in pigs.

There was a suggestion that the sire of a litter may have a small effect on litter size at birth but not at three weeks or eight weeks.

Culling decisions in the herds examined were shown to be influenced by considerations of litter size but only to a limited extent. A number of model culling schemes were considered and it was found that even at relatively high culling levels the improvement in overall herd mean performance is very small.

II. INTRODUCTION

Litter productivity is an extremely important economic aspect of commercial pig production. The most common measurements of litter productivity are the size and the weight of the litter at various stages between birth and weaning. From an economic point of view, the really critical measurements are those made at weaning. Characters such as the number of pigs born alive and the piglet mortality between birth and weaning are important because they have a large effect on measurements of litter productivity made at weaning.

It is convenient to regard all litter productivity traits as sow traits. Thus litter size, for example, becomes a measurement of the phenotype of the sow rather than of the piglets themselves. Such an approach is biologically justified if the variation in the trait is caused by either the genotype of the sow or the effect of the environment on her. With some traits such as litter size at birth this is almost certainly true. With others, such as litter weight at weaning, it is considerably less true.

A comprehensive plan to improve litter productivity will have two stages: firstly, to account for as much as possible of the variation in the traits in terms of measurable factors and secondly, to manipulate these factors, as far as possible, in such a way as to achieve maximum productivity. In accounting for the variation in the traits it is important to establish the relative importance of the sow's genotype and the environment, that is,

to find out to what extent the characters are inherited. If they are inherited to quite a considerable extent then it will be worthwhile pursuing a breeding policy designed to improve litter productivity. If not, the improvement will only be obtained by altering the environment.

In 1959 the British government set up the Pig Industry Development Authority (PIDA) and charged it with the responsibility of improving the efficiency of the British pig industry. From its inception PIDA has been operating a litter recording scheme for pig producers. As a result of this scheme it has accumulated a large amount of data on litter performance. The object of this study was to use this data to investigate the relative importance of various sources of variation affecting litter productivity, and in particular, to obtain estimates for some of the genetic parameters of litter productivity traits for use in recommending culling procedures and breeding plans.

III. REVIEW OF THE LITERATURE

In view of the economic importance of litter performance traits it is not surprising that a large number of studies on this subject can be found in the literature. A comprehensive review of the earlier work has been made by Smith et al (1936). In the present study, reference will only be made to more recent work.

In most herds sows farrow all the year round. The effect of the season of farrowing on litter performance has been looked at by a number of workers. There is general agreement that it has little or no effect on the number of pigs farrowed but does have an effect on the number of pigs weaned (Lush and Molln 1942, Korkman 1947, Bowman et al 1961 and Urban et al 1966). This implied effect on piglet mortality is confirmed by Braude et al (1954), Pomeroy (1960) and Shelby (1967) who found that piglet mortality was higher during the winter months. The analyses of Korkman (1947) and Urban et al (1966) show that the season of farrowing has a highly significant effect on litter weight at weaning. According to Korkman litter weights are high in the spring and low in the winter months.

The age of the dam at farrowing has been shown to have an important effect on litter performance. Usually gilts farrow at around twelve months of age. An increase in the age of the gilt at farrowing has been shown to result in an increase in the number of pigs farrowed (Olbrycht 1943, Korkman 1947, Brink 1960, and Sherrit 1962). According to Stewart (1945a) and

Pomeroy (1960) the increase is greatest in the period prior to twelve months and ceases completely after fifteen months. Pomeroy (1960) found a slight decline after fifteen months.

Bowman et al (1961) were unable to find any consistent pattern between litter size and age at first farrowing but found that it increased markedly with the weight of the gilt at mating. The effect of age at first farrowing on litter size may be partly a reflection of differences in the weights of gilts at mating. Stewart (1945a) found a correlation of 0.6 between age at first farrowing and weight at mating. In practice, some breeders mate their gilts at a particular weight rather than age. Differences found in the literature between the effects of age at first farrowing on litter performance may be partly a reflection of whether or not the weight of the gilt at mating has been kept constant.

The effect of parity on sow performance has been studied extensively. In most data on litter performance sows survive to have different numbers of litters. Some might be culled after their first or second litters while others may survive to have many more litters. If sows are culled on the basis of their litter performance then it is obvious that those surviving to have later litters will be a highly selected group. If in such selected data the overall mean performance of the animals tends to increase with parity then this may be the result of culling rather than a genuine age effect. Some workers do not seem to have paid adequate attention to this point (Lush and Molln 1942 and Blunn and Baker 1949). Others have attempted to get round it

by working within groups of animals that have survived to have equal numbers of litters (Olbrycht 1943 and Korkman 1947).

There is general agreement on the broad relationship between the age of the sow and litter size. Gilts tend to have the smallest litters. This is followed by a progressive increase in litter size in the next few litters and finally in later litters there is a gradual decline (Lush and Molln 1942, Olbrycht 1943, Korkman 1947, Blunn and Baker 1949, and Braude et al 1954). Olbrycht and Korkman found that the number of pigs alive at birth reached a maximum at around the fourth or fifth litter. Olbrycht was able to show that a sow reached her peak performance at a certain age rather than at a certain parity. In other words sows having their first litter early in life reached their maximum performance at later litter orders than those having their first litter later in life. Litter size and weight at weaning were found to increase up to around the third litter and then to decline (Lush and Molln 1942, Olbrycht 1943 and Korkman 1947). Olbrycht found that the percentage mortality from birth to weaning increased consistently from the first to the tenth litter while Korkman (1947) and Pomeroy (1960) found that the increase was erratic after the fourth litter. The age of the sow was generally found to have a much smaller effect on the size of the litter at weaning than at birth (Lush and Molln 1942, Korkman 1947, Blunn and Baker 1949 and Braude 1954).

The number of pigs weaned is of course very dependent on the number born alive and Bereskin et al (1966) and Shelby (1967), not surprisingly,

found a high positive correlation between those two traits. The percentage mortality of the pigs from birth to weaning also increases with the number of pigs born alive (Olbrycht 1943, Korkman 1947 and Pomeroy 1960). The increase in mortality in larger litters is such that the relationship between the number of pigs at weaning and at birth is quadratic rather than linear. Piglet mortality increases with litter size to such an extent that litters with the largest number of pigs at birth do not produce the largest number of pigs at weaning; there is an optimum size of litter at birth which, on average, gives rise to the maximum number of pigs weaned.

Olbrycht (1943) and Pomeroy (1960) have concluded that the optimum number of pigs farrowed alive is twelve or thirteen. In Pomeroy's data the percentage mortality increases extremely sharply in litters with more than thirteen pigs born alive. Olbrycht on the other hand, found that the increase in mortality with litter size was more gradual and an examination of his results indicates that the optimum number of pigs born alive is between fifteen and seventeen. The results of Korkman (1947) point to a figure of sixteen as the optimum number of pigs born alive. Pre-weaning mortality can be expected to vary from herd to herd depending, among other things, on the level of management. Since the optimum number of pigs born alive depends on the pre-weaning mortality it is not surprising that there is no general agreement among authors on a single figure. It would appear, however, that an optimum greater than thirteen is to be expected.

The total weight of the litter has been shown to be determined largely by the number of pigs in the litter. A high positive correlation

between litter size and weight has been found at all stages from birth to weaning (Korkman 1947, Bereskin et al 1966 and Shelby 1967). The relationship between the number of pigs in the litter and the average individual piglet weight is not so clear cut. Coey (1955) found a highly significant decrease in average piglet weight at weaning as the size of the litter increased while Bereskin et al (1966) obtained a small positive correlation between the two characters.

Since sows usually have several litters, a litter performance trait can be measured a number of times on the same animal and the correlation between the different measurements calculated. Such an intra-sow correlation is called the repeatability. If a trait such as litter size has a high repeatability then it follows that sows which have large first litters will tend to have large later litters. The parameter is of considerable economic importance for culling decisions. If a trait has a high repeatability then one would profitably cull an animal which performs badly in its first litter as it is not likely to do much better in later litters. On the other hand, if the trait has a very low repeatability nothing is to be gained by culling such an animal as its first litter is a poor guide to its performance in later litters.

The repeatability of the number of pigs born alive has been calculated by a number of authors and estimates from thirteen sources have been obtained (Hallqvist 1942, Lush and Molln 1942, Stewart 1945b, Korkman 1947, Blunn and Baker 1949, McClung 1953, Taketomi 1953, Van Oers 1964,

Urban et al 1966, Legault 1967, Shelby 1967 and King and Gajic 1968). The estimates range from 0.12 (Korkman 1947) to 0.26 (Taketomi 1953) and have a mean value of 0.19. Most authors who have also calculated the repeatability of litter size at or near weaning have found that it is considerably lower than for the number of pigs alive at birth (McClung 1953, Urban et al 1966, Shelby 1967, and King and Gajic 1968). The estimates range from 0.06 (Urban et al 1966) to 0.25 (Blunn and Baker 1949) with a mean value of 0.12. The lower repeatability for litter size at weaning is in line with the results of Hallqvist (1942) who has calculated the repeatability of litter size at birth and at weekly intervals up to six weeks and has found a progressive decrease from birth to six weeks. The repeatability estimates for litter weight at weaning are rather more variable and range from 0.05 (Urban et al 1966) to 0.53 (Blunn and Baker 1949) with a mean value of 0.19. It would appear that in general litter productivity traits have very low repeatabilities.

The heritability of a character is the fraction of the observed or phenotypic variance in the character which is caused by the differences between the genotypes of the individuals. The genes may interact with each other in non-additive ways, so that in certain combinations they have effects quite different from their average effects in the population. In the present study, the heritability is taken to include only the average effects of the genes, and is thus an extremely important parameter as it indicates the improvement which can be achieved in a character by selecting superior offspring.

It is interesting to note that, from evolutionary considerations, litter size might be expected to have a low heritability. Litter size, particularly at weaning, is a trait which one would expect to be closely connected with fitness. In his fundamental theorem of natural selection, Fisher (1929) states that the rate of change of fitness of a population is proportional to the additive genetic variation remaining in it. A population which has had an opportunity to reach equilibrium with its present environment should have had all its additive genetic variation in fitness exhausted by natural selection. It might be argued that, with modern husbandry practices, a pig's present environment is radically different from what it was in the wild and consequently the genes having an effect on litter size in its present circumstances differ from those that were subjected to natural selection during the centuries it spent in the wild. At any rate it would seem prudent to approach the question of the heritability of litter size with an open mind.

One reason for low heritability estimates may be a maternal effect operating to reduce heritability estimates of litter size that have been calculated by comparing a daughter's performance with her dam's performance. Working with mice, Falconer (1960) found that animals born in very large litters tended to have very small litters and vice versa. He was able to show that this was because mice born in large litters had their growth retarded and their small body size led them to have small litters. There is no record in the literature of anyone having looked for such a maternal effect in pigs.

Two convenient methods are available for estimating the heritabilities of litter productivity traits. One consists of carrying out a variance component analysis on groups of sows with the same sire and is usually referred to as the paternal half-sib method. The other involves calculating the regression coefficient of a daughter's performance on her dam's performance and multiplying it by two to obtain an estimate of the heritability. In the case of characters, like litter productivity traits, which are not expressed by the sire, Lush and Straus (1942) have concluded that the daughter-dam regression method makes the best use of the data.

In order to obtain heritability estimates with reasonably small standard errors by the daughter-dam method a considerable number of daughter-dam pairs is required. In the case of a trait with a low heritability and where the variance of the daughters' records is approximately equal to the variance of the dams' records, the standard error of the heritability estimate is approximately equal to $2/\sqrt{n}$ where n is the number of daughter-dam pairs (Falconer 1961). This means, for example, that a heritability estimate of 0.10 will generally not be significantly different from zero (at the 95% confidence level) if it is based on less than 1,600 daughter-dam pairs.

The great majority of the heritability estimates in the literature are based on too few animals to be at all reliable taken individually. In some cases, for example, the standard errors of the estimates are more than twice the size of the estimates themselves (Boylan 1961 and Noland et al 1966).

Estimates of the heritability of litter size at birth from eighteen sources are listed below, according to whether they have been calculated by the daughter-dam regression method or the paternal half-sib method.

SOURCE	DAUGHTER-DAM		HALF-SIB	
	h^2 *	s.e.*	h^2	s.e.
Stewart (1945b)	0.15	0.22	0.18	-
Cummings et al (1947)	0.22	0.13		
Korkman (1947)	0.04	-		
Blunn et al (1949)	0.24	-		
Cockerham et al (1952)	-0.11	0.07		
Lauprecht et al (1953)			0.13	-
McClung (1953)	0.03	-		
Boylan et al (1961)	0.03	0.07		
Siler (1962)	0.11	-		
Abarca (1963)			0.11	-
Van Oers (1964)			0.12	-
Louca et al (1965)	0.05	-		
Ferencz (1965)	0.08	-	0.15	-
Noland et al (1966)			0.11	0.23
Stockhausen et al (1966)	0.20	0.15	0.59	0.29
Urban et al (1966)	0.08	0.04		
Shelby (1967)			0.31	-
Legault et al (1967)	0.10	0.03	0.07	0.02

* h^2 = heritability *s.e. = standard error

The overall mean value of the estimates is 0.14. There is a suggestion that estimates calculated by the half-sib method may be higher than estimates calculated by the daughter-dam method; the means of the estimates calculated by the two methods are 0.20 and 0.09 respectively. In view of the large standard errors of most of the estimates it would be unwise to attach too much importance to this apparent difference; after all, the estimates obtained by Legault (1967) have the lowest standard errors and his daughter-dam and half-sib estimates were 0.10 and 0.07, respectively.

Heritability estimates in the literature for the number of pigs weaned are of a similar order of magnitude to those for litter size at birth: they range from -0.09 (Cockerham et al 1952) to 0.28 (Shelby 1967) and have a mean value of 0.12. Estimates for the total litter weight at weaning range from -0.19 (Comstock 1942) to 0.62 (Noland et al 1966) and have a mean value of 0.15. There is thus general agreement in the literature that litter productivity traits tend to have very low heritabilities.

The genetic correlation coefficient between two characters is important because it indicates the effect selecting for an improvement in one of the characters will have on the other. Cockerham (1952) and Louca and Robinson (1965), both with rather limited amounts of data, obtained results which suggested a positive genetic correlation between litter size and weight. This was confirmed by Legault (1967) who calculated the genetic correlations between the number of pigs alive at birth, the number of pigs weaned and litter weight at weaning and found them all to be very high and positive.

In the past, it has been generally agreed by scientists but not breeders that the sire of the litter has no influence on the size of the litter (Musson 1940). A number of recent analyses of data on boars used by artificial insemination have revealed that the boar can have a significant effect on litter size at birth (Aamdal 1964, Ollivier and Legault 1967, and Minkema 1967). In each case the influence of the boar is small; the proportion of the total variation in litter size attributable to the boar being of the order of 3%. Skjervold (1963) seems to have been the only person in recent years to find significant differences in litter size between boars used in natural service. Recent evidence thus indicates that the boar can have a significant but small effect on litter size.

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Fifth International Congress of Reproduction,
IV, 147-177.

Ollivier, Land Legault G. 1967 L'influence directe du
verrat sur la taille et le poids des
portées obtenues par insemination artificielle.
Ann. Zootech., 16 247-254.

Minkema, D. 1967. Some factors affecting litter size
in pigs. Anim. Breed. Abstr., 35, Abstr.
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IV. MATERIALS AND METHODS

1. The Data

All the data used in the study were obtained from the Pig Industry Development Authority's litter recording scheme. The farmers taking part in the scheme filled in a form giving particulars on each litter farrowed in their herd. Information was obtained on the number of pigs farrowed and the size and weight of the litters at three and eight weeks of age. A copy of the form, which was retained at the PIDA regional office, provided the source of the information for this study.

Information was obtained on a total of 38,092 Large White litters. For some of the litters the recorded details were incomplete and the information at three and eight weeks was based on 37,469 and 30,151 litters, respectively. The litters were farrowed in 146 herds between October 1959 and September 1965. At the outset it was decided that it would be convenient to only use litters farrowed in large herds. In order to obtain sufficient data however, it was necessary to make use of many of the smaller herds as well. About a dozen herds had to be rejected either because their records were illegible or because their method of ear numbering their pigs gave rise to ambiguities.

