A SIRE-LINE OF PIGS.

by

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A thesis presented to the University of Edinburgh for
the degree of Doctor of Philosophy.

November 1973.

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SUMMARY

The aim of this study was to provide an evaluation of a specialised sire-line of pigs developed at the Animal Breeding Research Organisation (A.B.R.O.), Edinburgh.

The A.B.R.O. sire-line was developed in 1959 from a cross of 4 breeds with the intention of producing a strain of pigs with exceptional qualities of lean meat production to act as the sires of pigs destined for slaughter. In subsequent years the line was thrown open to stock from any source thought to offer further improvement, ignoring breeds. Potential immigrants to the line were mated to native sire-line animals and their progeny allowed to compete for selection in the normal way. In 1966 selection for X-ray predicted body length and average ultrasonic backfat was superseded by selection on an index combining growth rate, food conversion ratio and backfat. No attention was paid to reproductive performance.

By 1971 the line was little more than 5% inbred and contained genes from 9 pure breeds and 1 commercial hybrid, 70% of the genes being contributed by the Large White and British and Norwegian Landrace breeds. Population size averaged 30 gilts and 8 boars, approximately one third of matings involving immigrants. With the exception of teat number there was no consistent decline in reproductive performance over the first 12 generations.

After a strong initial phenotypic decline in backfat, the apparent response to selection on the index was rather poor. In addition the central testing station performance of the line was only slightly better than that of Large Whites. Possible causes of a diminished selection response could have been a lack of additive genetic variation, inconsistencies in the performance testing procedure or alternatively a high incidence of incorrect selection decisions on immigrants. These three eventualities were investigated in more detail.

Estimated heritabilities of growth rate on test and average backfat in the sire-line were respectively 0.26± 0.13 and 0.63 ± 0.13 from a half-sib analysis, and 0.65 ± 0.11 and 0.30 ± 0.09 by daughter-dam regression. It was therefore concluded that additive genetic variation was unlikely to have been a barrier to selection, or to have increased in a measurable amount as a result of continued hybridisation.

An examination of the performance testing procedure and selection index indicated that under past conditions genetic progress could have been expected in a closed population of the same size as the A.B.R.O. sire-line. In a small trial in 1972 the repeatability of average ultrasonic backfat in the live pig was estimated as 0.92, and the correlation between the averages of live ultrasonic and corresponding carcass introscope fat depths was 0.72. Genotype by boar performance test environment interactions among immigrants and natives were tentatively ruled out. Addition of half-sib family averages to the current selection index increased its efficiency by only 3%.

It was shown that the selection of potential immigrants by performance testing their F_1 sire-line cross progeny alongside natives was biased, firstly as a result of ignoring genetic differences between native and immigrant populations, and secondly as a consequence of heterosis in the crossbred immigrant progeny. An expression was derived for the total bias which demonstrated that, in the presence of favourable heterosis, the net bias would be greater when the immigrants were worse on average than the natives. Between 1965 and 1970 there was evidence that the mean performance of all potential immigrants to the sire-line lagged behind that of natives, so that a high proportion of erroneous selection decisions could have resulted. For relatively large samples of immigrants the bias could be removed in future generations by making adjustments for the estimated mean difference between native and immigrant subpopulations, and for heterosis which could be estimated experimentally.

It was concluded that the "open synthetic" approach to pig improvement, employed in the A.B.R.O. sire-line, would be hard to justify and difficult to put into practice. In the future it was recommended that potential immigrant populations should be tried at the rate of one per generation in the sire-line, and it was suggested that genetic progress might be monitored through an unselected control line.

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ACKNOWLEDGEMENTS

Thanks are principally due to Dr. J.W.B. King for placing records on the A.B.R.O. pig sire-line at the disposal of the author, for suggesting areas of interest, and for considerable guidance and encouragement throughout.

The author is also particularly indebted to the following: Dr. W.G. Hill, Institute of Animal Genetics, who gave much helpful advice and read the manuscript; Mr. R. Thompson, A.R.C. Unit of Statistics, who wrote the computer programme for the hierarchical analysis of variance and advised on the design and analysis of the heterosis experiment; Mr. D.T. Wilson, who provided general statistical advice and assisted with the writing of the computer programme for offspring-parent regression; and Miss H. Maclean, who assisted with data preparation and calculation of inbreeding coefficients.

The managers of A.B.R.O.'s two pig farms, Mr. I. Will and Mr. A.T. Faulkner, and their staffs provided invaluable co-operation on matters of experimental design and data recovery. Carcass introscope measurements were obtained with the kind permission and co-operation of Mr. D. Lockie at Gorgie slaughterhouse, Edinburgh.

The author wishes to record special thanks to his wife, for assistance with the drawing of graphs, for reading the manuscript and for providing an endless source of encouragement.

The work was carried out while in receipt of a post-graduate studentship from the Ministry of Agriculture,

Fisheries and Food. Permission for the use of A.B.R.O. facilities was granted by Professor H.P. Donald.

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Chapter 1. General Introduction

In the past decade pig producers have come under increasing economic pressure to step-up their efficiency. Rising feed and labour costs have encouraged the rapid adoption of new production techniques which in turn have favoured the larger enterprise. Between 1960 and 1968 there was a 40% reduction in the number of holdings with pigs in England and Wales, and during this time the average herd size more than doubled (Ridgeon and Sturrock, 1969). Against this tightening economic background has come the realisation that genetic potential for improving efficiency has not been fully exploited.

Two of the main factors through which genetic improvement may affect profitability are sow productivity and food conversion rate. These two traits influence different stages of the production cycle and, because sow productivity is largely a maternal quality whereas food conversion is a quality of the offspring, they are each open to genetic improvement by different methods. Following the lead of the poultry industry this distinction has led to the concept of specialised lines of stock to act as the sires and dams of market pigs (Smith, 1964).

Adopting the unusual strategy of completely ignoring breed barriers a specialised "sire-line" of pigs has been developed by Dr. J.W.B. King at the Animal Breeding Research Organisation (A.B.R.O.), Edinburgh, and forms the basis of this study.

Chapter 2. Review of Literature

2.1 Methods of Genetic Improvement in Pigs.

From the point of view of the animal breeder traits of economic importance in pig production fall into two categories: traits of medium to high heritability that may be changed by selection, and traits of low heritability that may not easily be changed by selection. Table 2.1, abridged from Fredeen (1971), illustrates heritabilities for 8 important characters

Table 2.1

Heritability Estimates (%) for Important Performance Traits (abridged from Fredeen, 1971).

Trait	median value	range
Litter size at weaning	7	0 - 25
Average weaning weight	8	5 - 15
Daily gain post-weaning	30	6 - 50
Food conversion ratio	30	10 - 60
Average backfat	50	20 - 70
Carcass length	55	20 - 90
Loin eye area	45	20 - 80
Lean meat yield (%)	45	14 - 76

and shows that moderate heritabilities are generally associated with growth and carcass composition, while low heritabilities are associated with reproduction and viability. Traits of low heritability will respond slowly to selection and probably involve some form of progeny testing, so that improvement may be more easily obtained through controlled heterozygosity (Donald, 1955).

Crossbreeding experiments with a variety of breeds in different countries have yielded consistent evidence for useful levels of heterosis in pre-weaning and growth characters (e.g. Fredeen, 1957; Smith and King, 1964; Skarman, 1965). Some average levels are shown in Table 2.2, reproduced from Sellier (1970) who has reviewed published estimates. It

Table 2.2

Heterosis For Characters of Economic Importance In The Pig: Observed Mean Values In Crossing Experiments Between Non-Inbred Pure Breeds. Mid-Parent value = 100.(From Sellier, 1970).

Characters	Single Cross (Pure bred dam)	3-Way Cross* (Crossbred dam)
Maternal Performance		
No pigs born alive	102	108
Proportion of pigs weaned	106	108
No pigs weaned	108	116
Litter weight at birth	104	110
Litter weight at weaning	115	125
Offspring Performance		
Individual weight at weaning	106	107
Daily gain post-weaning	106	106
Individual weight at 154 days	110	110
Food conversion ratio	103	103
Proportion of lean in carcass	100	100

* relatively few trials involved

can be seen that heterosis is expressed both in offspring and maternal genotypes.

There are thus two methods by which genetic improvement may readily be brought about in pigs. The first, selection, utilises additive genetic variation and may be used to effect permanent and cumulative changes in traits of moderate heritability. The second, heterosis, makes use of non-additive genetic variation in traits of low heritability and must be regenerated by repeated crossing in each new generation. The task before the animal breeder is to design a breeding programme which will bring one or both methods to bear in such a way as to give the maximum financial advantage.

Choice of the optimum breeding system will usually begin with a survey of the available breeds and strains. Their number and relative performance levels will largely determine the type of system adopted. It may entail selection within one breed or strain, or within a so-called 'synthetic' derived from a crossbred foundation and subsequently maintained 'pure', or alternatively it may involve some form of crossbreeding accompanied by selection within the parent breeds. Unless one breed is particularly superior in terms of production capactity, some form of cross-breeding will be profitable (Jakubec and Fewson, 1970 a), Considering the case for a 'synthetic' Hill (1970) concluded that while this method may have the long-term advantage of a higher selection limit, it may take years to surpass the best pure breed and is therefore unlikely to be cost effective. For these reasons it seems very likely that the optimum breeding plan for pigs will include systematic cross-breeding. As well as heterosis this would provide an opportunity to combine the desirable attributes of two or more breeds in the end-product.