2. The Analysis

The analysis was carried out on the following nine characters:-

- (1) Number of pigs born alive
- (2) Number of pigs alive at 3 weeks
- (3) Litter weight at 3 weeks
- (4) Average pig weight at 3 weeks
- (5) Mortality from birth to 3 weeks
- (6) Number of pigs alive at 8 weeks
- (7) Litter weight at 8 weeks
- (8) Average pig weight at 8 weeks
- (9) Mortality from birth to 8 weeks

The number of pigs born alive, rather than the total number of pigs born, both alive and dead, was selected as a character because the recording of the number of still-born pigs by the farmers was most unreliable. The litter weights were expressed in pounds and weights which were not taken on the exact day were appropriately adjusted using correction factors obtained from PIDA. Fostering was rare but when it did occur the fostered pigs were included in the number of pigs at three and eight weeks but not in the number at birth. An arcsine transformation was used for the mortality characters and is explained as follows: if b is the number of pigs alive at birth and w is the number of pigs alive at eight weeks, then the mortality from birth to eight weeks is r radians where

$$r = \sin^{-1} \sqrt{(b-w) / b}$$

A table for this transformation is given by Quenouille (1950) and the advantages of using the transformation are discussed by him and Clark and Leonard (1939).

The performance of a sow is of course influenced by the herd, the season and the year in which it farrows. For most of the analysis it was desirable to remove the effects of these three environmental factors from the data as far as possible. The data were adjusted in the following manner. The six years spanned by the data were broken down into twelve "six-month" periods by splitting the year into two seasons, one stretching from October to March and the other from April to September. For each herd the mean value for each of the nine characters was calculated for each of the twelve periods. The individual values for each litter were then adjusted by expressing them as deviations from their corresponding "herd-period" mean.

Before calculating the repeatability, the data were adjusted for the effect of parity by the following method. For each character the mean values for litters one to ten were calculated from data which had previously been adjusted for the effects of herd, season and year. The third litter was arbitrarily selected as the standard parity and correction factors were obtained for the other nine parities by subtracting their mean values from the third litter mean value. These correction factors were then used to adjust the individual values for each litter to the third litter standard and so remove the variation in the data due to parity. The repeatability was estimated by carrying out an analysis of variance on the differences between sows and calculating the intraclass correlation as described by Snedecor (1956).

The heritability and its standard error were calculated by the daughter-dam regression method. All the daughters in the daughter-dam pairs had performed in the same herds as their dams. Many of the dams, of course, had more than one daughter and the question arose as to what was the best way to make use of the information from these daughters. Two simple methods have been commonly used in the past. The first method is to repeat the dam for each daughter, and so a dam with four daughters, for example, will give rise to four daughter-dam pairs. The second method is to substitute the mean of the daughters for the daughter value, and so have one daughter-dam pair per dam, regardless of how many daughters she had. An improvement on the second method, evolved by Kempthorne and Tandon (1953) and called the weighted regression technique, assigns a weight to the daughter mean, which, among other things, is a function of the number of daughters the dam has. Bohren et al (1961) have concluded that, although the weighted regression technique is theoretically the optimal method, it has little advantage in practice over the repeated dam method. A similar conclusion has been reached by Brown and Turner (1968). It was thus decided to use the repeated dam method.

The genetic correlation coefficients between the characters were calculated by a method given by Hazel (1943). The genetic correlation (r_G) between two characters (X and Y) is given by the formula:

$$r_G = \frac{\frac{1}{2} (r_{y_2x_1} + r_{y_1x_2})}{\sqrt{r_{y_1x_1} \times r_{y_2x_2}}}$$

where $r_{y_2x_1}$ = correlation between character Y in the daughter and character X in the dam,

$r_{y_1x_2}$ = correlation between character Y in the dam and character X in the daughter

3. The Computing Facilities and Procedure

The data from the litter recording forms were punched on to paper tape by PIDA staff and a private agency. The programmes were written in ALGOL and punched on to paper tape by the Edinburgh University Regional Computing Centre. Some of the programme development was done using an NCR-Elliott 4120 computer at the Department of Machine Intelligence and Perception at Edinburgh University. Most of the programme development and the running of the programmes were carried out on PIDA's NCR-Elliott 4120 at Stotfold in Hertfordshire.

The computer read in the litter records from paper tape and transferred them on to magnetic tape. The records were filed according to herd and sow. The overall means and the effects of seasons, years and herds were calculated from this first data file.

The "herd-period" means described above were calculated from the first data file and held on an intermediate file. The litter records on the first file were adjusted by subtracting their corresponding herd-period means. The adjusted litter records were written on to another magnetic tape

to create the second data file. Apart from the estimation of the genetic parameters and the effects of seasons, years and herds, all the calculations were carried out using the second data file.

A third data file was made in order to obtain estimates of the genetic parameters. A list of those sows whose dams' records were also included in the data and a list of the dams themselves were prepared on an intermediate file. This intermediate file and the second data file were used to produce the third data file which comprised a sequence of pairs of sow records, a dam's record followed by her daughter's record. Where a dam had more than one daughter, the dam's record was repeated.

V. RESULTS

1. The Mean Values of the Characters

The mean values and the standard deviations of the nine characters are given in Table 1. For the purpose of calculating the mean values the mortalities were expressed as percentages and not transformed. All subsequent analyses were carried out on the transformed values.

Table 1. Means and standard deviations

CHARACTER	MEAN	STANDARD DEVIATION
Number of pigs born alive	10.9	2.8
Number of pigs at 3 wks.	9.0	2.3
Litter wt. at 3 wks. (lb.)	116.2	32.5
Average pig wt. at 3 wks. (lb.)	13.1	2.4
Percentage mortality from birth to 3 wks.	16.5	15.6
Number of pigs at 8 wks.	8.8	2.3
Litter wt. at 8 wks. (lb.)	317.2	109.6
Average pig wt. at 8 wks. (lb.)	37.0	10.0
Percentage mortality from birth to 8 wks.	18.4	16.2

2. The Effects of Seasons, Years and Herds

(1) The effect of season.

The effect of season was looked at by comparing the means for different months. The monthly means for each of the nine characters are given in Table 2. Fairly marked seasonal effects are discernible. The mortality is low from April to August and high during the winter months of December, January and February. This is reflected in the numbers of pigs at three and eight weeks which are high in the summer and low in the winter but average pig weights do not show any consistent seasonal trend.

An analysis of variance was carried out on the differences between months. The differences were significant at the 1% level for seven of the nine characters. The exceptional characters were the number of pigs born alive, where the differences between months were not significant, and the average pig weight at eight weeks, where the monthly differences were significant only at the 5% level.

The percentage of the total variation in each of the characters attributable to the effect of month was calculated by a method described by Snedecor (1956). This method is more appropriate to random effects rather than fixed effects such as monthly effects. It does, however, give an indication of the importance of the effect on the character relative to the total amount of variation in the character. The results are given overleaf.

CHARACTER	Percentage of variation attributable to months
Number of pigs born alive	0.0
Number of pigs at 3 wks.	0.6
Litter wt. at 3 wks.	0.6
Average pig wt. at 3 wks.	0.3
Mortality from birth to 3 wks.	0.8
Number of pigs at 8 wks.	0.7
Litter wt. at 8 wks.	0.2
Average pig wt. at 8 wks.	0.0
Mortality from birth to 8 wks.	1.0

It can be seen that the month of farrowing is a relatively unimportant source of variation.

TABLE 2

Month means of litter performance traits

CHARACTER MONTH	Number of pigs at birth	Number of pigs at 3 wks.	Litter wt. at 3 wks. (lb.)	Average pig wt. at 3 wks. (lb.)	Mortality from birth to 3 wks.	Number of pigs at 8 wks.	Litter wt. at 8 wks. (lb.)	Average pig wt. at 8 wks. (lb.)	Mortality from birth to 8 wks.
January	10.83	8.66	113.8	13.24	0.386	8.46	312.0	37.67	0.420
February	10.91	8.82	114.5	13.12	0.374	8.63	310.7	36.97	0.408
March	10.99	9.03	118.1	13.21	0.359	8.81	317.1	37.04	0.387
April	10.85	9.14	118.8	13.15	0.324	9.00	324.8	37.06	0.352
May	10.89	9.17	118.8	13.13	0.320	9.03	322.2	36.70	0.345
June	10.87	9.21	118.6	13.04	0.313	9.01	322.9	36.75	0.337
July	10.96	9.13	118.9	13.19	0.330	8.91	322.9	37.22	0.363
August	10.95	9.07	115.7	12.88	0.338	8.85	317.7	36.83	0.374
September	10.94	9.05	116.1	12.98	0.348	8.86	318.8	37.02	0.378
October	10.94	9.01	115.0	12.92	0.351	8.83	316.3	36.76	0.386
November	10.89	8.94	113.9	12.91	0.356	8.73	314.9	36.96	0.388
December	10.77	8.65	110.5	12.89	0.380	8.41	303.3	36.67	0.414

(2) The effect of year.

The means for the six years for each of the nine characters are given in Table 3. No marked trends over the years are discernible although there is a suggestion of a gradual decrease in the mortality over the six years. An analysis of variance was carried out on the differences between years. The differences were significant at the 1% level for all of the nine characters. As for the effect of month, the percentages of the total variation in each of the nine characters attributable to the effect of year were calculated and are listed below.

CHARACTER	Percentage of variation attributable to years
Number of pigs born alive	0.0
Number of pigs at 3 wks.	0.2
Litter wt. at 3 wks.	0.0
Average pig wt. at 3 wks.	0.3
Mortality from birth to 3 wks.	0.3
Number of pigs at 8 wks.	0.2
Litter wt. at 8 wks.	0.1
Average pig wt. at 8 wks.	0.0
Mortality from birth to 8 wks.	0.2

It can be seen that the year of farrowing is a relatively unimportant source of variation; if anything, even less important than the month of farrowing.

TABLE 3

Year means of litter performance traits

YEAR CHARACTER	59-60	60-61	61-62	62-63	63-64	64-65
Number of pigs born alive	10.96	10.92	10.86	10.94	10.96	10.82
Number of pigs at 3 wks.	8.93	8.88	8.88	8.97	9.12	9.11
Litter wt. at 3 wks. (lb.)	115.1	114.9	116.3	117.3	116.6	116.4
Average pig wt. at 3 wks. (lb.)	13.04	13.08	13.23	13.23	12.93	12.92
Mortality from birth to 3 wks.	0.363	0.362	0.355	0.358	0.341	0.322
Number of pigs at 8 wks.	8.74	8.68	8.68	8.82	8.94	8.91
Litter wt. at 8 wks. (lb.)	311.6	313.0	315.0	320.3	322.3	320.2
Average pig wt. at 8 wks. (lb.)	36.4	36.8	37.3	37.3	37.0	36.9
Mortality from birth to 8 wks.	0.390	0.393	0.384	0.378	0.376	0.356

(3) The effect of herd.

A separate analysis of variance was carried out on the difference between herds. Since all the herds had litters in each of the six years, the yearly differences were unlikely to give rise to apparent herd differences in the analysis. The differences between herds were significant at the 1% level for all of the nine characters. The percentages of the total variation in each of the nine characters attributable to the effect of herd were calculated and are listed below.

CHARACTER	Percentage of variation attributable to herds
Number of pigs born alive	5.6
Number of pigs at 3 wks.	5.4
Litter wt. at 3 wks.	15.7
Average pig wt. at 3 wks.	22.8
Mortality from birth to 3 wks.	7.4
Number of pigs at 8 wks.	5.7
Litter wt. at 8 wks.	5.3
Average pig wt. at 8 wks.	5.9
Mortality from birth to 8 wks.	7.0

It can be seen that the herd of farrowing is quite an important source of variation for all nine characters. The influence of the herd is particularly high for the weight of the litter and the average weight of the pigs at three weeks.

3. The Effect of Age

(1) The age of the gilt at first farrowing.

Two approaches were adopted to investigate the effect the age of a gilt at its first farrowing had on its first litter: one involved dividing the gilts into groups according to their age at first farrowing and comparing the mean performance of the different groups, the other consisted of calculating the correlation and regression coefficients for the age at first farrowing and each of the nine characters.

The mean values of each of the nine characters for the different age at first farrowing groups are given in Table 4. As stated previously the values of the characters have been expressed as deviations from their respective "herd-period" means. Two thirds of the gilts in the sample first farrowed between 330 and 420 days of age. Almost all the mean values in the table are negative indicating that gilt litters tend to be smaller, lighter, and have a lower mortality than sow litters. An analysis of variance was carried out on the variation between the age groups and the differences between the age groups were found to be significant at the 1% level for all the characters except the number of pigs at eight weeks and the mortalities from birth to three weeks and birth to eight weeks. The results for litter size at birth, three weeks and eight weeks of age are illustrated in Figure 1. It can be seen that there is a progressive increase in the number of pigs born alive as the age of the gilt increases. There are corresponding increases in the numbers of pigs at three weeks and eight weeks but in the case of the number of pigs at eight weeks the increase

is much smaller and, as stated above, is not significant. The mortality does not seem to be influenced by the age of the gilt. Both the litter weights and the average pig weights at three and eight weeks of age increase with the age of the gilt at its first farrowing.

The correlation and regression coefficients for the age at first farrowing and each of the nine characters are listed in Table 5. None of the correlation coefficients exceed 0.10. The results confirm the conclusions that were drawn from the previous table. An increase in the age of the gilt causes an increase in the number of pigs born alive but not a significant increase in the number of pigs at eight weeks. The largest effects are on the litter weight and the average pig weight at three weeks, both of which are increased by increasing the age of the gilt.

10.9

TABLE 4

Age of gilt at first farrowing and litter performance

	AGE IN DAYS					
	300-329	330-359	360-389	390-419	420-449	450-479
% IN EACH CLASS*	4	16	27	25	14	7
CHARACTER						
Number of pigs born alive	9.55 - 1.35	9.75 - 1.15	- 1.01	- 0.72	- 0.81	- 0.51
Number of pigs at 3 wks.	- 0.82	- 0.65	- 0.48	- 0.34	- 0.38	- 0.18
Litter wt. at 3 wks. (lb.)	-16.0	-12.2	- 8.5	- 5.9	- 6.0	- 2.2
Average pig wt. at 3 wks. (lb.)	- 0.71	- 0.48	- 0.26	- 0.19	- 0.07	0.07
Mortality from birth to 3 wks.	- 0.03	- 0.05	- 0.05	- 0.04	- 0.03	- 0.04
Number of pigs at 8 wks.	- 0.69	- 0.61	- 0.46	- 0.35	- 0.43	- 0.22
Litter wt. at 8 wks. (lb.)	-26.3	-31.5	-15.6	- 9.0	-11.6	- 3.2
Average pig wt. at 8 wks. (lb.)	- 0.93	- 1.31	- 0.18	0.01	0.15	0.39
Mortality from birth to 8 wks.	- 0.02	- 0.04	- 0.05	- 0.03	- 0.02	- 0.04

*Percentages do not add up to 100 as gilts which farrowed before 300 days or after 479 days were excluded.

FIGURE 1. Age at first farrowing and litter size at birth three weeks and eight weeks.