Smith (1966) indicated that the advantage of heterosis in maternal and offspring genotypes would only be realised from a 'three-way' cross of a purebred sire on a crossbred dam, but the total heterosis from a back-cross to one of the dam breeds is expected to be only slightly lower (e.g. Hill, 1971). Smith pointed out that 'continuous', or 'rotational', back-crossing of hybrid females to two or more pure sire breeds might also yield a relatively large proportion of possible F_1 heterosis, 93% for a 4-breed system, but would be difficult to organise in small herds where the breed composition of individual sows might differ. On the other hand the advantage of a 'rotational' system is that dams would be replaced cheaply from the progeny of the previous generation, whereas in other 'non-continuous' systems a fresh supply of crossbred females would be required for each new generation.

The opportunity for subsequent improvement within a particular crossing programme will influence the choice of system adopted. Reviewing work with laboratory animals Roberts (1965) concluded that complex schemes aimed at selection for combining ability, such as the crossing of inbred lines or reciprocal recurrent selection, should be avoided in favour of methods of utilising additive genetic variation, which are relatively uncomplicated by genetic or environmental interactions. For example, the cost of an inbred line-crossing programme would be excessive as a result of inbreeding depression, and further improvement by within-line selection would become increasingly difficult (King,1966). In pigs reciprocal recurrent selection would have little to offer while the genetic correlation between purebred and crossbred performance is high and while there is sufficient additive variation in growth and carcass characters (Standal, 1968). Smith (1966) indicated that the easiest means of improvement within a crossing programme would be to select within the best pure breeds, when crossbred performance would approximate the average of 'parental' breeds. This would allow selection for different objectives within the various 'pure' parental breeds, except in the case of 'rotational' forms of crossing where each breed contributes both as a dam and as a sire.

Robertson (1971) suggested four factors which might govern decisions regarding the suitability of a crossing programme. The first two are the extent of heterosis in offspring and maternal performance. As already seen (Table 2.2), there is considerable heterosis in litter productivity, a point of some importance in pigs since extra progeny reared serve to 'spread' the maintenance costs of the parental stock. A third factor to be taken into account is the proportion of the total cost incurred by each offspring before becoming independent of its parents. Due to the relatively high reproductive rate of pigs, the extra parental stock required for crossbreeding will be less than in other livestock species, and the pre-weaning cost per pig reared will not be greatly increased. The final factor affecting the decision on a crossing programme is the genetic incompatibility between offspring and parental performance. For example, if maternal and offspring performance were negatively correlated there might be an advantage in a 'non-continuous' crossing scheme with distinct sire and dam lines (Smith, 1964). The case for separate parental lines will be discussed shortly.

2.2 The British Pig Industry.

At present the British pig industry is dominated by the Large White and Landrace whose overall performance exceeds that of other pure breeds. Litter productivity of the F_1 "white cross" exceeds the better parent, and further advantage may be gained from using the crossbred dam in a back-cross or 'three-way' cross (King and Smith, 1964). In order to fully exploit heterosis a three-breed cross of the form C x (A x B) would be required (Bichard and Smith, 1971), but with existing British breeds there is a danger that the introduction of a third inferior breed might lower, rather than increase, the overall merit of the cross in spite of the additional heterosis, through a reduction in carcass quality.

The present bacon grading system, based principally on backfat measurements, would therefore favour a 'third' breed which, as well as maximising heterosis, would improve the carcass leanness of pigs destined for slaughter. As a result there has been much interest in newly imported breeds such as the Lacombe, Hampshire and Pietrain (King, 1966a).

Pig breeding in the U.K. has traditionally been organised on a three-tier pyramidal structure (Bichard, 1971) in which pigs for slaughter are born on 'commercial' units from parents produced in 'multiplier' herds, who in turn purchase breeding stock from a select group of 'nucleus' herds. This structure particularly favours the three-breed cross since crossbred females of type (A x B) may be produced in the 'multiplier' herds from highly selected pure-breds obtained from the 'nucleus' herds. The crossbred females are then sold to 'commercial' farms as replacement breeding stock. Boars of type C may come direct from the 'nucleus', from the 'multiplier' or by artificial insemination.

At the same time the pyramidal structure aids overall genetic improvement, because any advance made in the relatively managable 'nucleus' will eventually be passed downwards to the other 'layers', which although lagging behind will improve at the same rate (Smith, 1959; Bichard, 1971). In 1966 the Meat and Livestock Commission, then the Pig Industry Development Authority (P.I.D.A.), introduced a scheme for genetic improvement based on central performance testing in the 'nucleus' herds, from which estimates of genetic progress have been positive (Cook, Smith and Steane, 1971). The market for hybrid female replacements coupled with the demise of old-style "pedigree" breeding has prompted the formation of over twenty private breeding companies, some of which are of sufficient size to provide their own performance testing facilities.

2.3 The case for Specialised Sire and Dam Lines.

Sire and dam lines are simply terms given to the different breeds or strains acting as the parents of pigs for slaughter, which are the end-product of a crossbreeding programme. Traits affecting the profitability of meat production may be divided into those concerned with 'reproduction' in the dam and those affecting 'production' in the offspring. 'Reproduction' infers an aggregate of characters determining the number and weight of pigs weaned, and 'production' here refers to the growth and carcass characteristics of market animals. In the past some producers have chosen sire and dam lines on the basis of their productive or reproductive ability alone, hoping to capitalise on a certain specialisation of function.

Smith (1964) algebraically compared rates of improvement obtained by selecting either for overall performance in a single line or for different objectives in sire and dam lines, for a number of different selection schemes with a range of genetic and economic parameters. The major finding was that selection in specialised sire and dam lines is always at least as efficient as selection within a single line, but may well be more so under certain conditions. In addition, 'reproduction' may conveniently be ignored in the sire line, whereas if 'production' is neglected in the dam line efficiency may fall below that of a single line. Smith showed that the circumstances which favoured a higher rate of gain from the use of sire and dam lines were, firstly, a low or negative genetic correlation between 'production' and 'reproduction' and, secondly, a balance between the economic improvements that could be made in the two traits whereby their economic selection responses are roughly equal. Because of the low heritability of 'reproduction' and the nature of the economic weightings Smith concluded that specialised sire and dam lines in pigs could only be expected to give a marginal improvement in efficiency over selection within a single line. Only if an unfavourable genetic correlation is demonstrated between reproductive performance and growth and carcass characters would the rate of improvement be usefully increased. From these observations it would appear that creation of new specialised lines would not be worthwhile, and selection in existing ones would only serve to maintain the status quo.

Smith's approach was later extended by Moav who took into account changes in profitability (Moav, 1966; 1966a; 1966b; Moav and Hill, 1966). Moav expressed profit (P) as a function of 'productivity' (y) and 'reproductivity' (x), so that assuming genetic additivity an equation of the following form was obtained:

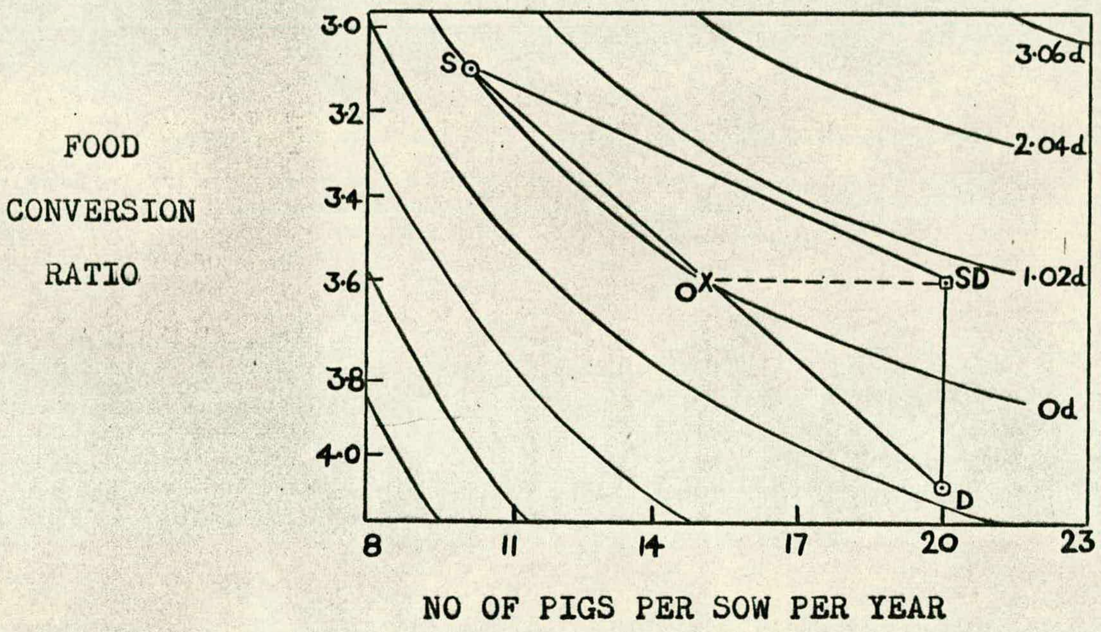
$$P = C - Gy - N/x \quad ,$$

where C, G and N are appropriate economic constants. In pigs, for example, y might represent food conversion ratio (lbs. feed/lb gain) and x might represent the number of marketable pigs per sow per year. By rearranging the equation y may be expressed as a function of x, which can then be plotted on a graph for a given value of P and referred to as a 'profit contour' as shown in Figure 2.1, taken directly from Moav (1966). On the diagram S denotes the sire line, with the best 'productivity' and D signifies the dam line, while SD is the profitability of the progeny when used as slaughter animals. It is clear that the combination of the two lines is more profitable than either one on its own.