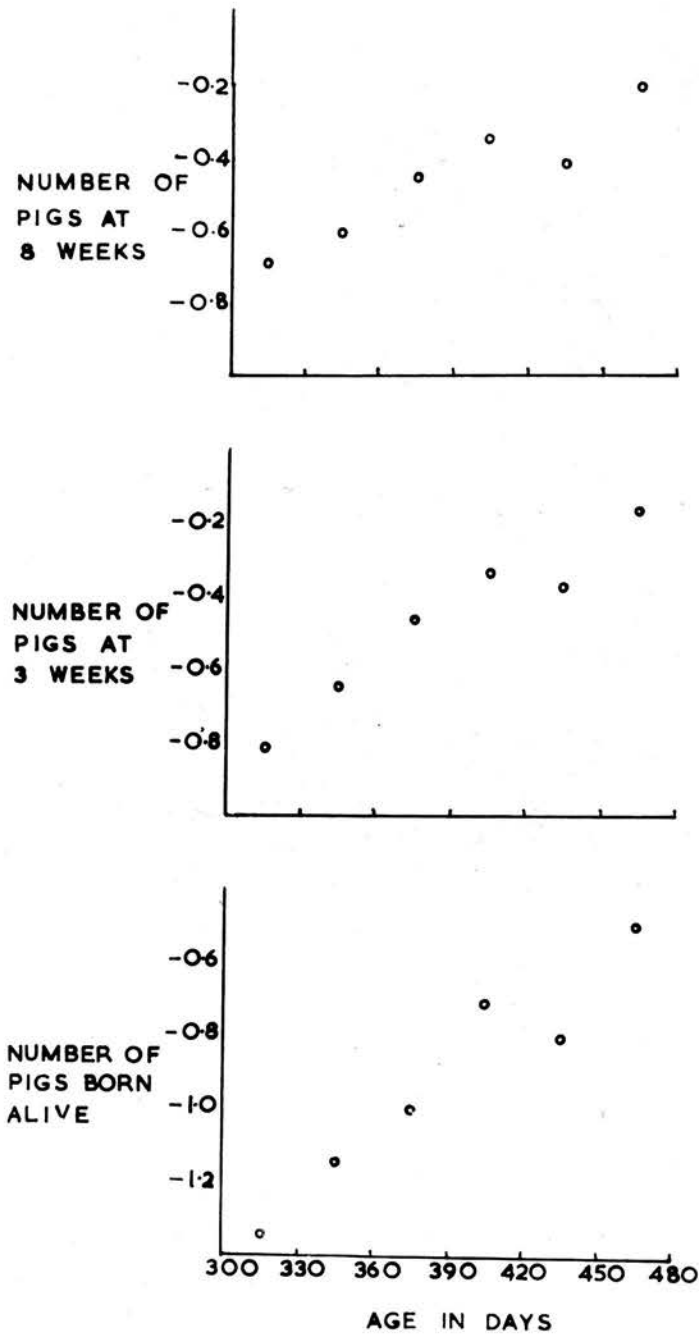


TABLE 5

Regression and correlation coefficients between age of gilt
in days at first farrowing and first litter performance

CHARACTER	NUMBER OF PAIRS	CORRELATION COEFFICIENT	REGRESSION COEFFICIENT	REGRESSION S.E.
Number of pigs born alive	6473	0.06	0.003	0.001
Number of pigs at 3 wks.	6364	0.05	0.002	0.001
Litter wt. at 3 wks. (lb.)	6364	0.10	0.062	0.008
Average pig wt. at 3 wks. (lb.)	6364	0.09	0.004	0.001
Mortality from birth to 3 wks.	6364	0.01	0.000	0.000
Number of pigs at 8 wks.	4867	0.03	0.001	0.001
Litter wt. at 8 wks. (lb.)	4867	0.06	0.123	0.031
Average pig wt. at 8 wks. (lb.)	4867	0.05	0.009	0.003
Mortality from birth to 8 wks.	4867	-0.00	-0.000	0.000

(2) The parity of the sow.

The relationship between parity and litter performance was investigated. The overall mean values of the characters for the first eight parities are given in Table 6. The differences between the mean values for the different parities may not simply reflect the effect of parity on sow performance; some of the differences, such as the increase in litter size in the early litters may be due to culling.

In order to find out whether the overall mean values for the different parities give a true picture of the relationship between parity and performance an alternative approach was adopted. The mean values of the different parities were calculated, as above, but for each parity, the only animals included were those which had survived to have one or more litters. For example the mean values obtained for the first litter were calculated from animals which had also had a second litter; animals which had only one litter were excluded. The results are given in Table 7.

A variation of the approach just described was also employed. Sows which had been culled after their seventh litter were extracted from the data and the mean values for their first six litters were calculated. The seventh litter was not included as many of the sows were probably discarded because of some ailment at that stage in their life. The results are given in Table 8. An advantage of this approach is that only records of the same sows are compared at the different parities. A disadvantage is that it only makes use of a small selected fraction of the data.

The question of how to eliminate culling bias from estimates of biological parameters is complicated and has been discussed by a number of authors including Lush and Shrode (1950), Henderson et al (1959) and Curnow (1961). It has already been stated that a straightforward comparison of the averages of all litter records at the different parities (method A) gives a biased picture of the relationship between parity and performance if culling on the basis of litter performance has been taking place. The alternative approach of only comparing records made by the same animals at two successive parities (Method B) introduces a bias in the other direction. Consider the true parity difference in performance between the first and second parities and the apparent parity differences indicated by methods A and B. The bias introduced by these methods can be defined as the true parity difference minus the apparent difference. Lush and Shrode (1950) have shown that the bias in method A is

$$t \cdot \frac{c}{N} \cdot (C-K)$$

and the bias in method B is

$$-(1-t) \cdot \frac{c}{N} \cdot (C-K)$$

where

N is the number of animals having a first litter,

c is the number of animals culled after the first litter,

C is the mean performance of the c culled animals in their first litter,

K is the mean performance of the (N-c) survivors in their first litter,

and t is the repeatability of the particular performance trait.

Estimates of the parameters required to calculate the biases have been obtained and are given in later sections of this thesis. It is also shown later that culling decisions are influenced by litter size at three weeks rather than at birth. Methods A and B will both, therefore, give biased estimates of the effect of parity on litter size at three weeks. For example, consider the apparent differences in litter size at three weeks between first and second litters indicated by methods A and B. Using the above formulae it has been calculated that the biases in the differences are -0.01 pigs and 0.09 pigs for methods A and B, respectively.

It can be concluded that the biases in the observed differences between successive parities in Tables 6, 7 and 8 are very small. It is worth noting that the biases are in opposite directions: the differences between the means in Table 6 (method A) overestimate the true parity differences while the differences in Tables 7 and 8 (method B) underestimate them. Method B as defined by Lush and Shrode (1950) refers to the situation where only the same animals are compared at successive parities and strictly speaking applies to the results in Table 8, where all the sows had seven litters but not to Table 7 where different numbers of sows contributed to the different parity means. In fact the approach employed to give the means listed in Table 7 is fundamentally the same as that in Table 8, and as already stated both tables should underestimate the effect of parity if culling on the basis of performance has been practised.

The means for the different parities listed in Tables 6, 7 and 8 have been plotted separately for the nine characters in Figures 2 to 10. For convenience the relationship defined by the means in Table 6 is referred

to as method A and those for Tables 7 and 8 as methods B1 and B2, respectively. For all of the characters it can be seen that the overall relationship between parity and performance indicated by each of the three methods is very similar. Since method A is expected to overestimate the true parity effects and methods, B1 and B2 to underestimate them, it seems likely that figures 2 to 10 give a reliable picture of the broad relationship between parity and sow performance for each of the nine characters.

It can be seen that the number of pigs born alive is low in the first litter. It increases sharply to a maximum in the fourth or fifth litters and then declines progressively in later litters. The numbers of pigs at three and eight weeks are also low in gilt litters but reach a maximum in the third litter before declining with increasing parity. The litter weights at three and eight weeks follow a similar pattern to litter number: very low in the first litter, a sharp increase up to the third litter, and a progressive decrease at later parities.

The influence of increasing parity on the average pig weight at three weeks is very different from that on the average pig weight at eight weeks. The average pig weight at three weeks is very low in the first litter, rises steeply to a maximum in the second litter and then declines steeply but erratically with increasing parity. Some of the means for the first four litters for the average pig weight at eight weeks are rather

erratic but it would appear that the average pig weight at eight weeks is fairly stable for the first four litters and then increases progressively with increasing parity. The mortality from birth to three weeks and from birth to eight weeks is at its lowest in the first litter, and then increases progressively with increasing parity.

Table 6. Mean performance for parities one to eight

LITTER CHARACTER	1	2	3	4	5	6	7	8
Number of pigs born alive	-0.88	0.03	0.47	0.56	0.54	0.40	0.24	-0.01
Number of pigs at 3 wks.	-0.44	0.26	0.36	0.27	0.16	-0.03	-0.20	-0.43
Litter wt. at 3 wks. (lb.)	-7.4	4.8	5.6	3.9	2.1	-0.1	-3.3	-6.3
Average pig wt. at 3 wks. (lb.)	-0.19	0.18	0.11	0.05	0.01	0.04	-0.10	-0.11
Mortality from birth to 3 wks.	-0.04	-0.03	0.01	0.02	0.03	0.05	0.05	0.06
Number of pigs at 8 wks.	-0.43	0.25	0.36	0.25	0.19	-0.03	-0.18	-0.41
Litter wt. at 8 wks. (lb.)	-15.5	7.2	8.7	6.4	6.7	1.2	0.1	-2.5
Average pig wt. at 8 wks. (lb.)	-0.25	-0.09	-0.31	-0.12	0.10	0.30	0.69	1.33
Mortality from birth to 8 wks.	-0.03	-0.03	0.00	0.02	0.03	0.04	0.04	0.05

Table 7. Mean performance of animals surviving to have a later litter for parities one to eight

LITTER CHARACTER	1	2	3	4	5	6	7	8
Number of pigs born alive	- 0.82	0.16	0.56	0.73	0.73	0.67	0.50	0.21
Number of pigs at 3 wks.	- 0.34	0.43	0.54	0.49	0.43	0.32	0.12	- 0.06
Litter wt. at 3 wks. (lb.)	- 6.0	7.7	8.2	7.2	5.9	4.9	1.4	- 0.4
Average pig wt. at 3 wks. (lb.)	- 0.17	0.24	0.15	0.09	0.05	0.06	- 0.01	0.06
Mortality from birth to 3 wks.	- 0.05	- 0.04	- 0.01	0.01	0.02	0.03	0.03	0.04
Number of pigs at 8 wks.	- 0.33	0.43	0.54	0.51	0.42	0.33	0.17	-0.05
Litter wt. at 8 wks. (lb.)	-12.3	12.2	14.8	13.1	10.9	12.3	12.1	15.6
Average pig wt. at 8 wks. (lb.)	- 0.26	- 0.25	- 0.34	- 0.38	- 0.26	0.10	0.62	1.87
Mortality from birth to 8 wks.	- 0.04	- 0.04	- 0.01	0.01	0.02	0.02	0.02	0.03

Table 8. Mean performance of animals culled after seven litters for parities one to six

CHARACTER	LITTER					
	1	2	3	4	5	6
Number of pigs born alive	-0.59	0.23	0.65	0.89	0.78	0.50
Number of pigs at 3 wks.	0.07	0.61	0.72	0.69	0.50	0.07
Litter wt. at 3 wks. (lb.)	-1.7	9.6	10.6	8.9	6.0	1.0
Average pig wt. at 3 wks. (lb.)	-0.27	0.15	0.13	- 0.03	-0.04	0.02
Mortality from birth to 3 wks.	-0.08	-0.05	- 0.02	0.00	0.02	0.04
Number of pigs at 8 wks.	0.05	0.63	0.77	0.77	0.48	0.08
Litter wt. at 8 wks. (lb.)	-3.7	19.8	22.6	11.7	7.9	3.2
Average pig wt. at 8 wks. (lb.)	-0.67	- 0.29	- 0.31	- 1.37	-0.68	0.11
Mortality from birth to 8 wks.	-0.06	- 0.05	- 0.04	- 0.00	0.01	0.04

FIGURE 2. The relationship between parity and the number of pigs born alive.

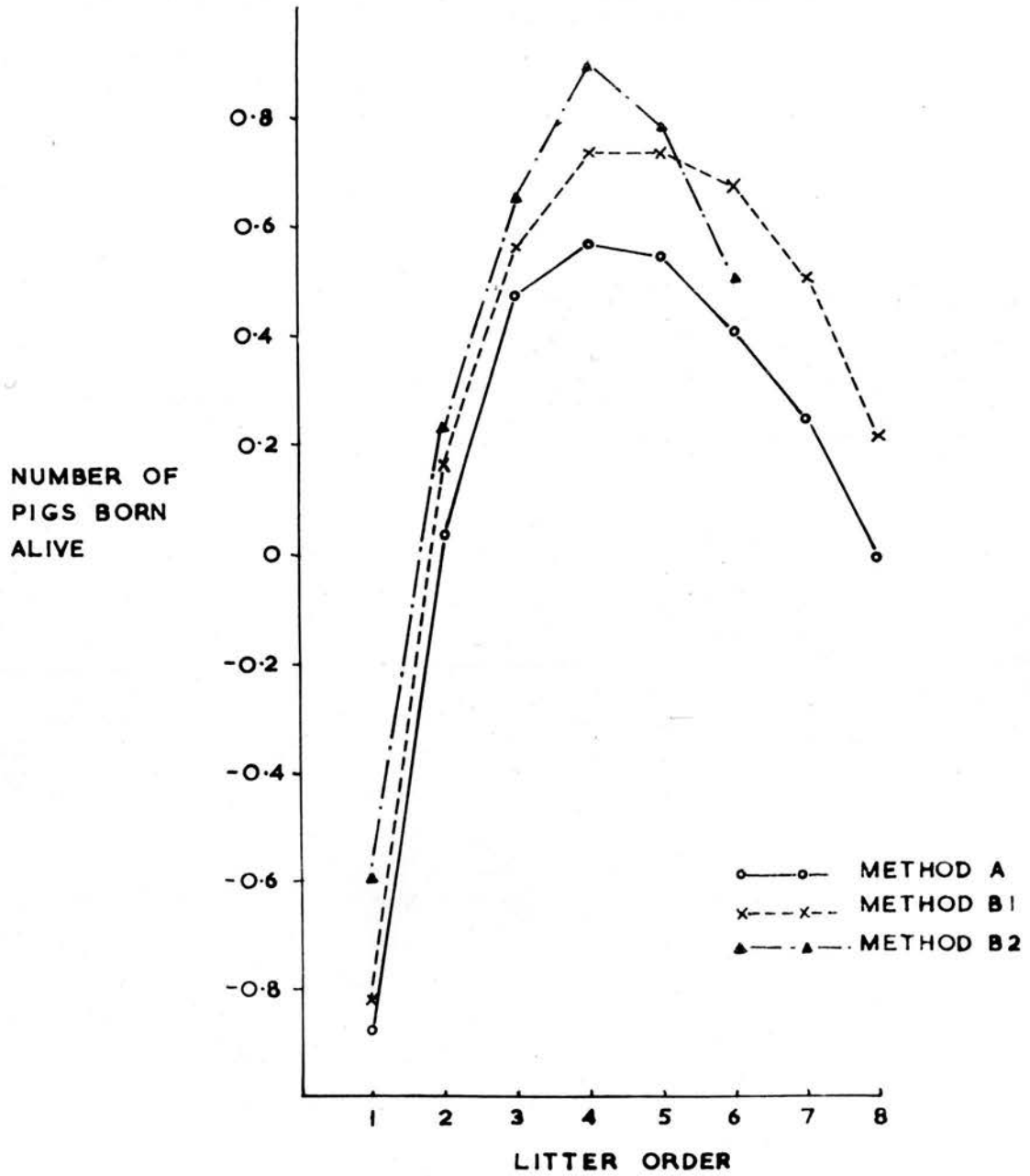


FIGURE 3. The relationship between parity and litter size at three weeks.

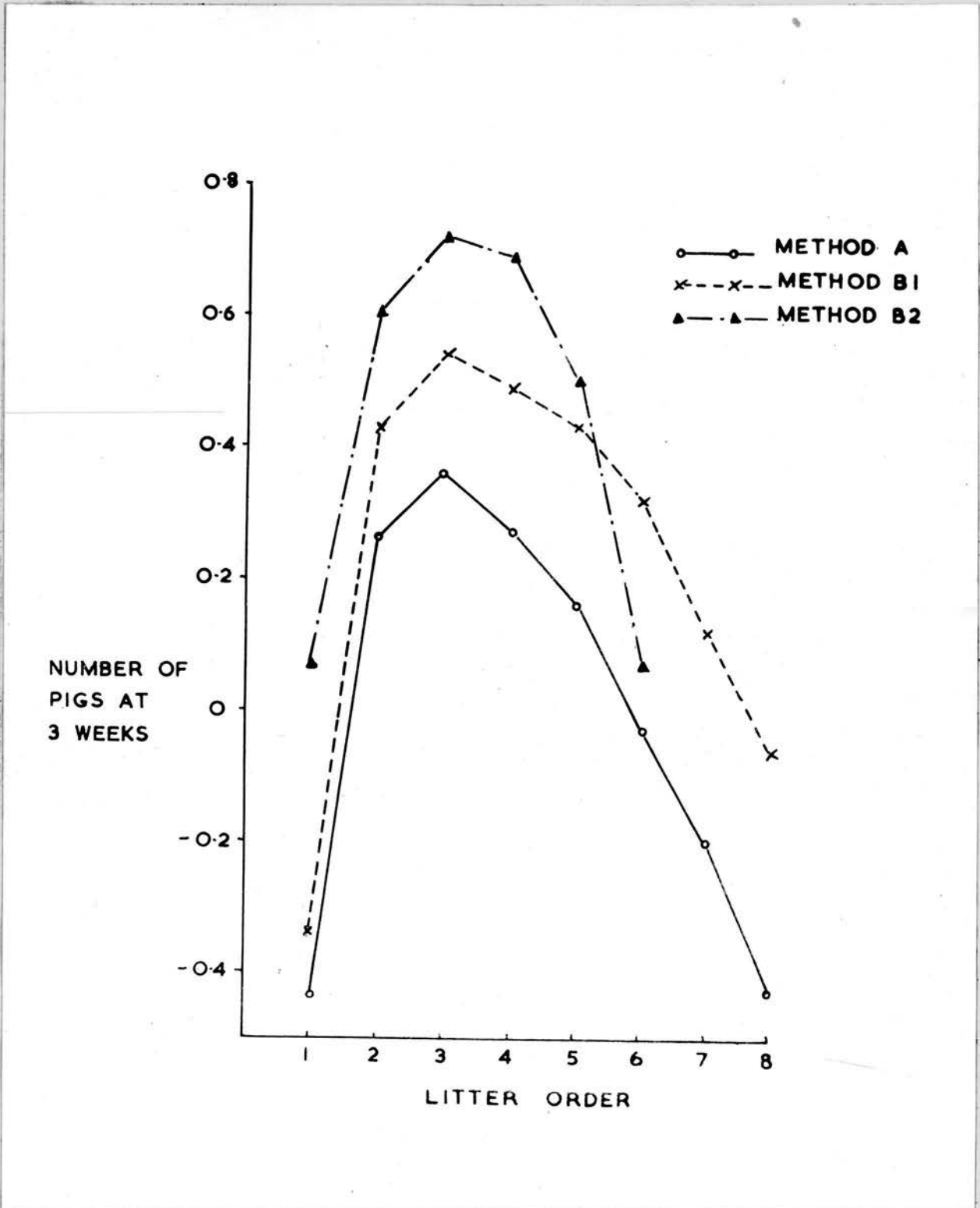


FIGURE 4. The relationship between parity and litter weight at three weeks.

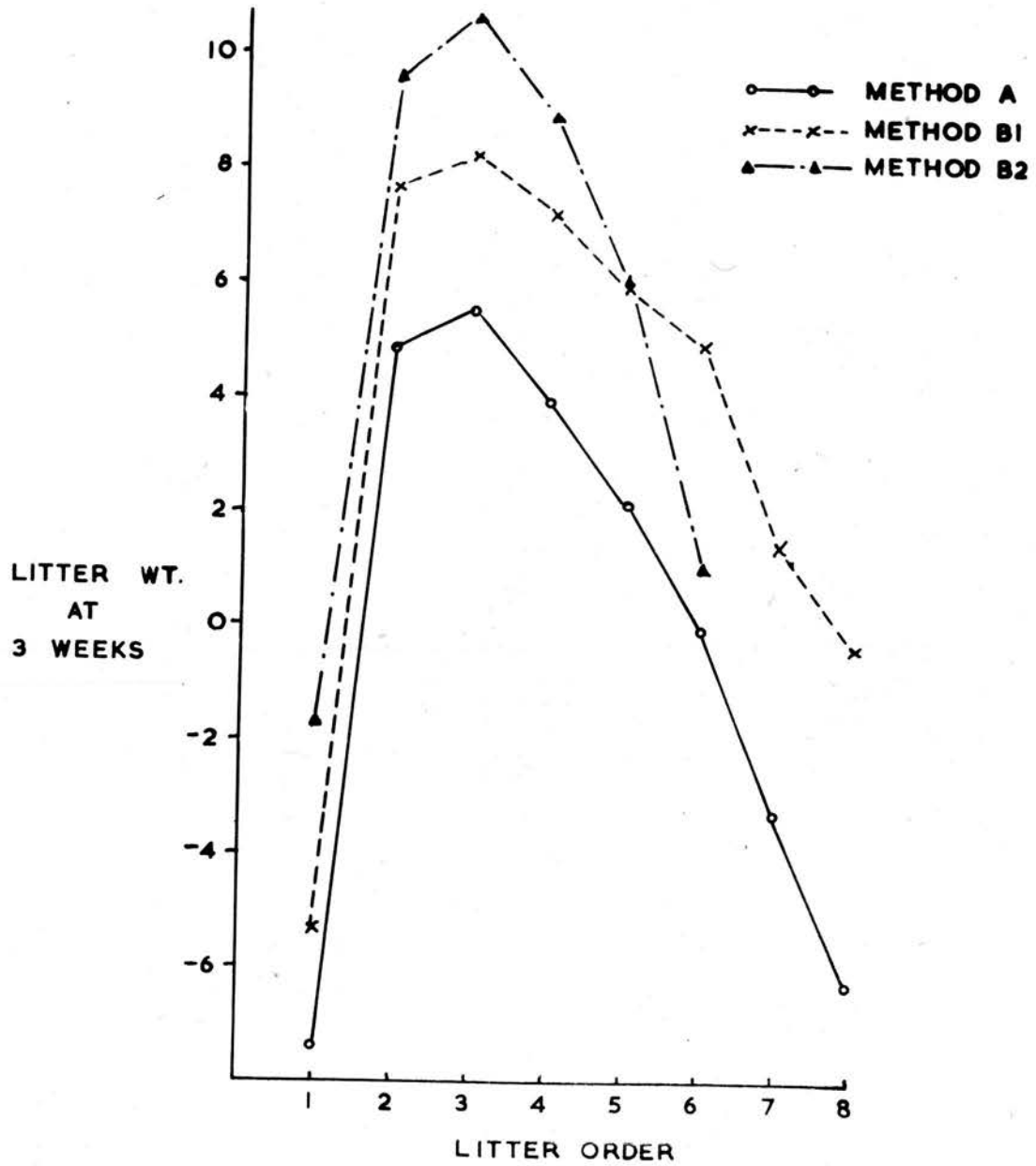


FIGURE 5. The relationship between parity and average pig weight at three weeks.

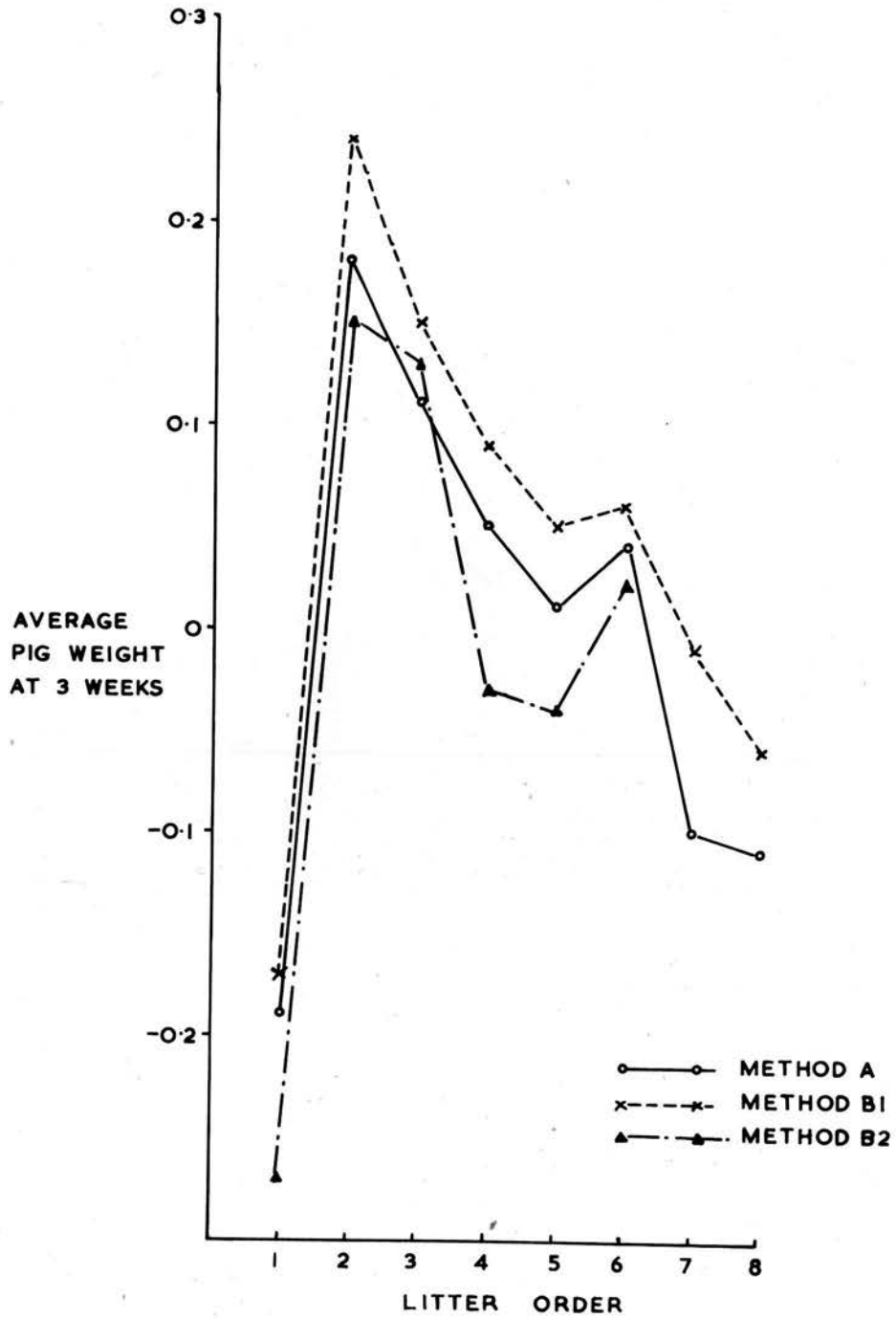


FIGURE 6. The relationship between parity and mortality from birth to three weeks.

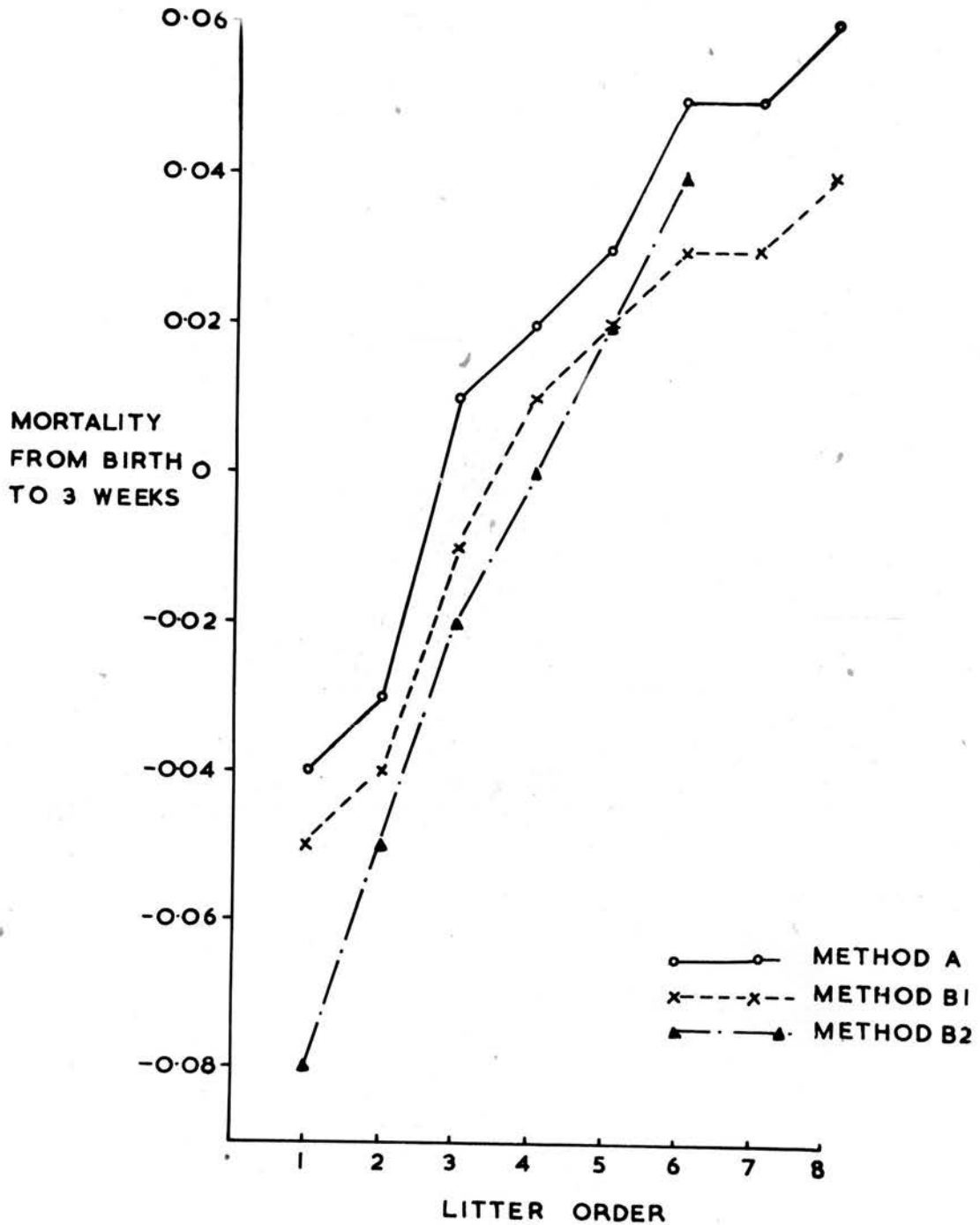


FIGURE 7. The relationship between parity and litter size at eight weeks.

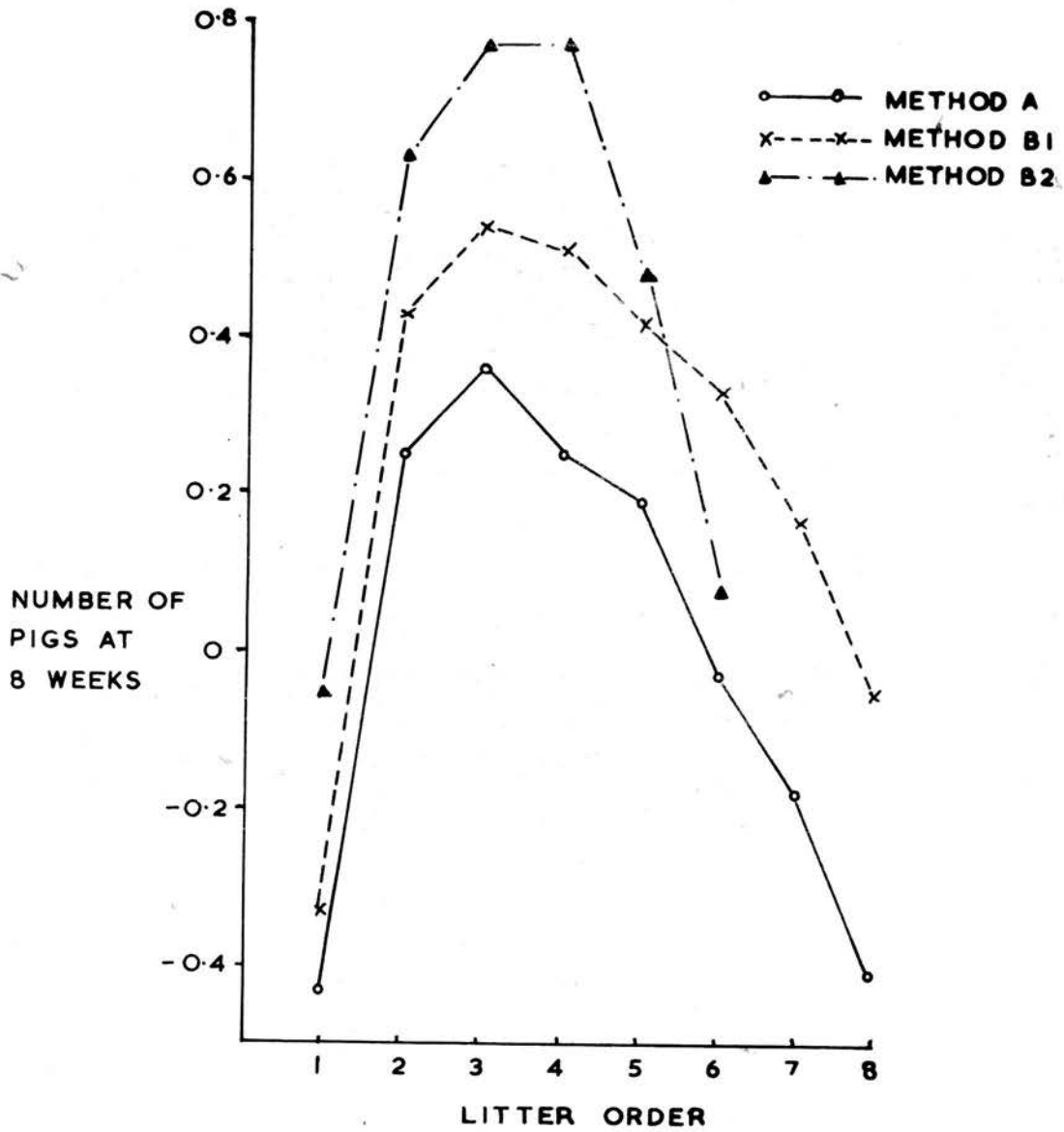


FIGURE 8. The relationship between parity and litter weight at eight weeks.