Moav defined the deviation of the SD profitability from

Figure 2.1

Profit diagram for heavy pigs (250 lb.) (From Moav, 1966).



$$P = C-3.4y - \frac{52}{x} .$$

(Profit is expressed in pence per lb. live-weight, C is chosen arbitrarily, y = food conversion ratio, x = number of offspring per sow per year).

the arithmetic mean of the two parents as "profit heterosis" which may stem from five different classes of 'heterosis'. The first, heterosis in the component traits, would arise through non-additive gene action. For example both traits in Figure 2.1 would be expected to show heterosis, in which case their values on the graph would be slightly increased so that the SD point would move in the direction of higher profit . The second and third classes are sex-linkage and maternal effects, which might mean for example that the cross B x A would be more profitable than its reciprocal A x B. The fourth class, "non-linearity heterosis", results from the curvilinear nature of the profit equation on a scale which is genetically additive. This means that the change in profit per unit change in a component trait may not be the same for all values of the trait, and probably that the extra profit from successive improvements may be expected to decline. The fifth factor, "sire-dam heterosis", may contribute to profit in the absence of "component-trait" and "non-linearity" varities, and arises simply from the diversity of function of the two lines. Moav regarded this final point as a major justification for cross-breeding even when there is no "component-trait" heterosis.

Using profit equations Moav and Hill (1966) compared the efficiency of selecting sire and dam lines on specialised indices with the efficiency of selecting males and females within a single line, either on the same or different indices, over five generations. Their conclusion supported that of Smith (1964) in finding that separate lines were theoretically the most efficient means of improvement. They also pointed out that in single lines or dam lines where 'reproductivity' is already high, selection on food conversion alone is nearly as efficient as selection on the optimum index.

Before attempting to make practical decisions on the basis of these theoretical studies it is important to point out their inherent assumptions and limitations. Of the two characters considered, 'reproduction' was fairly adequately summarised by the number of pigs per sow per year, whereas 'production' was only partly represented by food conversion since carcass traits were ignored. The same selection indices were applied to both males and females within a line, which were selected with equal intensity and had the same generation interval. Heterosis was omitted from the calculations.

Moav and Hill's (1966) approach demonstrates that, when starting from a single base population, the advantage of separate sire and dam lines depends on a response to selection for reproductive rate in the dam line, which may be hard to achieve in practice. It is likely that suitable pure or cross-bred "dam lines" may already be available with adequate reproductive performance so that substantial overall improvement could be obtained by selection for 'production' alone in both lines. The utilisation of existing breeds or crosses as sire or dam "lines" would allow any negative genetic correlation between the two groups of traits which may exist between breeds to be exploited. The effect of type of production, pork, cutter, bacon or heavy, on the suitability of separate lines was not considered.

The general conclusion is therefore that no attention need be paid to 'reproduction' in producing a line of pigs to act as the sires of animals destined for market.

Attention should be paid to 'production' in the dams of slaughter pigs, whose 'reproduction' should be maximised by selection between breeds and exploitation of heterosis. In Britain the Large White x Landrace cross, while exhibiting heterosis in 'reproduction', suffers no set-back in growth or carcass quality in which the two breeds are very similar (e.g. Bichard and Smith, 1971) and is therefore especially suited to be the dam of commercial pigs. There is clearly a place for a sire-line which would further enhance the growth and carcass merit of the final progeny.

2.4 Development of Specialised Lines.

There are three distinct alternatives for the development of sire or dam lines. The first is to select among current breeds for the best parental lines, and to discard the remainder. The second is to maintain a series of specialised lines selected either for the same or differing objectives. The third alternative is that all promising genetic material be included in a single 'synthetic' sire or dam line. The advantages of these procedures will now be considered more fully.

2.4.1 Selection of Best Existing Breeds or Lines.

The greatest initial benefits from the use of specialised sire and dam lines would come from the correct choice of parental strains. Although maintenance of the best current strains would maximise present gains, it may be disadvantageous in the long run because there would be no possibility of responding to changes in market requirements and management techniques (Hill, 1970). With Moav's (1966a,b) graphical procedure for the rational choice of suitable parental lines, candidates are simply manipulated so that the performance of the sire-dam combination is moved in the direction of higher profit (see Figure 2.1). Crossbred sire or dam lines could then add to profitability through improved parental performance.

While a '4-way' cross offers maximum heterosis, the increase in male reproductive performance would have to be dramatic to justify the extra maintenance costs of a fourth pure breed (Bichard and Smith, 1971). In seeking to further reduce the number of 'pure' populations, Bichard and Smith pointed out that sire-breed C in their C x (A x B) scheme could not be dispensed with because of the negative correlation between meat production and reproductive performance between breeds. Nor could (A x B) be replaced by a single dam breed without loss of heterosis, but the dam line could be maintained as a rotational cross of the form (A x B) x A) x B) x A) x........(Robertson, 1971). The use of best current breeds as sire or dam lines would be the most straightforward method, and may involve only a slight modification of existing crossing systems.

2.4.2 Retention of Alternative Lines.

Changes in consumer demand could be catered for by maintaining a number of alternative sire or dam lines, and substituting them where necessary. The disadvantage of this course is that facilities for selection would have to be provided for each of the spare lines, which would be of less value if allowed to lag behind. If testing facilities were limited, this could result in an overall reduction of selection intensity, and it is unlikely that many British commercial pig breeding operations are of sufficient size to tolerate expenses on this scale.

Watson (1968) indicated that the type of specialisation suggested by Smith and Moav, involving 'production' and 'reproduction', may be less important than other types of specialisation separating, for example, food conversion and lean percentage. In addition, Fredeen (1971) drew attention to evidence from several sources of an inverse genetic relationship between meat quality and quantity. Assuming a case exists, it is difficult to see how specialisation among growth and carcass characters could be organised within the present framework. Diversity of selection objectives between the two breeds used to produce crossbred dams would confer only $\frac{1}{4}$ of any improvement on the final progeny. Introduction of further sire breeds for production of crossbred sire lines has already been excluded on the grounds of cost.

2.4.3 Formation of Synthetic Lines.

The creation of a specialised synthetic line from an initial cross of two or more breeds would avoid the necessity of maintaining the 'pure' parental stock required for simple crossbreeding systems. The population could then either be maintained 'closed', meaning that like a breed it is kept pure, or 'open' in which case new genes would be admitted at any time. Discussion will be confined to the development of a synthetic sire line.

Closed Synthetic Lines.

The aim of setting up a synthetic sire line would principally be to combine the desirable attributes of a number of existing breeds or lines (Winters, Comstock and Dailey, 1943) in the hope of obtaining individuals superior for all the required traits by fortuitous recombination. Theoretically, it is intended to adjust the gene frequencies in the population to the desired levels at a faster rate than is possible by selection in the best existing population Success in this respect would depend on the gene frequency differences between breeds relative to the changes possible by selection (e.g. Willham, 1970). James (1966), comparing selection from one or several foundation flocks in sheep, found that for a single trait selection within many flocks gave the greater gain only when the genetic variation between populations was small. The conclusion may be tentatively applied to "multi-breed" foundations, but James warned that unless the best single population is quickly surpassed by the new 'hybrid', the crossbred foundation would be unjustified.

A synthetic may show greater genetic variation, and therefore greater selection response, than the mean of the pure breeds from which it was constituted. Assuming additive gene action and ignoring linkage and epistasis, the genetic variance in the synthetic is expected to be at least as high as the average of parental lines (Hill, 1970). At loci showing complete dominance the additive variance is only higher in the synthetic when the mean frequency of the recessive allele is greater than about 0.5. Hill concluded that averaged over all loci the synthetic would probably have a higher variance. James (1971) discussed the effect of linkage on the genetic variance in a mixed population. If the gene frequencies at loci affecting a particular trait are positively correlated, recombination after the F_1 would gradually erode the correlation and genetic variance would decline. Conversely if the gene frequencies were negatively correlated, the variance would increase with time. James' view is that the average correlation is positive since animal populations have been selected in different directions or in the same direction with widely different intensities. Intense selection immediately after synthetic formation would then tend to pick out blocks of genes from the best population and so reduce the chances of combining the best alleles from all populations. At the same time positive association between favourable alleles would raise their chances of fixation. Winters (1955) suggested that selection be postponed in order to allow recombination to take place, but this met with little success in Drosophila (Osman and Robertson, 1968).

As well as a faster response the synthetic may have a higher selection limit than the average of its foundation breeds (Hill, 1970). Osman and Robertson (1968) demonstrated that the introduction of inferior genetic material may be of some benefit as a means of increasing both the variance and selection limit in a highly selected strain. On the other hand, synthetic populations of Drosophila yielded no greater rates of genetic gain or selection limits than their parental lines, which suggests that observed differences between parental stocks are the result of differences in gene frequency rather than the presence or absence of particular alleles (Lopez - Fanjul, 1972). Even if livestock breeds differ only in gene frequency Comstock (1960) pointed out that a synthetic might shift the gene frequency to a new and possibly higher "adaptive peak". Hill warned that extrapolation from laboratory species may be dangerous since there is no similar history of purposeful selection.

Any heterosis in the initial stages of the development of a synthetic line may help to lower reproduction costs. The "selection and multiplication overhead" (Bichard, 1971) of a closed synthetic sire line would be the same as for a pure-bred sire line, and the selection intensity would be no less. However, there may be a case for having a larger synthetic population than would otherwise be necessary in order, firstly, to increase the probability of favourable gene combinations and, secondly, to avoid inbreeding since no 'outside' synthetic animals can be brought in as is the case with a pure breed (Sumption, Rempel and Winters, 1961).

The development of synthetic pig populations from a crossbred foundation is not a new idea. In the 1940's and '50's a large number of new 'breeds' were developed in the U.S.A. and Canada, and many were based on the newly acquired Danish Landrace as shown in Table 2.3. Genetic parameter estimates from the new breeds are unfortunately scarce, but would be of doubtful validity due to varying amounts of inbreeding. In any case Hill (1970) indicated that estimated heritability differences between synthetic and pure populations would suffer from low precision and be expensive to obtain. In the mildly inbred Minnesota No 3 heritabilities of growth rate and litter size were similar and slightly higher respectively than in less heterozygous populations (Rempel and El-Issawi, 1959; Sumption, Rempel and Winters, 1961).

Table 2.3

New Pig 'Breeds'

'Breed' Name	Breed Contribution (%)		Author
Minnesota No 1	Danish Landrace	48	
	Tamworth	52	Zeller (1952)
Minnesota No 2	Yorkshire	40	
	Poland China	60	Zeller (1952)
Minnesota No 3	Gloucester Old Spot	31	
	Poland China	21	
	Welsh	13	
	Large White	12	
	Beltsville No 2	6	
	Minnesota No 1	6	
	Minnesota No 2	5	
	San Pierre	5	Mason (1969)
Montana No 1	Danish Landrace	55	
	Hampshire	45	Zeller (1952)
Beltsville No 1	Danish Landrace	75	
	Poland China	25	Zeller (1952)
Beltsville No 2	Danish Yorkshire	58	
	Duroc	32	
	Danish Landrace	5	
	Hampshire	5	Zeller (1952)
Maryland No 1	Danish Landrace	62	
	Berkshire	38	Zeller (1952)
Palouse	Danish Landrace	67	
	Chester White	33	Fowler and Ensminger (1959)
Lacombe	Danish Landrace	57	
	Chester White	21	
	Berkshire	22	Fredeen and Stothart (1969)

Table 2.3 contd.

Managra	Swedish Landrace	45	
	Wessex Saddleback	20	
	Welsh	12	
	Berkshire	23	
	Minnesota No 1		
	Tamworth		
	Yorkshire		Stockhausen and Boylan (1966)
San Pierre	Danish Landrace	-	
	Chester White	-	Mason (1969)

There was no apparent increase in the heritability of backfat thickness in the Managra (Roy, Boylan and Seale, 1968) or in the "Red Line", a mixture of Minnesota No 1, Tamworth and Duroc (Berruecos, Dillard and Robison, 1970). On the other hand introduction of Guam stock into a slightly inbred, small line of pigs for medical research increased the heritability of 140-day weight from 0.21 to 0.41 (Dettmers, Rempel and Comstock, 1965). There was no evidence of increased genetic variation in the Romnelet sheep, developed from the Romney Marsh, Rambouillet, Targhee and Romeldale (Vesely and Slen, 1961).

Open Synthetic Lines.

It has not been the general practice to allow fresh immigration into synthetic pig populations after their formation. In a sire line this policy would permit superior genes to be incorporated at any time and would hopefully lead to greater economic merit.

Watson (1968) suggested two methods of utilising outstanding individuals thrown up by selection programmes in order that their superiority should not be wasted. The first would be to sample their genes for incorporation into a germ plasm bank or 'gene pool' and the second would be the formation of small inbred lines by close matings, followed by line-cross testing. Admission to a 'gene pool' would be on the basis of a progeny test in competition with animals already in the pool, ignoring breeds, and may have the advantage over inbreeding methods where reproductive losses may be high

(King, 1966). Considering how best small samples of imported breeds of particular merit in one or more aspects of production should be used, King (1966a) concluded that rather than be maintained pure these breeds hould be used as a source of germ plasm for incorporation into existing stocks. It would therefore be justifiable to keep a commercial sire line 'open' on the grounds that individuals of high merit from any source might provide a faster means of genetic improvement than selection in the closed population.

The suggestion has been made that such an 'open' synthetic line might act as a reservoir of genetic material as an insurance against future change in the industry (M.L.C. Scientific Study Group, 1970). Sumption (1963) indicated that the best way to guard against long-term changes in demand would be to preserve genetic variability in the form of separate unselected populations from breeds of low contemporary utility which are in danger of total elimination. On this assessment a highly selected specialised sire-line, developed from small samples of a number of breeds, would be of little value as a long-term reservoir of genetic variation since it would preserve only the genes suited to the management and market requirements of the day, and the very genes which would ensure against major changes in the future would be lost.

In Drosophila attempts to introduce genetic material into a synthetic from 'pure' laboratory populations were unsuccessful except in the case of one recently collected population, which probably contained "useful" variation absent in the others (Lopez - Fanjul, 1972). In pigs the introduction of new genes into a potentially closed synthetic would have the added advantage of reducing inbreeding and may boost reproductive performance through heterosis. A practical disadvantage of continual immigration would be the introduction of disease, but this might be overcome by the use of artificial insemination (Fredeen and Martin, 1967). A number of other practical questions are unanswered at present. Suppose, for example, that stock from breed B are to be introduced into synthetic line S. Decisions must then be made as to what proportion of the line should be given over to S x B matings, the merit of S animals mated to B immigrants and the rate at which B genes should be spread through the line.

2.5 Selection for Meat Production Within a Sire Line.

Fredeen (1971) divided the traits to be considered in a pig improvement scheme into four components: reproductive performance, physical soundness, carcass quality, and feed conversion and growth rate. As already discussed reproduction may be ignored in a sire line, and less emphasis meed be placed on physical soundness since the commercial 'cross' progeny will not be retained for breeding. All the selection pressure will therefore be placed on growth rate, food conversion ratio and carcass quality. The heritabilities of growth and carcass traits are sufficiently high to permit some form of performance or sib testing, and carcass quality may be assessed either indirectly from measurements taken on the live animal or directly from the carcasses of slaughtered sibs. For a given size of breeding herd Martin and Fredeen (1967) showed that a performance test in which backfat was measured in the live animal allowed greater selection advance than a sib test involving carcass measurements, because of the inherent reduction in population size resulting from loss of the sibs. The mechanical probing technique of Hazel and Kline (1953) and the ultrasonic probe are the most commonly used methods of measuring carcass quality in the live pig. Hazel and Kline (1959) showed a correlation of 0.900 for the average of three ultrasonic probe sites, two inches off the midline at the shoulder, mid-back and rear of the loin, with dissected lean percentage.

Estimates of genetic correlations between growth rate, food conversion and average backfat thickness have generally been favourable (e.g. Smith and Ross, 1965). The most efficient method of selection would be to combine the performance test traits on an index of overall merit (Young, 1961). The efficiencies of various indices have recently been compared for a situation where sib dissection data are available (Cunningham and Power, 1971). The boars' own backfat and food conversion contributed the most to economic gain, whereas part-dissection of two full-sibs contributed very little. Exclusion of all full-sib information from the index resulted in a 14% loss of efficiency, while exclusion of the half-sib data sacrificed only 4%. Deletion of food conversion from the optimum index reduced efficiency by 10%. Individual food conversion data are expensive and laborious to obtain, whereas growth rates are relatively simple. Fredeen (1971) concluded that food conversion would have a place in the selection programme only where it could be measured cheaply and accurately.

Although no attempt would be made to improve the reproductive performance of a sire-line, an adverse relationship between intense selection for meat production and litter productivity would clearly be a disadvantage. Hetzer and Miller (1970) found no indication of a consistent decline in reproductive fitness after 10 generations of selection for high and low backfat in Durocs and Yorkshires. However in the same lines Gerrits, Hetzer and Richardson (1969) showed that selection had altered either the secretory rate or the ability of the tissues to respond to somatotrophic hormone (STH). The longterm implications of physiological changes of this nature are not clear, but it is conceivable that they may be connected with an increasing incidence of various undesirable physical conditions such as leg weakness. Fredeen (1971) cited an instance where the pale, soft, exudative (PSE) syndrome of pig meat has defin~~a~~itely been associated with hormone deficiencies.

Primary control of the rate of genetic progress in a sire-line would be through the intensity of selection and the generation interval. In an 'open' synthetic line the introduction of superior stock from outside would be a means of maximising the selection differential. Choice of potential immigrant parents will be difficult if they have been measured in different herds, and, except in the case of small untested imports of exotic breeds, may therefore be limited to individuals which have been centrally tested. King and Smith (1968) described a method of evaluating candidate immigrants by performance testing their F_1 sire line cross progeny alongside animals already in the line. Two sources of bias may affect selection decisions on immigrants made in this way.

The first affects the estimation of an F_1 immigrant cross animal's breeding value. If the immigrant population mean differs from the synthetic population mean, as it very probably will, then the breeding value of F_1 individuals calculated from a deviation from the sire line mean will be incorrect Secondly, if there is genetic diversity between the two populations, heterosis may be expressed in the cross between then (Cress, 1966), so that a bias will result in favour of the F_1 immigrant progeny, particularly in the case of growth rate and food conversion (Table 2.2).

Chapter 3. The A.B.R.O. Sire-Line.

3.1 Selection History.

The A.B.R.O. sire-line was started in 1959 from a cross of Large White, Landrace, Wessex Saddleback and Tamworth in roughly equal proportions. It was designed to confer carcass length and leanness on the progeny of linecross sows which, although satisfactory in maternal performance, were rather short and fat. At first the carcass quality of the line was poor and it was therefore thrown open to stock of any breed offering further improvement. Potential immigrant animals of either sex were chosen on the basis of records taken either at A.B.R.O. or national testing stations, but measurements were not always available on the individuals themselves. Immigrants were mated to sire-line animals and their progeny, F_1 sire-line crosses, were allowed to compete for selection with native sire-line progeny. Over the years a variety of breeds, some imported and some themselves crossbred, have been successful in leaving progeny in the line. The percentage breed composition of the sire-line by years is shown in Table 3.1. The object has been to introduce animals of potential merit rather than simply to pool a range of diverse genotypes. Generation turnover has been at the rate of one per year.

For the first six generations selection was for length and backfat only. During this time the number of breeding animals in the line was approximately 30 gilts and 8 boars, with slightly more than a third of matings involving one immigrant parent. Table 3.2 shows the size of the breeding population, the proportion of immigrant litters and the

Table 3.1

Percentage Breed Composition of the A.B.R.O. Sire-Line Breeding Population by Years.