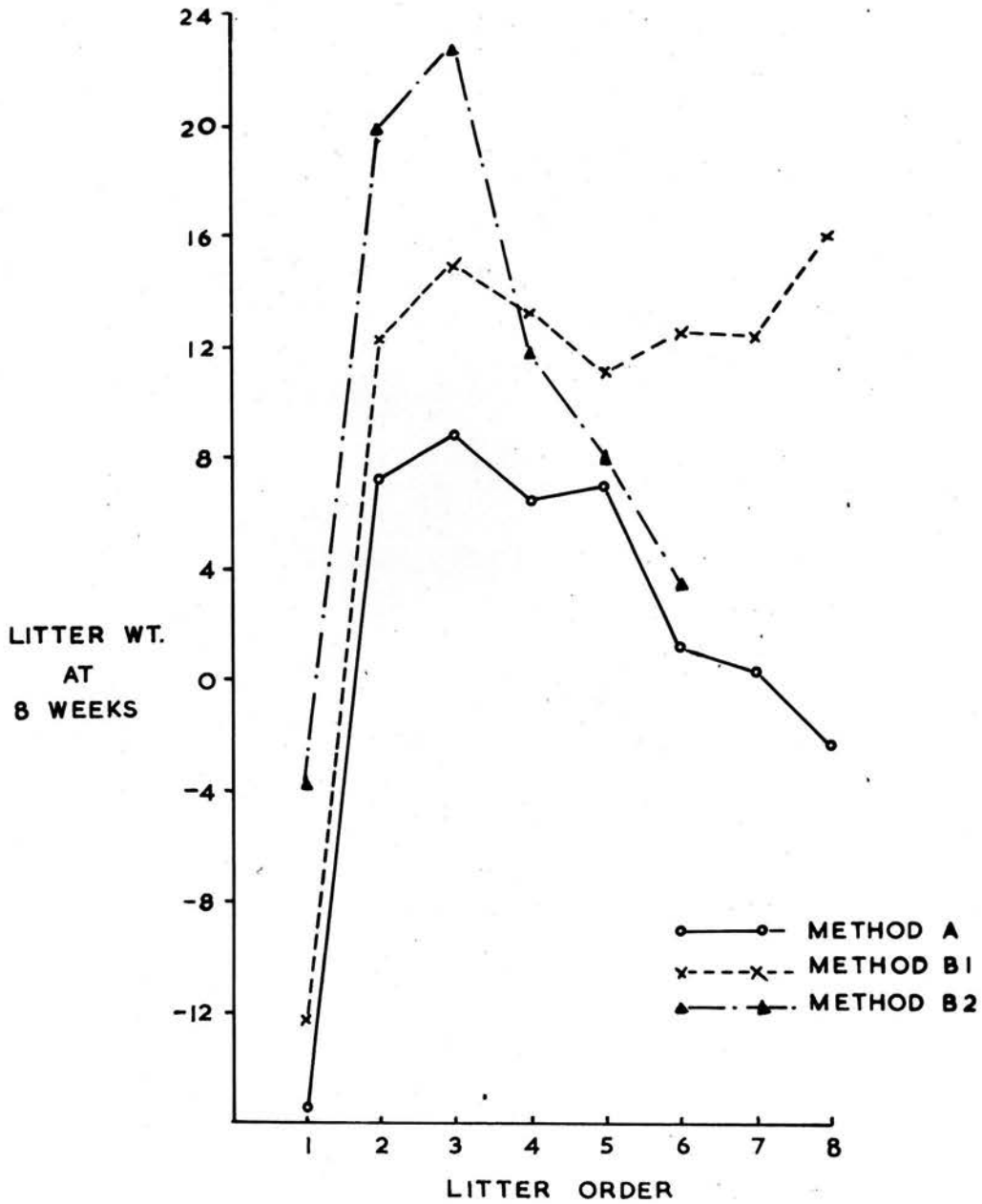


FIGURE 9. The relationship between parity and average pig weight at eight weeks.

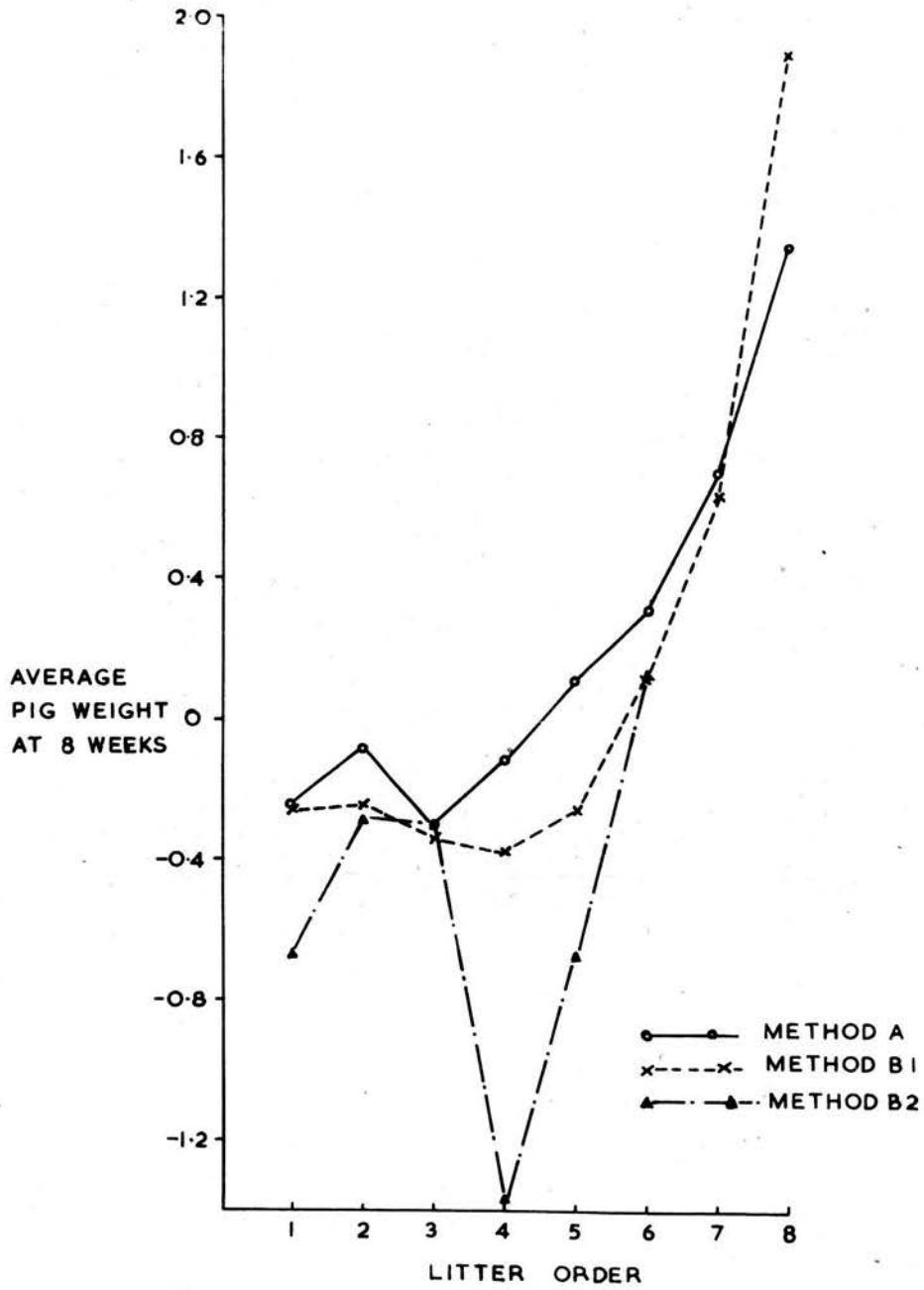
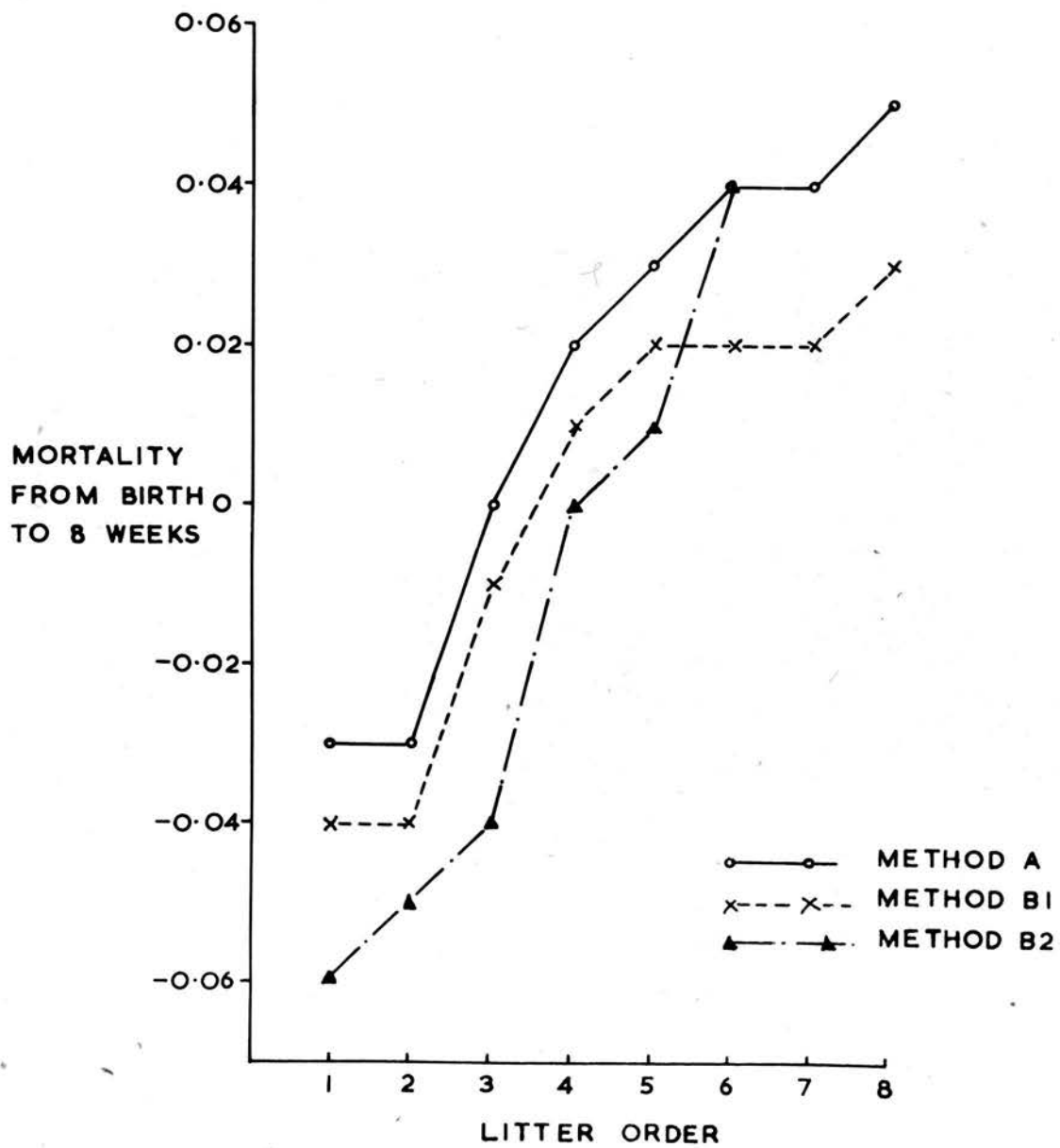


FIGURE 10. The relationship between parity and mortality from birth to eight weeks.



4. The Phenotypic Relationships between the Characters

The number of pigs born alive can be regarded as the most fundamental of the nine characters in that the values of all the other characters are dependent on it to some extent. The litters were classified according to the number of pigs born alive, and the mean values for each class of the other eight characters are given in Table 9. The relationships between the number of pigs born alive and the other eight characters are illustrated in Figures 11 to 14 and are summarised below. As the number of pigs born alive increases:-

- (1) the numbers of pigs at three and eight weeks increase,
- (2) the total litter weights at three and eight weeks increase,
- (3) the average piglet weights at three and eight weeks decrease,
- (4) the mortalities from birth to three weeks and birth to eight weeks increase.

The overall regression and correlation coefficients for the various combinations of the nine characters are given in Table 10. The standard errors of the regression coefficients were all extremely small, i.e. roughly a hundred times smaller than the corresponding regression coefficient. A rough guide to the broad relationships between the various characters can be obtained from the correlation coefficients. They confirm the relationships between the ~~number~~ number of pigs born alive and the other characters described above: the number of pigs born alive is positively correlated with the

litter size, weight and mortality at three and eight weeks and negatively correlated with the average pig weights at three and eight weeks. The relationships between litter size, litter weight and average pig weight are similar at both three and eight weeks and are summarised below.

- (1) There is a positive correlation between the weight of the litter and the number of pigs in the litter.
 - (2) The average pig weight is negatively correlated with litter size.
 - (3) The average pig weight is positively correlated with litter weight.
- Corresponding characters at three and eight weeks (e.g. number of pigs at three weeks and number of pigs at eight weeks) are positively correlated.

The results described above indicated that, although piglet mortality increased with litter size at birth, there was still a progressive increase in the number of pigs at three and eight weeks as the number of pigs born alive increased. The results however, did not show in detail what the relationship was with extremely large litters. Other workers, have found that there is a point at which a further increase in litter size at birth is more than offset by the associated increase in mortality.

Table 11 gives details on the relationship between the number of pigs born alive and litter size at three weeks in large litters for parities one to five, and the overall relationship for the first five litters is illustrated in Figure 15. It can be seen that there is a point at which an increase in the number of pigs born alive results in a decrease in the

number of pigs at three weeks. The optimum number is between four and five pigs above the mean. Since the mean number of pigs born alive is 10.9, it can be concluded that litters with between 15 and 16 pigs born alive give the maximum number of pigs at three weeks. In Table 11, there is a suggestion that in the case of parities three and five, at any rate, the optimum may be even higher.

Table 9. Mean values of eight characters for litters with different numbers of pigs born alive

PERCENTAGE OF LITTERS IN RANGE CHARACTER	NUMBER OF PIGS BORN ALIVE									
	Under -3.0	-3.0 - -2.9	-2.0 - -1.1	-1.0 - -0.1	0 - 0.9	1.0 - 1.9	2.0 - 2.9	3.0 and over		
Number of pigs at 3 wks.	12	9	13	15	16	13	10	12		
Litter wt. at 3 wks. (lb.)	-3.0	-1.5	-0.8	-0.1	0.6	1.1	1.5	1.9		
Average pig wt. at 3 wks. (lb.)	-29.9	-14.4	-7.3	-0.5	6.6	10.6	13.8	16.5		
Mortality from birth to 3 wks.	1.4	0.6	0.3	0.0	-0.2	-0.4	-0.7	-0.9		
Number of pigs at 8 wks. (lb.)	-0.14	-0.08	-0.05	-0.02	-0.00	0.04	0.08	0.17		
Litter wt. at 8 wks. (lb.)	-2.9	-1.5	-0.8	-0.1	0.5	1.1	1.4	1.8		
Average pig wt. at 8 wks. (lb.)	-71.0	-22.5	-5.7	7.3	19.9	21.6	21.7	13.8		
Mortality from birth to 8 wks.	4.8	3.3	2.2	0.7	-0.5	-2.0	-3.2	-4.9		
	-0.14	-0.08	-0.05	-0.02	0.00	0.04	0.08	0.16		

FIGURE 11. The relationship between the number of pigs born alive and litter size at three weeks and eight weeks.

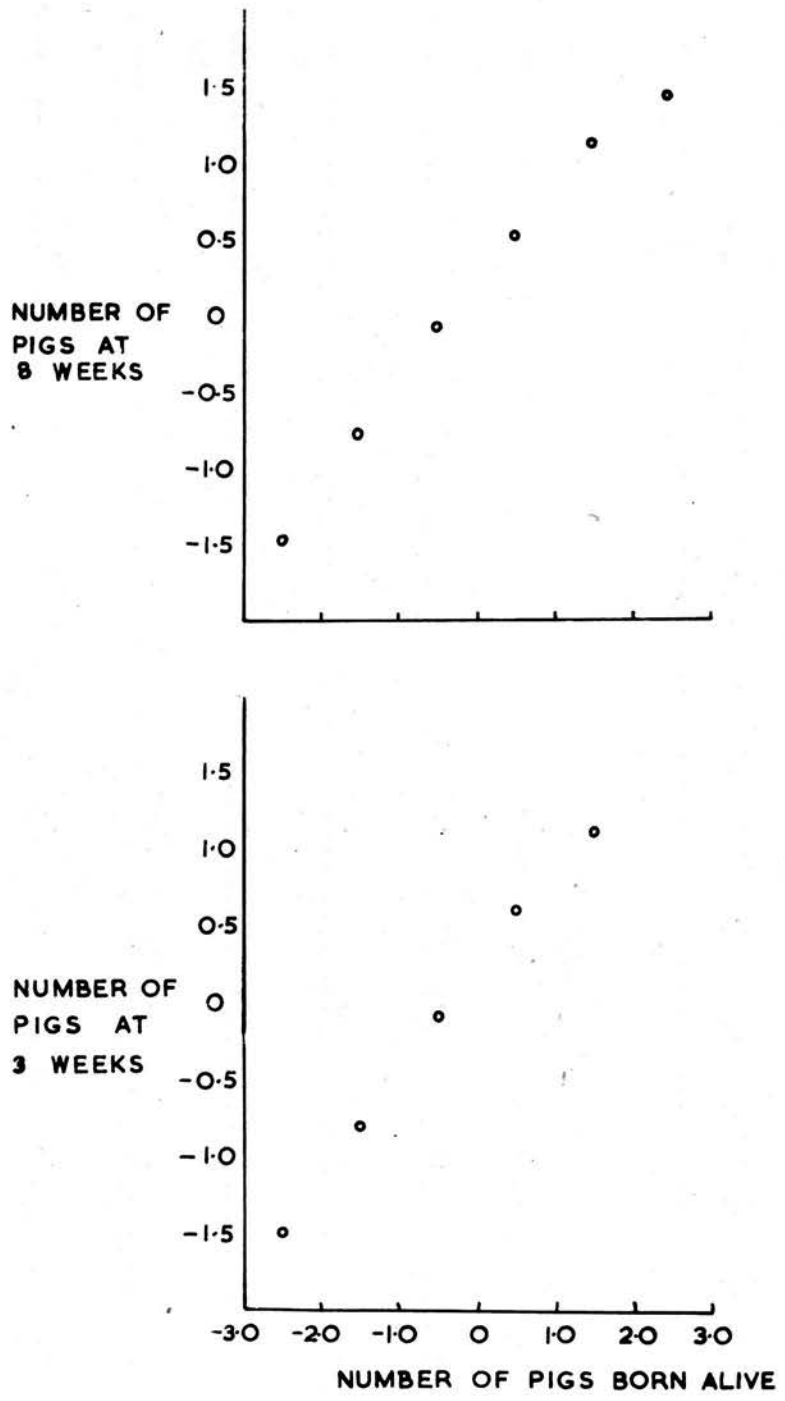


FIGURE 12. The relationship between the number of pigs born alive and litter weight at three weeks and eight weeks.

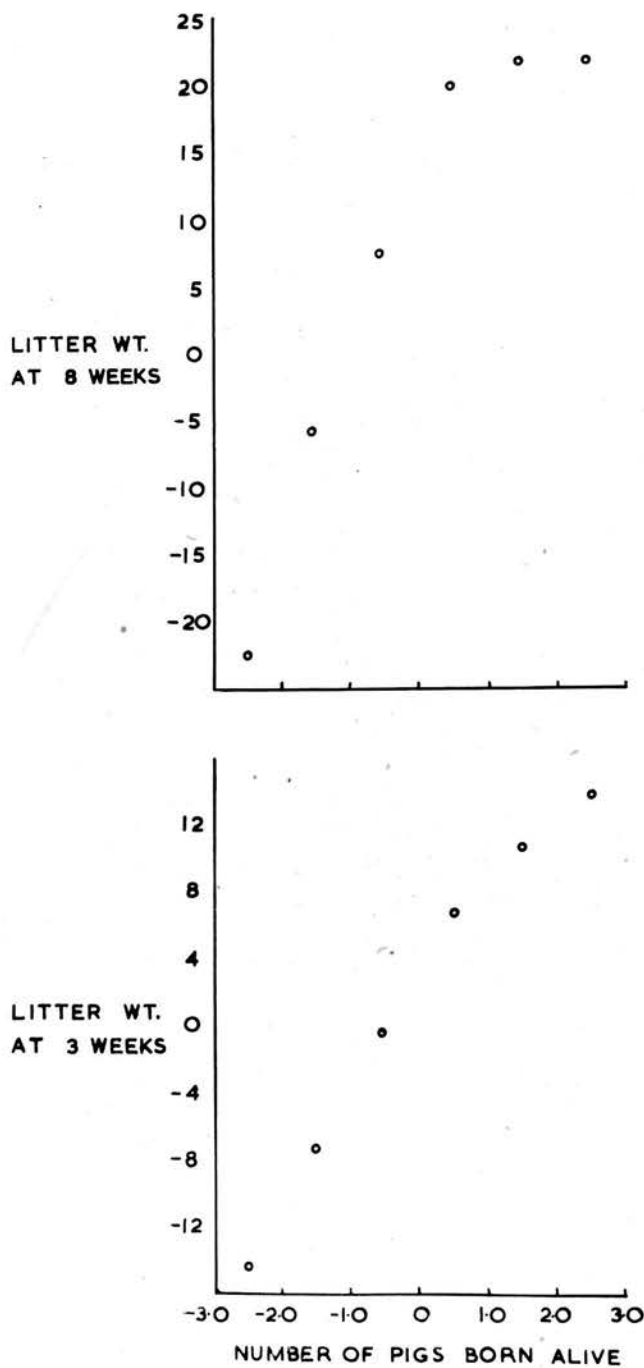


FIGURE 13. The relationship between the number of pigs born alive and average pig weight at three weeks and eight weeks.

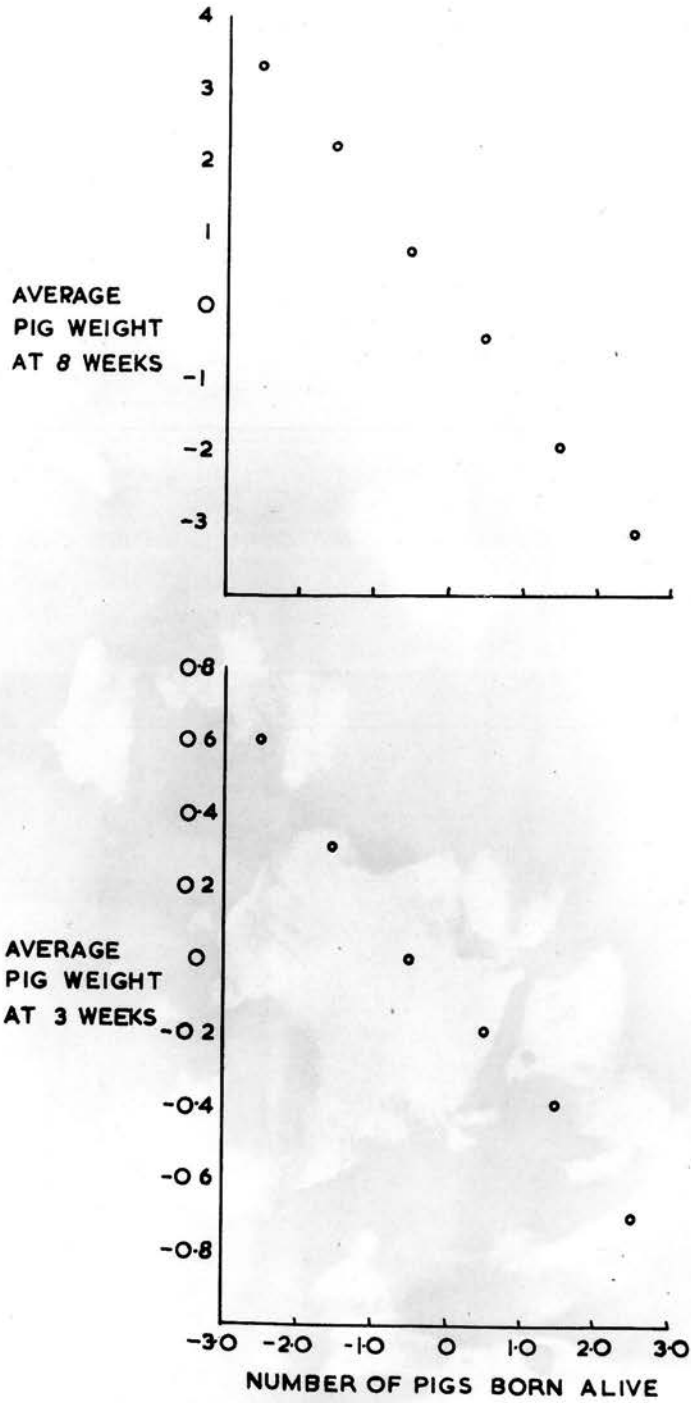


FIGURE 14. The relationship between the number of pigs born alive and mortality from birth to three weeks and from birth to eight weeks.

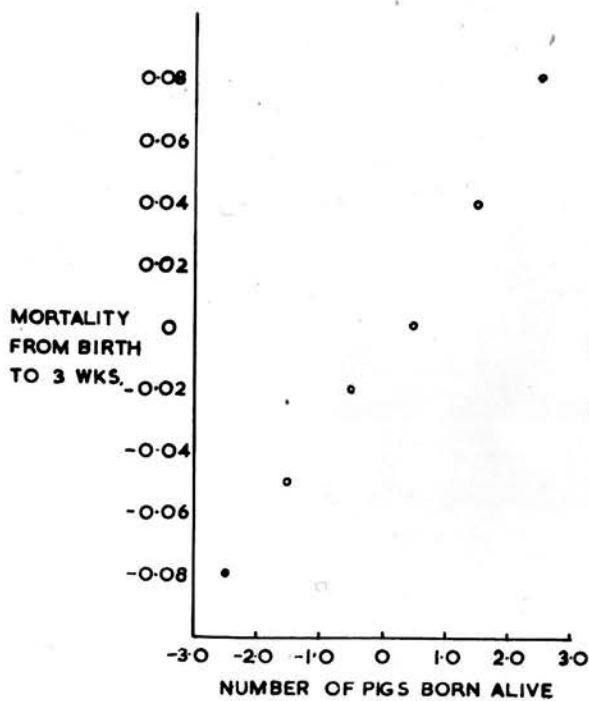
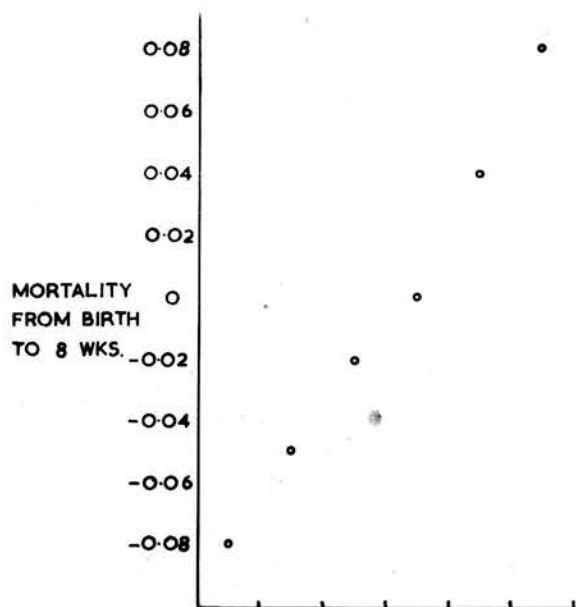


Table 10. Phenotypic *regression and correlation coefficients between the characters

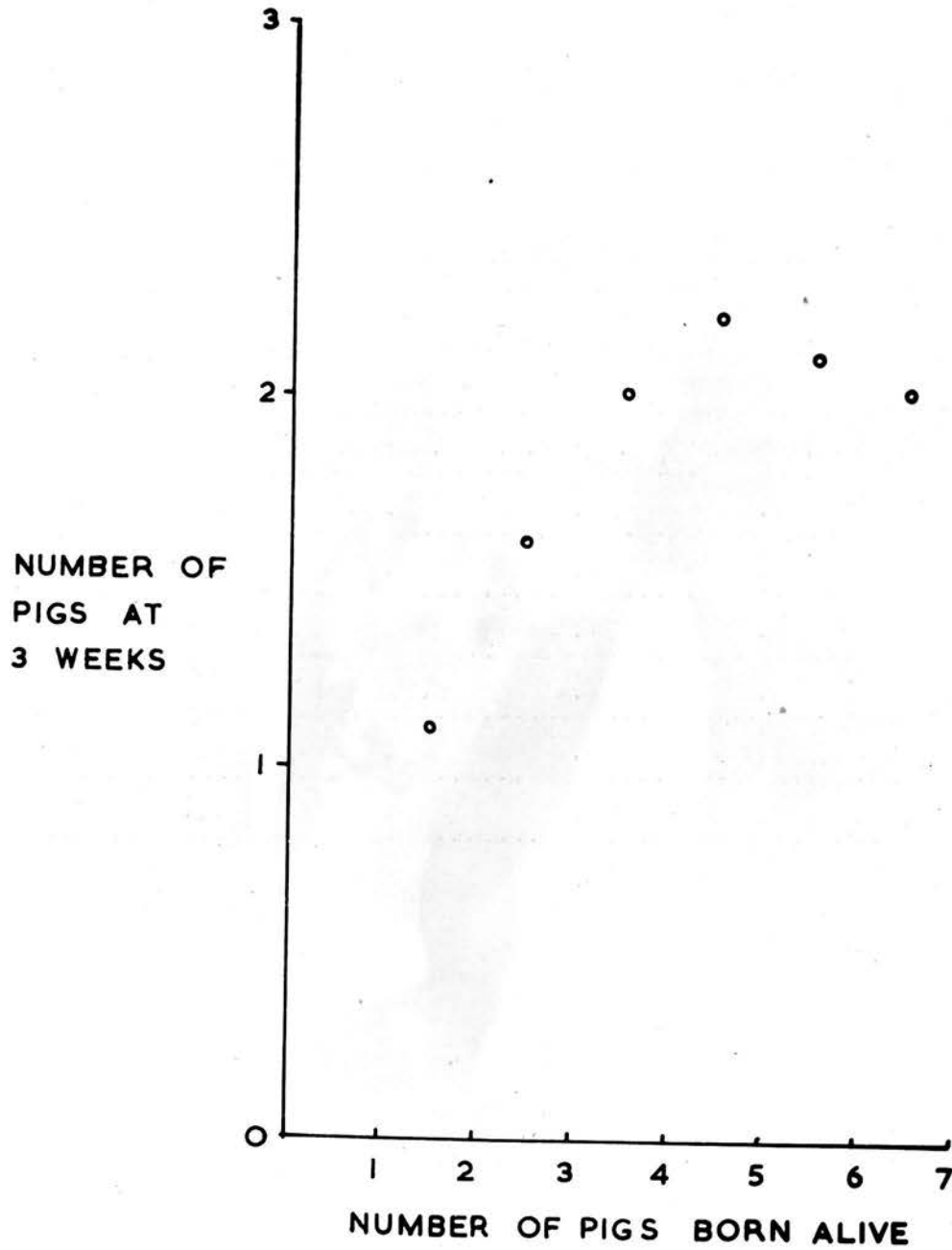
	Number of pigs born alive	Number of pigs at 3 wks.	Litter wt. at 3 wks. (lb.)	Average pig wt. at 3 wks. (lb.)	Mortality from birth to 3 wks.	Number of pigs at 8 wks.	Litter wt. at 8 wks. (lb.)	Average pig wt. at 8 wks. (lb.)	Mortality from birth to 8 wks.
Number of pigs born alive		0.6	5.3	-0.3	0.03	0.5	9.7	-1.1	0.03
Number of pigs at 3 wks.	0.7		10.7	-0.3	-0.03	1.0	19.6	-1.6	-0.03
Litter wt. at 3 wks. (lb.)	0.5	0.8		0.0	-0.00	0.1	1.5	-0.1	-0.00
Average pig wt. at 3 wks. (lb.)	-0.3	-0.3	0.3		-0.01	-0.3	1.5	1.5	-0.01
Mortality from birth to 3 wks.	0.4	-0.3	-0.3	-0.1		-2.8	-80.6	1.7	0.94
Number of pigs at 8 wks.	0.7	1.0	0.8	-0.2	-0.3		20.9	-1.6	-0.04
Litter wt. at 8 wks. (lb.)	0.2	0.4	0.4	0.0	-0.2	0.4		0.1	-0.00
Average pig wt. at 8 wks. (lb.)	-0.3	-0.4	-0.2	0.3	0.0	-0.4	0.6		-0.00
Mortality from birth to 8 wks.	0.4	-0.3	-0.4	-0.1	0.9	-0.4	-0.2	0.0	

*Regression coefficients above the diagonal: the characters listed on the left hand side are the independent variables and the characters in the top row the dependent variables.