Breed	1960	1961	1962	1963	1964	1965	1966	1967	1968	1969	1970	1971	1972
Wessex Saddleback	26.0	26.3	20.8	19.5	10.5	11.4	5.6	3.5	2.9	2.4	2.2	2.1	2.0
Tamworth	27.0	20.3	13.8	9.9	7.4	6.6	4.7	3.0	2.4	2.1	1.9	1.7	1.7
Large White	24.0	26.3	29.2	35.7	42.8	36.4	40.6	40.5	42.6	35.7	34.6	29.8	37.2
British Landrace	23.0	27.1	36.2	34.9	33.1	32.0	25.1	22.8	20.1	24.1	22.9	22.4	20.4
Lacombe					3.1	3.4	4.0	2.6	4.9	4.4	1.6	1.7	1.6
Hampshire					3.1	5.7	6.0	6.5	7.7	5.2	4.5	4.3	3.8
Pietrain						4.5	14.0	15.9	9.7	14.6	11.4	9.8	9.4
Welsh								5.2	0.6	0	0	0	0
American Yorkshire									9.1	11.5	9.3	7.1	5.2
Norwegian Landrace											8.1	20.0	15.6
Commercial Hybrid											3.5	1.1	3.1

Table 3.2

Size of the Breeding Population, The Proportion of Immigrant Litters and the Numbers of Pigs Measured by Years in the A.B.R.O. Sire-Line.

Year	Generation No.	No. Parents Contributing Progeny		Proportion of Immigrant Litters		No. Progeny Measured for Selection	
		Sires	Dams (Litters)	Number	%	Boars	Gilts
1960	0	5	25	--	--	33	62
1961	1	10	29	15	52	39	73
1962	2	10	25	10	40	33	87
1963	3	7	17	7	41	38	63
1964	4	10	32	13	41	41	75
1965	5	8	20	7	35	35	65
1966	6	9	25	11	44	31	47
1967	7	12	29	17	59	58	88
1968	8	15	44	20	45	77	173
1969	9	11	37	9	24	76	109
1970	10	17	43	14	33	73	134
1971	11	17	44	8	18	120	141
1972	12	14	24	6	25	60	75

numbers of progeny measured in each generation. Until 1965 all male piglets were X-rayed at 7 - 10 days of age and the plates used to count the numbers of vertebrae and measure the length. Bacon Carcass length was predicted from a regression equation using X-ray data and piglet weights (King and Roberts, 1960). About 40 boars with the greatest body length and all the gilts were reared in paddocks, and at roughly 180lbs live weight they were measured ultrasonically for backfat thickness. Replacement breeding stock were those with least backfat, estimated as the average of six readings taken approximately 6.5 cms. off the mid-line at the shoulder, mid-back and loin corrected for live weight. Positive assortative mating was practised, but full- and half-sib matings were avoided. Because of immigration, inbreeding was maintained at a low level throughout the development of the line (Table, 3.3).

Published results for the initial 7 year period (King 1966; Smith, 1966) are shown in Table 3.4 and indicate that a moderate improvement in length was accompanied by a dramatic improvement in backfat thickness. In the absence of a control line it was impossible to tell how much of the change was genetic. Between 1960 and 1965 replacement breeding stock were raised on one of two feeding regimes; twice daily feeding to appetite or ad libitum, in order to compare their relative efficiencies for selection. Equal numbers of replacements were selected from each regime, with animals of like regime mated together. Their progeny were then pooled and the cycle re-started. The results have been analysed elsewhere but are as yet unpublished. The major finding appears to have been that, although there was a significant difference

Table 3.3

Average Inbreeding Coefficients of the A.B.R.O. Sire-Line Breeding Population by Years.

	1960	1961	1962	1963	1964	1965	1966	1967	1968	1969	1970	1971	1972
Average Inbreeding Coefficient %	0.50	2.28	2.63	2.64	4.29	5.46	3.61	3.30	2.45	3.21	4.22	5.10	4.21

Table 3.4

Year Means for Traits Under Selection in the A.B.R.O. Sire-Line. (From King, 1966).

Year	Estimated Carcass Length (mm.)	Average Backfat Thickness (mm.)
1959	797	30.4*
1960	804	29.4
1961	808	26.0
1962	809	23.0
1963	811	20.4
1964	812	19.7
1965	806	18.4

* measured by Lean-Meter instead of ultrasonics

in backfat thickness between ad libitum and restricted feeding neither regime produced a conclusively greater reduction in backfat from selection.

From 1966 selection for length was discontinued since it was considered adequate for current grading standards, and both males and females were performance tested on ad libitum feeding. In 1966 and 1967 all boars were tested singly in outdoor accommodation, between 1968 and 1970 they were tested outdoors either singly or in pairs, and in 1971 they were tested either outdoors singly or in pairs in separate indoor accommodation. From 1967 onwards gilts were tested indoors by litter groups. In any generation equal numbers of boars were selected from the different types of test environment. Selection was on an index combining individual growth rate, ultrasonic backfat thickness and group or individual food conversion ratio as available. The method of constructing the index is given in Appendix C. On completing performance test all pigs were preliminarily screened on a simple index consisting of backfat and food conversion added together. The policy of immigration continued so that in 1967 King and Smith (1968) reported contributions by the Lacombe, Hampshire and Pietrain. At this time, however, the gene content of the line was dominated by the two white breeds, and the contributions of the original Wessex and Tamworth had become very much reduced (Table 3.1). In the same year a sample of 20 hog-gilt pairs from the line were tested at P.I.D.A.'s Stirling testing station. Although the sire-line pigs grew slightly slower and had about the same food conversion as Large Whites, they were roughly 4 mm better in backfat at all sites measured (King and Smith, 1968).

The line has been continued in the same way, but with a slightly larger breeding population (Table 3.2), up until the time of writing. More recent immigrant successes have been the American Yorkshire and Norwegian Landrace, with further injections from high-pointed Large Whites at national A.I. centres.

3.2 Management.

All sire-line pigs were born and reared on one of the Animal Breeding Research Organisation's two pig farms: "Skedsbush" near Gifford, East Lothian and "Mountmarle" at Roslin, Midlothian. From its inception in 1959 until 1965 the line was confined to Skedsbush, but from 1966 onwards pigs were transferred postweaning to Mountmarle for performance testing. In 1968 and subsequent years a shortage of farrowing accommodation resulted in farrowings being split roughly half and half between the two farms. All farrowings producing piglets for the next generation took place in the summer months between late June and early September, and the objective of a 12 month generation interval meant that with few exceptions the line was bred entirely from first parity or gilt litters. It has therefore been possible to discount season of farrowing and parity effects as serious sources of variation between generations. A brief account of routine management procedures follows.

The breeding population of the sire-line has been maintained under fairly extensive, low cost conditions. Farrowing accommodation on both farms consisted of single wooden huts, each with farrowing rails, a covered creep area and an individual outside yard. The huts were sited in a clean grass field and moved up onto fresh ground once a week. Two weeks before farrowing gilts were washed, wormed, dressed for mange and installed in the huts. Immediately after farrowing, during which the sow was unrestrained and unattended, the piglets were ear-notched for identification. During lactation the dam was fed watered meal twice daily on a sliding scale according to the number of piglets, to a maximum of 2lb plus 1lb per piglet per day. Creep feed was introduced 14 days after farrowing. The compositions of the creep feed and the standard ration for breeding stock used throughout rearing, pregnancy and lactation are shown in Table 3.5 A little straw bedding was placed on the wooden floor of the hut, and both the dam and litter were permitted free use of the adjacent yard. No heating was supplied in the creep, and, although no iron injection was given, ferrous sulphate was added to the mother's diet and to a tray of earth which was placed in the creep. While farrowing conditions on the two farms were fairly well standardised, it is recognised that they may differ in ability of the stockmen and the spectrum of subclinical disease.

In the years following 1965 prospective breeding stock were chosen for performance testing after weighing at 50 days of age. They were nominated on the basis of live weight, and conformation. Boars from litters showing congenital abnormalities of possible genetic origin, such as splaylegs or hernias, were not tested and were thus excluded from the

Table 3.5

The Approximate Composition of Rations Fed to the A.B.R.O. Sire-Line.

Constituent %	Creep Feed	Breeding Stock*
Wheatings	40	50
Barley Meal	20	20
Oats	--	20
Flaked Maize	30	--
Fishmeal	10	10
Copper	--	++
Vitamins A and D	++	--
Energy (Mcals,M.E./kg D.M.)	3.16	2.85
Crude Protein (% fresh wt.)	17.2	17.8

++ included in ration as a proprietary supplement.

* The breeding stock ration was fed on performance test from 1966 until 1971, when a proprietary pelleted ration (McGregor and Co.,Leith) containing approximately 2.99 McalsM.E./kg. D.M. and 14.5% protein was introduced.

line. Numbers of boars and gilts tested from each litter were governed by the availability of testing space from year to year, and in general the heaviest, most well-matched representatives of each sex in the litter were selected. As a result there was a certain amount of pre-selection for weight at 50 days. Boars not required for testing were castrated and fattened to pork weight.

Pigs were weaned at 60 days of age by removal of the dam, at which time they were wormed and vaccinated against erysipelas. Before 1965, when the line was restricted to Skedsbush and selection based on length and backfat thickness, young pigs were transferred directly to paddocks at 74 days of age in groups of twenty boars and gilts. At this stage they were also vaccinated against swine fever with crystal violet vaccine. Each paddock was provided with a wooden hut containing straw bedding, and young pigs were fed the standard ration (Table 3.5) either ad libitum or to appetite on a scale rising to 3lb twice daily, as described earlier. After reaching 180lbs live weight they were measured ultrasonically for backfat thickness on which they were then selected and regrouped, the culls being sold for bacon at 200lbs live weight.

After 1965 pigs were transferred from Skedsbush to Mountmarle at 70 days of age for feed-recorded performance testing. Litter groups of up to 5 gilts, and pairs of boars in later years, were tested in a Danish-type fattening house. Pens in the house had no provision for individual feeding, and food conversion was therefore recorded on a full sib group basis. The temperature in the house was kept at roughly

60° F (15° C) by adjusting the ventilation and by the use of electric heaters. The majority of boars were tested either singly or in pairs in outdoor wooden huts equipped with separate runs. These huts were unheated, sited on grass and moved up regularly in the same way as the farrowing huts. They allowed the measurement of individual or full-sib pair food conversions. Straw bedding and unlimited drinking water were provided in both types of accommodation. Dry meal was fed ad libitum in order to create variability and give sufficient depth in ultrasonic backfat measurements. In 1971 the performance testing ration was changed over to a proprietory pelleted feed, rather than the home-mixed version. Testing took place during the winter months from October until March, and since the outside temperature frequently falls below freezing point at that time of year the two test locations were regarded as being quite different.

Weaners from both farms were sprayed with insecticide before being placed in testing pens at Mountmarle. Test recording was started at a pen average live weight of 60lbs so that the pigs had approximately one week in which to settle into their new quarters. After finishing test at 180lbs live weight the pigs were culled on the basis of their performance and then moved outdoors into paddocks in sex groups of 12. Once outside they were fed a slop consisting of 3lbs of meal (Table 3.5) and 6lbs of water per head twice daily from a communal trough, and this amount remained unchanged, throughout puberty, mating and pregnancy.

Maiden gilts were served at roughly 8 months of age. During the 6 week mating period, designed to allow a gilt to come on heat (oestrus) at least twice, one boar was placed in a small paddock with up to 6 gilts. At the end of 6 weeks the boars were removed and this resulted in a batch-farrowing spread over approximately 8 weeks. Where potential immigrant blood was introduced into the line by artificial insemination, as in the case of Large Whites, either a vasectomised boar was placed in the paddock or an entire sire-line boar was turned in at weekends. In 1967 10 litters were produced after oestrus synchronisation of their dams using "AImax" (I.C.I. Compound 33828 Methalibure.). Gilts were once again re-grouped into larger paddocks during pregnancy. As a rule boars and gilts were disposed of immediately after their first litters, unless required for re-mating in order to produce progeny groups for testing by the Meat and Livestock Commission.

3.3 Recording.

The following traits were recorded routinely for each individual pig in the sire-line since its creation in 1959:

(1) Number of Teats : scored at birth and confirmed at weaning,

(2) Birth Weight: weight of the newborn piglet up to twelve hours after birth, to the nearest ¼lb,

(3) 50-Day Weight: weight of the piglet at 50 days of age (approximately 10 days before weaning), to the nearest ¼lb,

(4) 150-Day Weight: weight of the piglet at 150 days of age (lbs).

Live weights at 50 and 150 days of age were subsequently combined to give growth rates over the intervening 100 day period. The presence of congenital abnormalities, such as hernias or atresia ani, was recorded.

The following measurements were taken on pigs competing for selection as parents of the next generation:

(1) Growth Rate on Test (lbs/day): individual liveweight gain from 60 to 180lbs liveweight; first measured in 1966,

(2) Food Conversion Ratio (lbs feed/lb liveweight gain): measured on a pen basis where boars were penned singly or in pairs, gilts in full-sib groups to a maximum of 5 per pen; first measured in 1966,

(3) Average Backfat Thickness (cms): predicted from 3 pairs of ultrasonic measurements taken 6.5 cms off the mid-line at the shoulder, mid-back and loin, and corrected to 180lbs liveweight by a linear regression of 0.01 cm of average backfat/lb liveweight. Prior to 1966 this measurement was the sole criterion for selection, after culling males on the basis of X-ray predicted length.

Reproductive performance in the sire-line was monitored through the following set of records for each dam farrowing:

(1) Number of piglets born alive,

(2) Total live birthweight of the litter; to the nearest ¼lb.,

(3) Average piglet live birthweight in the litter (lbs),

(4) Number of piglets alive at 50 days: includes piglets which have been fostered by the dam,

(5) Total liveweight of the litter at 50 days (lbs),

(6) Average piglet liveweight in the litter at 50 days (lbs).

For the purpose of this study all available data for the years 1960 to 1971 inclusive were collected together and placed in computer storage.

Chapter 4 Purpose of The Study

The A.B.R.O. sire-line has been developed with the aim of producing a line of pigs with exceptional qualities of lean meat production to act as the sires of the slaughter generation. The line has been built up over thirteen years by the relatively un-tried "open synthetic" approach of selection coupled with immigration, and without any attention being paid to reproductive performance. The purpose of this study is to provide an evaluation of the line, in an attempt to answer the following questions:

(1) Has selection with immigration resulted in a faster rate of genetic progress than would have been possible by selection alone in a closed population of the same size?

(2) Has there been any decline in the reproductive performance of the sire-line during its thirteen-year period of development?

(3) Has the continual introduction of new genetic material into the line resulted in an increase in the amount of genetic variability available for selection?

(4) How serious are the biasing effects of heterosis and unknown immigrant population means (Chapter 2) on the comparison of potential immigrant and native progeny, and how might these be lessened or removed?

(5) What should be the future of the A.B.R.O. sire-line, and what direction should this line of research now take? The alternatives are that the line could be discontinued, closed to immigration and selected, or retained on an "open synthetic" basis.

(6) Does this method of pig improvement have any general applicability to the British pig industry at the present time?

It would of course be difficult or impossible to give precise answers to these questions, but a fair amount of evidence has been obtained from past records, from theoretical considerations and by simple experimentation.

The investigation was divided into four parts (Chapters 5, 6, 7 and 8). In the first, all the available past and present production and reproduction records were examined for time trends to give an indication of the magnitude and direction of genetic change. Secondly, estimates of genetic and environmental variability and convariability in the line were obtained for comparison with other pig populations. The third part of the study centred on aspects of the selection procedure within the sire-line, in order to establish that any adverse effects on the rate of genetic progress could be expected to be the result of immigration rather than inaccurate performance testing. The testing procedure for the 1972 generation of the line was therefore slightly modified to permit two small trials: the first to assess the reliability of ultrasonic backfat measurements and the second to detect any genotype x test environment interactions. The final and most important part of the study was concerned with an investigation of the effects of bias on the selection or rejection of F_1 potential immigrant x native progeny, and with the general philosophy of immigration as a means of pig improvement. For this purpose an experiment was specially designed to measure heterosis in crosses of the sire-line with purebred Large Whites.

Chapter 5 Changes in Mean Performance.

5.1 Introduction

The purpose of this chapter is to examine phenotypic trends in the mean performance of the A.B.R.O. sire-line with a view to showing, firstly, whether the policy of selection coupled with immigration has been successful in reducing backfat and in later years increasing the efficiency of growth, and, secondly, whether there have been any adverse changes in reproductive performance and viability. One way of assessing the success or failure of the A.B.R.O. sire-line approach would be to compare its current performance with the best available contemporary material. To this end a sample of the 1971 sire-line generation was submitted for central performance testing by the Meat and Livestock Commission and the results are presented here.

5.2 Materials and Methods.

A computer programme was written to tabulate standard deviations, simple means and their standard errors for both sexes by years from 1960 to 1971 for all traits described in Chapter 3. Linear regression coefficients of mean performance on generation number were calculated giving equal weighting to generations, but levels of significance were not attached to the estimated responses because closed population theory cannot be applied to the "open" sire-line. Tentative levels of significance were, however, placed on within-year sex differences. Castrates were included in male means only for traits recorded at 50 days of age. At all other times male pigs were either uncastrated or the means were restricted to the population of entire males retained as potential breeding animals. As the generation interval remained at 1 year throughout, each generation will be referred to by its year of birth.

For the purpose of illustrating overall trends the effects of ad libitum versus restricted feeding between 1960 and 1966, and the effects of single versus double outdoor penning, or of indoor versus outdoor housing between 1968 and 1971 have been ignored. Selection on the two feeding regimes has already been examined by King (unpublished) who found an average difference of 1.7 ± 0.4 ~~g~~mms in backfat for ad libitum minus restricted feeding. A comparison of the carious methods of boar testing will be postponed until Chapter 7. X-ray predicted length between 1960 and 1965 will not be discussed, since results have already been published (King, 1966).

Carcass Data.

In some years during the development of the line a limited amount of simple carcass data was recovered from culls slaughtered at bacon weight (200 lbs liveweight). Although the information is scanty and from a selected sample of the line, it provided an indication as to the type of carcass produced and is included here for completeness. Measurements were taken at two factories by a variety of operators, but all measurements were taken at the same factory within any one year.

Pigs were slaughtered once a week and food was witheld for 24 hours before slaughter. The pigs were electrically stunned bled to death, scalded and scraped. The carcasses were eviscerated and weighed before being placed in a cold store overnight. Backfat and length measurements were taken on the cold, hanging right-hand side of the carcass on the following morning. Eye muscle area and 'C' and 'K' fat depths were obtained by cutting the side transversely at the base of the last rib, and tracing the cut face. Areas were later obtained using a planimeter. An important distinction is that the skin was removed for "Ayrshire Roll" curing at one factory, while it was left intact for whole-side "Wiltshire" curing at the other. The following were recorded:

(1) Weight of the warm eviscerated carcass (lbs.)

(2) Carcass length, from the _symphysis pubis_ to the anterior edge of the first thoracic vertebra

(3) Backfat thickness (mm.) in the mid-line at three positions:

    shoulder, maximum depth
    mid-back, level with the last rib
    loin, maximum depth over the _gluteus medius_

(4) Streak thickness: total thickness of the belly mid-way down the half carcass (mm.)