Table 11. Litter size at three weeks in litters with increasing numbers of pigs born alive for parities one to five

LITTER	NUMBER OF PIGS BORN ALIVE					
	1.0 - 1.9	2.0 - 2.9	3.0 - 3.9	4.0 - 4.9	5.0 - 5.9	6.0 - 6.9
1	1.2	1.7	2.2	2.8	2.4	2.2
2	1.3	1.8	2.3	2.6	2.1	2.1
3	1.1	1.7	2.1	2.1	2.2	2.5
4	1.1	1.4	1.6	2.0	1.9	1.5
5	0.9	1.4	1.8	1.7	1.8	1.9
1-5	1.1	1.6	2.0	2.2	2.1	2.0

FIGURE 15. The relationship between the number of pigs born alive and the number of pigs at three weeks in large litters.



5. The Repeatability

The repeatability estimates for the nine characters are given in Table 12. All the estimates are low but in the case of the litter weight at eight weeks and the average pig weight at eight weeks they are particularly low.

The repeatability estimates give an overall measure of the extent to which a sow's performance in her earlier litters can be used to predict her performance in later litters. A more direct measure for any particular combination of litters is obtained by calculating the appropriate regression coefficient (e.g. the regression of second litter performance on first litter performance).

The regression coefficients for three litter combinations are given in Table 13. They are very low and are generally in accordance with the repeatability estimates obtained above. The relationship between first and second litter performance is similar to that between second and third litter performance. The regression of the mean performance of the third and fourth litters on the mean performance of the first and second litters is, as one would expect, somewhat greater, but nevertheless, it could not be maintained that a sow's performance in her first two litters is a good guide to her later performance.

Table 12. Repeatability estimates for nine litter performance traits

CHARACTER	REPEATABILITY
Number of pigs born alive	0.15
Number of pigs at 3 wks.	0.14
Litter wt. at 3 wks.	0.15
Average pig wt. at 3 wks.	0.17
Mortality from birth to 3 wks.	0.10
Number of pigs at 8 wks.	0.14
Litter wt. at 8 wks.	0.04
Average pig wt. at 8 wks.	0.04
Mortality from birth to 8 wks.	0.12

Table 13. Regression coefficients of performance in succeeding litters on performance in previous litters

	LITTER ORDERS		
	2 on 1	3 on 2	$\frac{3+4}{2}$ on $\frac{1+2}{2}$
Number of pigs born alive	0.17	0.18	0.25
Number of pigs at 3 wks.	0.11	0.12	0.17
Litter wt. at 3 wks.	0.11	0.16	0.18
Average pig wt. at 3 wks.	0.13	0.14	0.20
Mortality from birth to 3 wks.	0.07	0.11	0.11
Number of pigs at 8 wks.	0.12	0.15	0.20
Litter wt. at 8 wks.	0.04	0.05	0.06
Average pig wt. at 8 wks.	0.09	0.07	0.12
Mortality from birth to 8 wks.	0.07	0.12	0.11

6. Investigations into a possible Maternal Effect

It was stated in the introduction that Falconer discovered a maternal effect in mice whereby females born in large litters tend to have small litters as a result of their reduced body weight. As the records used in this study did not contain any information on the weight of the gilts or the individual piglets, the question could only be investigated indirectly. Two methods were used to see if there was any evidence to suggest that such a maternal effect existed in pigs.

The first method involved dividing the daughter-dam first litter pairs into two groups: one group included those pairs where the daughter had been born in her dam's first litter, the other group consisted of those pairs where the daughter had not been born in her dam's first litter.

Consider those daughter-dam pairs where the daughter has been born in the dam's first litter. If litter size is inherited then the genetic relationship between a dam and her daughter will tend to give rise to a positive daughter-dam regression coefficient for litter size in first litters. If the maternal effect exists there will be a tendency for daughters which have been reared in large litters to have reduced body weights and thus have small first litters and vice versa. Since the daughters have been reared in their dam's first litters the maternal effect would in the absence of other effects give rise to a negative daughter-dam regression coefficient for litter size in first litters. The observed

daughter-dam regression coefficient for litter size in first litters will thus be the result of two opposing effects, a positive genetic effect and a negative maternal effect.

Now consider the second group of daughter-dam first litter pairs: those in which the daughter was not born in the dam's first litter. Once again we can expect the genetic relationship between a daughter and her dam to tend to give rise to a positive daughter-dam regression coefficient for litter size in first litters. If the maternal effect exists it will tend to produce a negative regression coefficient for the size of the daughter's first litter on the size of the dam's litter it was reared in. Since the daughters in this group have not been reared in their dam's first litters, the maternal effect will not affect the first litter daughter-dam regression coefficient as in the other group of daughter-dam pairs. In this group the observed daughter-dam regression coefficient will only reflect the positive genetic effect.

It follows from the above reasoning that if the maternal effect exists, the first litter daughter-dam regression coefficient for daughters born in their dams' first litters will be smaller than for daughters not born in their dam's first litters. The regressions coefficients for the number of pigs born alive for the two daughter-dam first litter groups are given in the table on the next page.

DESCRIPTION	REGRESSION COEFFICIENT	STANDARD ERROR
Daughter born in dam's first litter	0.07	0.03
Daughter not born in dam's first litter	0.04	0.02

The regression coefficients are not significantly different. It can be seen that the observed difference is the opposite of what would be expected if the maternal effect existed.

The second method used to investigate the possible existence of the maternal effect in pigs approached the question from rather a different angle. If such an effect operates in pigs it means that gilts, which have been reared in large litters, will have small litters because their weights have been reduced as a consequence of having been reared in large litters. The regression of the litter size of the gilt's first litter on the weight of the gilt when it was three weeks old will thus be positive. The data do not contain information on a gilt's individual weight at three weeks of age, but its weight at three weeks would presumably be fairly highly correlated with the average three week piglet weight of the litter it was reared in. Thus a significant positive regression coefficient for the number of pigs born alive in the gilt's first litter on the average three week weight of the pigs in the litter the gilt was reared in could be taken as indirect evidence for the existence of the 'maternal effect'. Such a regression coefficient was calculated; it had a value of -0.0004 pigs/lb. with a standard error of 0.0004 and was thus not significantly different from zero.

7. The Genetic Parameters

Separate heritability estimates for litter orders one to five were obtained for each of the nine characters. Overall estimates, calculated within litters one to five, were also obtained by pooling the sums of squares and cross products. The estimates and their standard errors are given in Table 14. As the data include fewer litters at the higher parities, the standard errors of the estimates are larger for the higher parities. For discussion purposes it is advantageous to have a single overall estimate of the heritability of each of the nine characters; the heritabilities calculated within litters one to five represent such estimates. The most striking fact about these estimates is that they are all extremely low. The heritabilities of the mortality characters are particularly low, as is the heritability of litter weight at eight weeks. The average pig weight at eight weeks, on the other hand, has a slightly higher heritability than the other characters.

A close examination of the heritability estimates in Table 15 leads one to suspect that the heritabilities of the characters may vary to some extent with litter order. The rather variable estimates for the fourth and fifth litters are almost certainly a reflection of their relatively high standard errors. It is noticeable that the heritability of a character in the first litter is invariably higher than the heritability of the character in the second litter. There is, in fact, a definite tendency for the first litter heritabilities to be relatively high and for the second litter heritabilities to be relatively low.

Heritability estimates of a sow's mean performance after two, three, four and five litters have been calculated for the nine characters and are listed in Table 15. The first litter estimates have been included for comparison. The estimates for the means of the first four and the first five litters are somewhat erratic owing to their relatively high standard errors. As expected, the heritability estimates tend to increase as the number of litters contributing to the mean increases.

The genetic correlation coefficients between the characters were calculated and are listed in Table 16. It can be seen that there are favourable positive correlations between the characters relating to litter size and litter weight. The positive correlations between litter size and mortality are of course unfavourable. Unlike the average pig weight at three weeks, the average pig weight at eight weeks has a negative genetic correlation with litter size.

Table 14. Heritability estimates calculated separately for the first five litters and overall estimates calculated within litters one to five

CHARACTER		LITTER					
		1	2	3	4	5	1-5
Number of pigs born alive	h^{2*}	0.10	0.06	0.03	0.10	0.07	0.07
	s.e.†	0.03	0.04	0.05	0.07	0.08	0.02
Number of pigs at 3 wks.	h^2	0.11	0.07	0.02	0.02	0.08	0.07
	s.e.	0.03	0.04	0.05	0.07	0.08	0.02
Litter wt. at 3 wks.	h^2	0.14	0.03	0.05	0.07	0.06	0.08
	s.e.	0.03	0.04	0.05	0.06	0.08	0.02
Average pig wt. at 3 wks.	h^2	0.10	0.05	0.04	0.09	0.04	0.07
	s.e.	0.03	0.04	0.04	0.06	0.07	0.02
Mortality from birth to 3 wks.	h^2	0.04	0.00	0.02	0.07	-0.02	0.03
	s.e.	0.04	0.04	0.05	0.07	0.08	0.02
Number of pigs at 8 wks.	h^2	0.13	0.08	0.07	0.01	0.09	0.09
	s.e.	0.04	0.05	0.06	0.08	0.10	0.03
Litter wt. at 8 wks.	h^2	0.02	-0.02	0.05	0.05	0.21	0.03
	s.e.	0.04	0.04	0.06	0.07	0.09	0.02
Average pig wt. at 8 wks.	h^2	0.12	0.02	0.14	0.18	0.21	0.11
	s.e.	0.04	0.04	0.05	0.07	0.09	0.02
Mortality from birth to 8 wks.	h^2	0.04	0.02	0.05	0.20	-0.08	0.04
	s.e.	0.04	0.05	0.06	0.09	0.10	0.03

* h^2 = heritability

†s.e. = standard error

Table 15. Heritability estimates of mean performance after one to five litters

CHARACTER		LITTERS INCLUDED IN MEAN				
		1	1, 2	1, 2, 3	1, 2, 3, 4	1, 2, 3, 4, 5
Number of pigs born alive	h^2	0.10	0.10	0.12	0.12	0.32
	s.e.	0.03	0.05	0.06	0.09	0.14
Number of pigs at 3 wks.	h^2	0.11	0.13	0.11	0.06	0.23
	s.e.	0.03	0.05	0.06	0.09	0.15
Litter wt. at 3 wks.	h^2	0.14	0.13	0.12	0.04	0.11
	s.e.	0.03	0.04	0.06	0.08	0.14
Average pig wt. at 3 wks.	h^2	0.10	0.09	0.05	0.01	0.04
	s.e.	0.03	0.04	0.06	0.08	0.13
Mortality from birth to 3 wks.	h^2	0.04	0.07	0.08	0.11	0.21
	s.e.	0.04	0.05	0.07	0.11	0.18
Number of pigs at 8 wks.	h^2	0.13	0.10	0.19	0.19	0.42
	s.e.	0.04	0.06	0.08	0.13	0.23
Litter wt. at 8 wks.	h^2	0.02	-0.04	-0.03	-0.06	0.07
	s.e.	0.04	0.05	0.08	0.14	0.20
Average pig wt. at 8 wks.	h^2	0.12	0.00	0.01	0.01	0.46
	s.e.	0.04	0.05	0.08	0.14	0.19
Mortality from birth to 8 wks.	h^2	0.04	0.09	0.10	0.21	0.16
	s.e.	0.04	0.06	0.09	0.17	0.28

8. The Effect of the Mate

The data were investigated to see whether the sire of the litter had an effect on any of the characters. The data had been adjusted for the effects of herd, season, year and parity as for the repeatability calculations. The analysis was confined to boars which had sired five or more litters. An analysis of variance was done for each of the nine characters and the ratios of the between and within boars mean squares are given in Table 17. The appropriate F-values were calculated using a formula described by Lindley and Miller (1953). The proportions of the variation in each of the traits attributable to the differences between mates were also calculated and are listed in Table 17.

It can be seen that the effect of the boar is significant at the 1% level for the average pig weights at three and eight weeks. As the differences between boars for the number of pigs born alive and the litter weights at three weeks are just significant at the 5% level and no more, it would be unwise to conclude categorically that the boar has a significant effect on these characters.

Table 17. Analyses of variance of the differences between mates for nine litter performance traits

CHARACTER	Number of litters	Number of boars	Ratio of between and within boars mean squares	F - 1%	F - 5%	Percentage of variation attributable to mates
Number of pigs born alive	33123	1544	1.07	1.09	1.06	0.3
Number of pigs at 3 wks.	32617	1544	0.96	1.09	1.06	-0.2
Litter wt. at 3 wks.	32617	1544	1.08	1.09	1.06	0.4
Average pig wt. at 3 wks.	32617	1544	1.15	1.09	1.06	0.7
Mortality from birth to 3 wks.	32617	1544	0.94	1.09	1.06	-0.2
Number of pigs at 8 wks.	26259	1383	0.92	1.09	1.06	-0.4
Litter wt. at 8 wks.	26259	1383	0.99	1.09	1.06	-0.0
Average pig wt. at 8 wks.	26259	1383	1.10	1.09	1.06	0.5
Mortality from birth to 8 wks.	26259	1383	0.97	1.09	1.06	-0.1

9. The Extent of Culling on the basis of Litter Size

It is of interest to know the extent to which farmers cull on the basis of litter size. Two methods were used to examine the data to this end. The first method involved looking at some of the earlier parities and comparing the mean performance for these parities of animals surviving to have later litters with the mean performance of animals which did not survive to have later litters. The second method consisted of dividing the sows in some of the earlier parities into groups according to litter size and calculating the proportions of the sows in the different litter size groups which survived to have later litters.

The mean values, comparing the animals surviving to have a later litter with those that were culled are given in Table 18. The mean values of the survivors and the culls are expressed as deviations from the overall mean of each parity. The comparisons were made for two characters, the number of pigs born alive and the number of pigs at three weeks, and for five litter order means, the first, the second, the third, the mean of the first two litters, and the mean of the first three litters. It can be seen that for both characters and for all five litter order means, the litter size of the females surviving to have a later litter was greater than for those which did not have another litter. The advantage the survivors have over the overall mean is not very much and in no case does it reach 0.2 of a pig. The difference between the mean performance of the survivors and the culls is always greater for the number of pigs at three weeks than the number of pigs at birth suggesting that the farmers are probably culling on the basis

of litter size at three weeks or weaning rather than at birth.

The proportions of animals culled after their first, second or third litters were remarkably similar, the actual percentages being 29, 27 and 29 respectively. The percentages of sows surviving to have a later litter for the different litter size groups are given in Table 19 for the number of pigs born alive and in Table 20 for the number of pigs at three weeks. For both characters it can be seen that a sow's chance of surviving to have another litter tends to increase with the size of the last litter she farrowed. Once again, it is apparent that the number of pigs at three weeks is more important than the number of pigs born alive in determining whether a sow will be culled or not. It can be seen in Table 20 that whether or not a sow survives to have a third or a fourth litter depends to a greater extent on her average performance in her previous litters than on her performance in the last litter she farrowed.