(5) Fat depths over the eye muscle and at right angles to the skin at the last rib (mm.):

    'C', normal to the longest axis of the eye muscle as seen in cross section
    'K', at the lateral extremity of the eye muscle

(6) Area of the eye muscle (_longissimus dorsi_) at the last rib (sq.cms.)

(7) Fat score: subjectivescore of firmness: 1 - soft; 2 - moderate; 3 - firm

(8) Age at slaughter (days)

Means and variability only have been tabulated, and no correction was made for either carcass or live-weight.

Meat and Livestock Commission Central Testing Station Results.

Twenty-one "combined test" groups, each comprising 2 boars, 1 castrate and 1 gilt, from the 1971 generation were submitted for central testing at the M.L.C.'s Stirling station. 7 groups were from first parity litters, and a further 14 groups were obtained 6 months later from second parity matings. The two batches of results were treated as a single sample.

Detailed accounts of the testing procedure will be found elsewhere (e.g. White, 1966; Steane, 1972), so that a very brief description will suffice here. Boars and sibs (castrate and gilt) are housed separately. The two boars are penned together in a kennel-type house and are fed and recorded individually. The two sibs are housed together in indoor accommodation and feed recorded on a "group" basis. The test starts when the pen average liveweight reaches 60 lbs. and finishes at 200 lbs., when the sibs are slaughtered for carcass evaluation. A sample dissection of the rump back is carried out on either the hog or gilt from each sib pair. Pigs are fed the standard diet shown in Table 5.1 twice daily to appetite.

Traits measured on M.L.C. performance test are as follows:

(1) Records taken on boars and sibs.

Food conversion ratio (kg. food/kg. liveweight gain)
Daily liveweight gain (gms./day)
Days on test

Fat depths (mm) - measured ultrasonically on boars, from cut carcass on sibs:

Mid-line

shoulder, maximum
mid-back, at last rib
loin 2, minimum over gluteus medius

Table 5.1

Standard Diet for Boars and Sibs at Meat and Livestock Commission Central Testing Stations (supplied by M.L.C. Pig Improvement Services, April 1971).

Constituent	%
Ground Barley	60.0
Ground Wheat	20.0
White Fish Meal	5.0
Extracted Soya Bean Meal	12.5
Molasses	2.5
Supplements:	
Di-calcium phosphate	0.75
Ground limestone	0.50
Salt (Na Cl)	0.25
Vitamins and Minerals*	++
Energy (Mcals M.E./kg. D.M.)**	3.33
Crude Protein (% fresh wt.)**	17.7

++ included in ration

* Amounts per ton:

Vitamin A	4.0 m. I.U.
Vitamin D	0.8 m. I.U.
Riboflavine	2.0 gm.
Calcium Pantothenate	5.0 gm.
Vitamin B 12	15.0 mg.
Copper Sulphate	800.0 gm.
Zinc Oxide	80.0 gm.
Ferrous Sulphate	280.0 gm.

** Estimated from tabular values taken from McDonald, Edwards and Greenhalgh (1966).

Off the mid-line at the last rib

'C' approximately 6½ cms. off the mid-line
'K' approximately 12 cms off the mid-line at the latero-dorsal corner of the eye muscle

(2) Slaughter data recovered from sibs only.

Conformation score - subjective assessment of general shape of carcass ranging from 1 (poor) to 7 (good)

Streak score - subjective assessment of appearance of the streak ranging from 1 (poor) to 7 (good)

Eye muscle (<u>longissimus dorsi</u>)area - at the last rib (sq. cms.)

% Lean in the rump back - obtained from sample dissection of either hog or gilt in each group

% Rump in the hind quarter - sample dissection

% Hindquarter in the side - obtained on both sibs after cutting the carcass at the last rib

Carcass length (mm.) - from <u>symphysis pubis</u> to anterior edge of first thoracic vertebra after removal of head

$$\text{Killing out \%} = \frac{\text{cold carcass weight}}{\text{last live weight}} \times 100$$

$$\text{Trimming \%} = \frac{\text{trimmed carcass weight}}{\text{cold carcass weight}} \times 100$$

where : cold carcass weight = weight of hot head and chine + twice the weight of the cold left side (including flare fat, kidney, feet and fillet)

last live weight = mean of last 3 liveweights.

trimmed carcass weight = twice the weight of the cold left side (excluding flare fat, kidney, feet and fillet)

For each boar tested the M.L.C. combine these data into two separate selection indices. The first, termed "Economy of Production", is an index of food conversion ratio, daily gain and killing out percentage. The second, "Carcass Quality", is an indicator of lean as a percentage of carcass weight, the distribution of lean in the carcass, and eye muscle area. The two indices, each scaled to a mean of 50, are then combined to give a Total Points Score with a mean of 100 and a standard deviation of 35, Boars with high scores are predicted to be genetically superior in terms of the overall economic genotype defined by the index.

Means for the 40 surviving sire-line boars and their 41 sibs are given as deviations from the contemporary Large White average. Differences were divided by their observed standard errors and compared with t-tables in order to test for significance.

5.3 Results and Discussion.

The means and variability of growth and reproductive traits for the sire-line recorded at A.B.R.O., together with the number of pigs involved, are tabulated by generations in Appendix A. In order to illustrate time trends, graphs of mean performance against generation number are presented in Figures 5.1 to 5.6 for the two sexes separately. Regressions of generation mean on generation number are given on the appropriate graph with their approximate standard errors. Ranges for the simple standard errors of year-sex means are also given, but should be treated with caution because the sire-line was not a closed population and may also have been liable to the effects of genetic drift as described by Hill (1972).

REGRESSION OF AVERAGE BACKFAT ON GENERATION NUMBER (cms./year):

	1960 - 1971	1960 - 1965	1965 - 1971
♂♂	-0.05 ± 0.02	-0.22 ± 0.04	+0.05 ± 0.02
♀♀	-0.06 ± 0.02	-0.20 ± 0.02	+0.05 ± 0.02
♂♂+♀♀	-0.06 ± 0.02	-0.21 ± 0.02	+0.05 ± 0.02