Table 18. Mean performance of survivors and culls for litter size at birth and three weeks

LITTER COMBINATION	NUMBER OF PIGS BORN ALIVE		NUMBER OF PIGS AT 3 WKS.	
	SURVIVORS	CULLS	SURVIVORS	CULLS
1	0.07	-0.15	0.11	-0.26
2	0.11	-0.29	0.19	-0.53
3	0.05	-0.14	0.16	-0.40
1, 2	0.09	-0.24	0.14	-0.41
1, 2, 3	0.02	-0.06	0.09	-0.23

Table 19. Percentage of survivors for different litter size at birth classes

LITTER	LITTER SIZE CLASS							
	Under -3.0	-3.0 - -2.1	-2.0 - -1.1	-1.0 - -0.1	0 - 0.9	1.0 - 1.9	2.0 - 2.9	3.0 and over
1	69	72	66	72	76	72	77	72
2	63	71	72	74	77	75	75	76
3	70	69	70	67	73	73	76	72
Mean of 1, 2,	63	71	73	73	76	77	75	78
Mean of 1, 2, 3	70	71	70	73	70	75	75	70

Table 20. Percentage of survivors for different litter size at three weeks classes

LITTER	LITTER SIZE CLASS							
	Under -3.0	-3.0 - -2.1	-2.0 - -1.1	-1.0 - -0.1	0 - 0.9	1.0 - 1.9	2.0 - 2.9	3.0 and over
1	65	65	70	72	73	75	76	74
2	59	63	67	73	77	76	82	79
3	61	62	64	73	75	72	77	78
Mean of 1, 2,	58	59	69	73	77	80	79	83
Mean of 1, 2, 3	39	64	69	71	72	76	76	87

DISCUSSION

The data used in this study came from roughly a third of the pure-bred Large White herds recording with PIDA. The mean values for litter size and litter weight are in line with those published annually by PIDA for all the Large White herds participating in their recording scheme. The herds recording with PIDA represent an extremely small fraction of the total pig population in Britain. Mean performance figures for the national herd are not available but it seems reasonable to expect the mean performance of PIDA recorded herds to be, if anything, somewhat higher than the national average. The fact, that even in these herds 18% of the pigs born alive are lost by the time they are eight weeks of age, is a sharp reminder that there is considerable scope for improving current husbandry techniques.

The seasonal differences in litter size and weight at three and eight weeks can all be accounted for by the increased mortality during the winter months. The results are very similar to those of Bowman et al (1961) who found that seasonal differences were important for litter size and weight at weaning but not for litter size at birth. The proportion of the variation in the traits attributable to seasonal differences is extremely small and is not comparable with that attributable to herd differences.

The differences between herds are considerable for all of the characters, but, in the case of litter weight and average pig weight at three weeks, the herd differences are very large indeed, accounting for 16%

and 23% of the total variation in the characters, respectively. The large herd differences for these two characters are almost certainly caused by differences in husbandry practices between herds.

Litter and piglet weights at three weeks depend to a large extent on the amount of milk available from the sow. The amount of milk a sow produces is very dependent on the amount of food she consumes and it is for this reason that sows should be fed liberally during lactation. The large herd differences in three week weights may be caused by some farmers not feeding their sows well enough at this stage. The herd differences in litter and pig weights are much less at eight weeks. After three weeks an increasing fraction of a pig's feed requirements are met from creep feed. It may be that the creep feed enables the lighter litters to catch up to some extent and the herd differences are thus reduced by the time the pigs are eight weeks of age.

The effects of age at first farrowing on the size and weight of a gilt's first litter are similar to those found by Korkman (1947) and Sherrit (1962). The regression coefficient of litter size at birth on age at first farrowing in days of 0.003 is comparable to the values of 0.009 and 0.005 obtained by Sherrit and Korkman, respectively. As found by Korkman, the effect of age is greater on litter weight than on litter size.

The differences in litter size at birth caused by age at first farrowing are considerably reduced at eight weeks. The results indicate that gilts farrowing at thirteen months will on average rear only an extra quarter of a pig compared with gilts farrowing at eleven months.

At current prices the marginal value of an extra quarter of a pig at weaning allowing for the extra sow and creep feed costs is about £1. The cost of feeding a gilt for two months on the other hand is roughly £4. Since approximately 40% of the gilts in the data first farrowed at over thirteen months of age, it seems likely that many farmers would profit from farrowing their gilts at a younger age.

The relationship found between parity and sow performance is in accordance with the general picture obtained by previous workers and described in the introduction. The progressive increase in litter size at birth up to the fourth or fifth litter followed by a progressive decline is precisely what was found by Korkman (1947), as is the increase in litter size and weight at three weeks up to the third litter followed by a decline. The consistent increase in mortality with parity is in agreement with the findings of Olbrycht (1943) but not Korkman (1947) who found little variation in mortality after the fourth litter. Since in most herds very few sows survive to have anything like eight litters, the decline in performance at higher parities is not of any practical importance. In the data used in the present study, for example, 74% of the litters were from the first ^{four} parities.

The values obtained for the phenotypic regression and correlation coefficients between the characters are in line with the findings of other workers. The increase in mortality with litter size is similar to that found by Korkman (1947). The correlation coefficient of 0.8 obtained between litter size and weight at three weeks is in close agreement with the value of 0.7 obtained by Korkman (1947). The correlation coefficient of 0.4

between litter size and weight at eight weeks, on the other hand, is rather lower than the value of 0.8 obtained by Omtvedt et al (1966) for litter size and weight at six weeks. The correlation of -0.4 between litter size and average pig weight at eight weeks is in good agreement with the value of -0.5 obtained by Omtvedt et al (1966) for the corresponding correlation at six weeks.

It has been shown that litters with between 15 and 16 pigs born alive give the maximum number of pigs at three weeks. Since only ten per cent of the mortality between birth and eight weeks occurs after three weeks it seems likely that litters giving the maximum number of pigs at three weeks will also give the maximum number of pigs at weaning. The optimum litter size at birth is somewhat higher than that found by Pomeroy, who concluded that it was between 12 and 13. It is in agreement with the results of Olbrycht (1943) and Korkman (1947) which suggest an optimum of between 15 and 17 pigs born alive.

The optimum litter size at birth described above is the one which gives the maximum number of pigs at weaning. Provided pigs reared in large litters do not have an inferior subsequent post-weaning performance, it is probably also the most desirable from an economic point of view. There is very little evidence in the literature on the relationship between litter size and subsequent post-weaning performance. Trulsson (1965) found that gilt litters, which are of course smaller than sow litters, had a slower rate of gain than sow litters, but found no difference between gilt and sow litters in carcass quality. Fredeen and Plank (1963) concluded that litter

size at weaning had no effect on post-weaning daily gain or on the carcass traits of length and loin area.

The low repeatability estimates obtained are in accordance with those found by other workers. A repeatability of 0.15 for litter size at birth was also obtained by Lush and Molln (1942). The estimates of 0.14 and 0.15 for the repeatabilities of litter size and weight at three weeks, respectively are slightly higher than the values of 0.07 and 0.11 obtained by Korkman (1947). The value of 0.04 obtained for the repeatability of litter weight at eight weeks is somewhat lower than most workers have found although Urban et al (1966) did obtain a value of 0.05.

The methods used to investigate the possible existence of a maternal effect in pigs similar to that found by Falconer in mice were necessarily rather indirect. The results suggest that such a maternal effect does not exist in pigs. It would not be surprising if pigs and mice differed in this respect. Falconer found that mice reared in large litters had reduced body weights at mating and this led them to have small litters. Mice are weaned at three weeks of age and mated at six weeks of age. Pigs on the other hand, are weaned by eight weeks of age and mated at eight months of age. Thus while the rearing period of a mouse accounts for half of its life before mating, the corresponding proportion in the pig is less than one quarter. Hence it is understandable that while the weight of a mouse at mating may be influenced by the size of the litter it has been reared in that of a pig should not be. Thus although the weight of a gilt at mating influences the size of its first litter (Bowman et al 1961) as in

mice, this need not give rise to the type of maternal effect found in mice.

The low heritability estimates obtained for litter performance traits are in agreement with the results of other workers. The heritability estimate for litter size at birth of 0.07 is in close agreement with the value of 0.08 obtained by Urban et al (1966). The estimates of 0.07 and 0.09 for litter size at three and eight weeks, respectively, agree with the values of 0.10 and 0.09 obtained by Siler (1962). The estimate of 0.08 for litter weight at three weeks is somewhat lower than the values of 0.18 and 0.17 obtained by Korkman (1947) and Siler (1962). The estimate of 0.03 for litter weight at eight weeks is low. It is in accordance with the estimate of 0.05 obtained by Legault (1967) but is considerably lower than the estimates of 0.19 and 0.21 obtained by Urban et al (1966) and Siler (1962) respectively. The estimates of 0.03 and 0.04 for litter mortality from birth to three weeks and birth to eight weeks suggest that the heritability of litter mortality is somewhat lower than the heritability of litter size. The estimates are considerably lower than the value of 0.40 obtained by Cummings et al (1947) for the heritability of survival from birth to weaning.

The repeatability of a trait sets an upper limit to its heritability. The repeatabilities and heritabilities of the nine traits are listed, side by side, in the table on the next page for comparison. It can be seen that, with one striking exception, the repeatability estimates are invariably higher than the heritability estimates. The striking exception is the

CHARACTER	REPEATABILITY	HERITABILITY
Number of pigs born alive	0.15	0.07
Number of pigs at 3 wks.	0.14	0.07
Litter wt. at 3 wks.	0.15	0.08
Average pig wt. at 3 wks.	0.17	0.07
Mortality from birth to 3 wks.	0.10	0.03
Number of pigs at 8 wks.	0.14	0.09
Litter wt. at 8 wks.	0.04	0.03
Average pig wt. at 8 wks.	0.04	0.11
Mortality from birth to 8 wks.	0.12	0.04

average pig weight at eight weeks which has a repeatability of 0.04 and a heritability of 0.11. The divergence between the two estimates seems to be slightly too great to be attributable to sampling errors. There would appear to be some systematic environmental factor operating either to reduce the repeatability or increase the heritability. It has not been possible to make a satisfactory suggestion as to what form such an environmental factor might take.

In a short review on the inheritance of productivity and growth in pigs, Rendel (1950) has argued that, since most of the variation in sow characters is due to differences between litters of the same sow, a more accurate measure of a sow's potential is obtained from two or more litters. Berge (1934) has derived the following formula for calculating the heritability of a mean of repeated records

(h_n^2) :-

$$h_n^2 = \frac{nh^2}{1+(n-1)r}$$

where r represents the repeatability and n the number of records. For example, if the heritability of litter size is 0.10 and the repeatability 0.15 then the heritabilities of the mean of two and three litters are 0.17 and 0.23, respectively.

The above reasoning assumes that the heritability of litter size is the same for different parities. That may not be so with the data used in this study. There is a suggestion that the heritability of a trait is higher when expressed in a first litter than when expressed in a second litter. Legault (1967) who calculated the heritabilities of four litter performance traits, separately for

parities one to five, also obtained lower heritability estimates for the second litter. The results obtained by Korkman (1947), who also calculated the heritabilities of a number of litter performance traits for different parities, were quite the opposite; he concluded that the heritabilities of the traits tended to be somewhat higher in the second litter.

The estimates obtained for the heritability of a sow's mean performance after different numbers of litters suggest that little is to be gained in practice from selecting on the basis of the mean of several records. The heritability estimates of the mean performance of the first two litters or the first three litters are not appreciably greater than for the first litter alone. The heritability estimates for mean performance after four or five litters are not of much practical consequence as an animal's genetic merit has to be assessed long before it has had five litters.

In the past sufficient data has not been available to facilitate the calculation of the heritability of litter performance traits in British pigs. The results obtained are the only reliable estimates available of the heritability of litter productivity in a British breed of pigs. The magnitude of the estimates and their standard errors makes it quite clear that the heritability of litter productivity traits in the Large White breed is extremely low.

The heritability of a character determines the rate of improvement which can be achieved in the character by selection. To obtain some idea of the rate at which litter size can be improved, let us consider an ideal

situation where a farmer establishes a nucleus of say twenty females within his herd and selects solely on the basis of the number of pigs born alive. The females have only one litter before moving out of the nucleus into the general herd and so the generation interval is one year. The replacement females are the daughters of the best third of the gilts in the previous generation. To avoid rapid inbreeding the boars were obtained from outside the nucleus and are thus not subjected to selection for litter size.

If a character is assumed to have a normal distribution then knowing the proportion of the animals selected as parents and the standard deviation of the character, it is possible to calculate the average superiority of the selected animals or the selection differential (Falconer 1961). As no selection is being practised on the male side, the selection differential is reduced by half. The rate of improvement per generation, or per year in this case, is calculated below.

$$\begin{aligned} \text{Rate of improvement} &= \text{Selection differential} \times \text{heritability} \\ &= 1.54 \times 0.07 \\ &= 0.11 \text{ pigs per generation.} \end{aligned}$$

Thus even with the fairly ideal set up described above ten years of selection will be required to increase litter size at birth by one pig.

The estimates obtained for the genetic correlation coefficients between the characters are similar to the values obtained for the corresponding phenotypic correlation coefficients. The high positive genetic correlations obtained between litter size and litter weight are in agreement

with the results obtained by Legault (1967). The genetic correlation between litter size and average pig weight at three weeks would appear to be small and positive but that between litter size and average pig weight at eight weeks is decisively negative.

The finding that the average pig weights at three and eight weeks are influenced by the sire of the litter is not surprising. The growth rates of the pigs, even at this early stage, are, apparently, influenced to some extent by the genes they have received from their sire. The results indicate quite definitely that the sire of the litter has no influence on litter size at three or eight weeks of age. The suggestion that the sire may have an effect on the number of pigs born alive is not of much practical importance, since if the effect does exist, it is extremely small and is lost before weaning.

The importance which pedigree breeders attach to information on litter size when buying or selling breeding stock is well known. It is thus not surprising to find that sows which survive to have later litters have on average produced larger litters than their contemporaries. What is perhaps surprising is to find that culling decisions are influenced by considerations of litter size to only a limited extent.

If, for example, we take litter size at three weeks, we find that, although 29% of the animals were culled after their first litter, the mean performance of the survivors in their first litter was only 0.1 pigs greater than the overall first litter mean. It was calculated that if culling had

been on the basis of litter size at three weeks only, then the culling differential would have been 1.0 pigs. It is obvious that many of the animals were culled for reasons other than litter size.

The low repeatability of litter performance traits raises the question of whether culling on the basis of litter size is justified. The effect of culling for litter size at three weeks was considered for five different culling schemes. Knowing the proportion of animals selected to have another litter and the standard deviation of the trait, the culling differential (s) was calculated, as described by Falconer (1961). The improvement in mean performance (I) obtained in the next litter order as a result of culling is given by the formula:

$$I = s \times r,$$

where r is the repeatability of the trait. When culling is based on the mean of a number of records (r), Lush (1945) has shown that the appropriate formula is:

$$I = s \times \sqrt{\frac{n}{1+(n-1)r}} \quad + \quad +$$

When culling is based on the mean of several records the accuracy of culling is increased. The culling differential on the other hand is reduced since the variation between the means is less than between the individual records.

In order to calculate the effect of the five different culling schemes on herd performance, the following assumptions were made:

1. The herd size was maintained at 100 sows and all female replacements were gilts.
2. Sows which had farrowed five litters were automatically discarded.
3. The proportions of animals which had to be culled for reasons other than poor performance were 10%, 15%, 20% and 25% after the first, second, third and fourth litters, respectively.
4. The relationship between parity and litter size at three weeks was assumed to be the same as that in Table 6 on page 42.
5. Litter size at three weeks was taken to have a standard deviation of 2.4 and a repeatability of 0.14.

The overall mean litter size at three weeks which would prevail in the herd under each of the five culling regimes was calculated and compared with that which would prevail in the absence of any voluntary culling. The descriptions of the culling schemes and the respective herd mean performances are given in the table on the next page. The herd means have been expressed as deviations from the uncultured herd mean.

It can be seen that the improvement in herd mean performance is extremely small for all of the culling schemes. There are two reasons why the increase is small: firstly, the repeatability of litter size is low, and secondly, since gilt litters are smaller than sow litters, the increased proportion of gilt replacements required at higher culling levels depresses the herd mean performance. The net cost of providing

additional gilt replacements must be set against this small increase. It can be concluded that culling on the basis of litter size is not to be recommended.

CULLING SCHEME	Herd mean litter size at three wks. minus uncullled herd mean
30% culled after the first litter	0.05
30% culled after the second litter on the basis of their mean performance in the first two litters	0.03
30% culled after the first litter, 30% culled after the second litter on the basis of their second litter performance	0.06
50% culled after the first litter	0.04
50% culled after the second litter on the basis of their mean performance in the first two litters	0.01

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