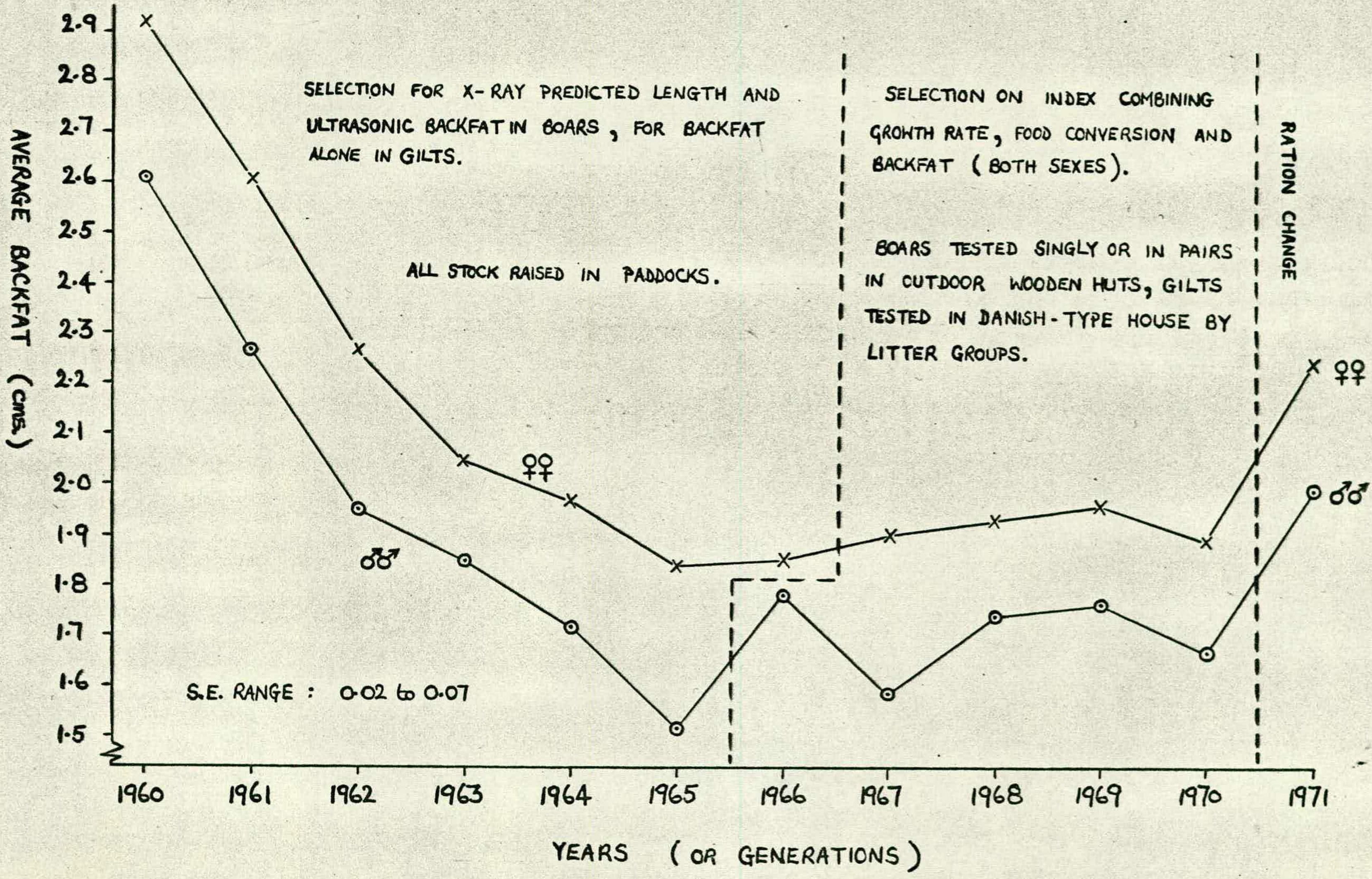


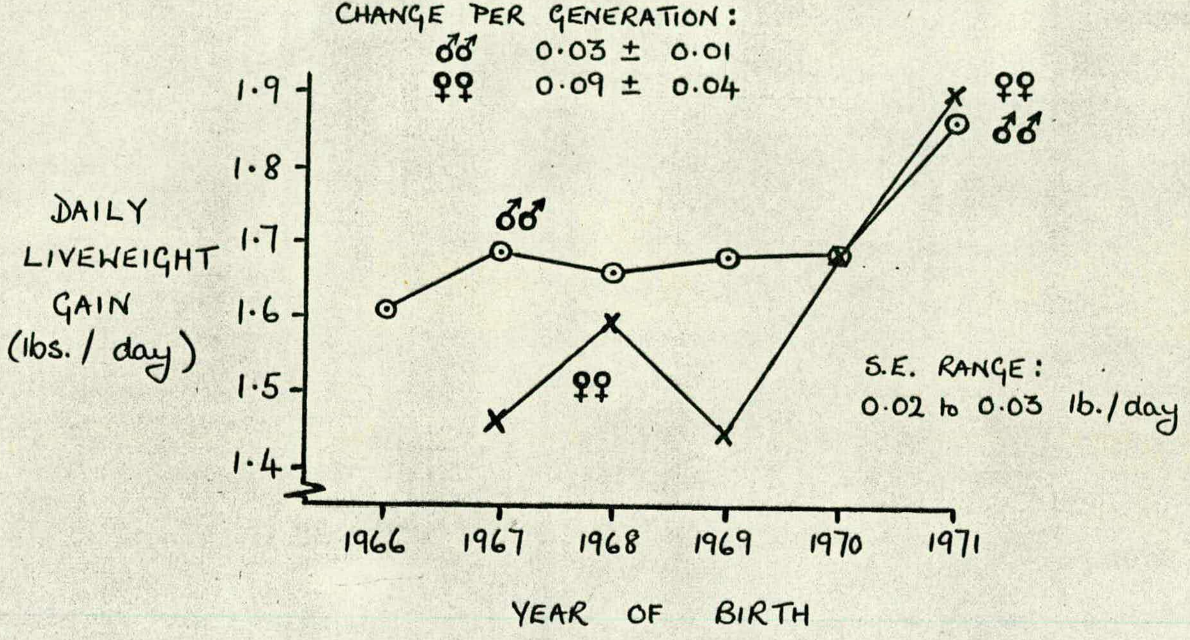
Figure 5.1

Average Ultrasonic Backfat Thickness (cms.) of Boars and Gilts in the A.B.R.O. Sire-Line by Years (Generations)

FIGURE 5.2

MEAN PERFORMANCE TEST RESULTS FOR SIRE-LINE BOARS AND GILTS, BY YEARS (GENERATIONS).

(a) DAILY LIVEWEIGHT GAIN (lbs. / day)



(b) FOOD CONVERSION RATIO (lbs. feed / lb. liveweight gain)

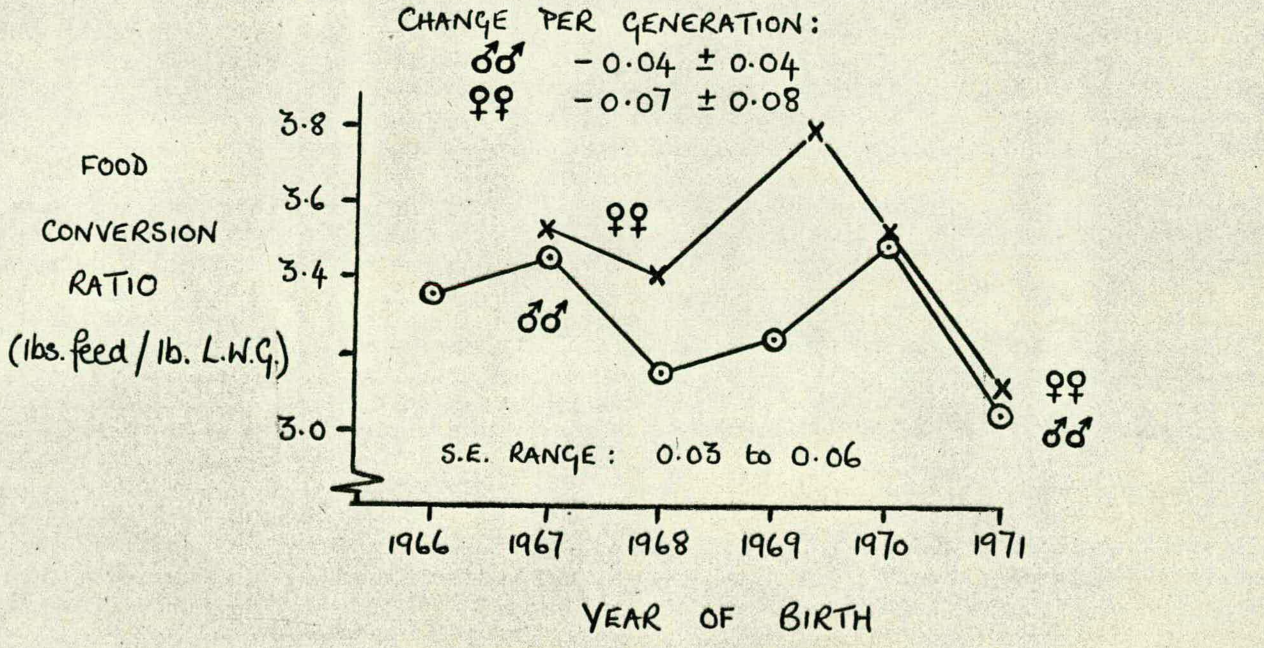
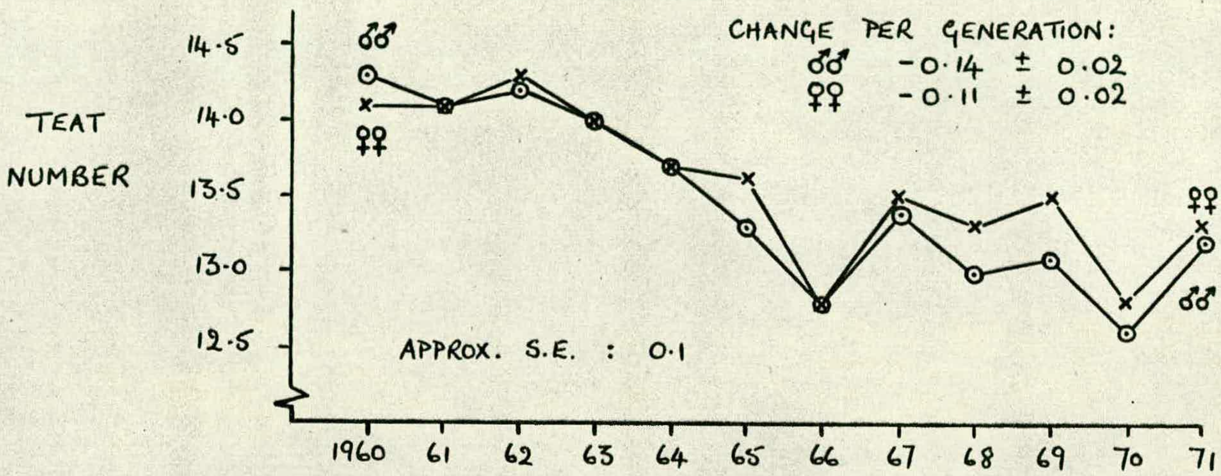


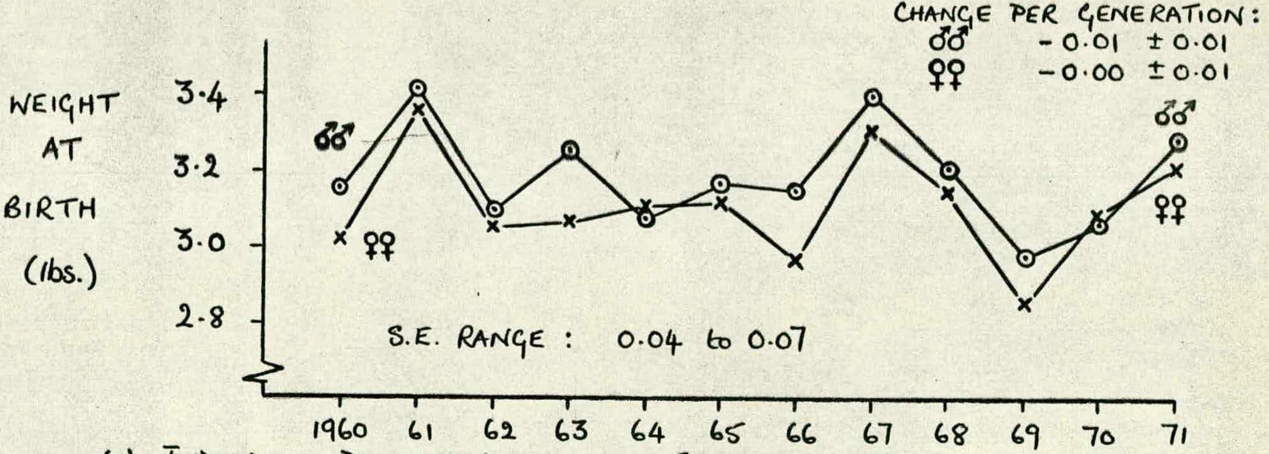
Figure 5.3

Mean Pre-Weaning Performance of Sire-Line Pigs by Years (Generations).

(a) TEAT NUMBER AT 50 DAYS



(b) INDIVIDUAL PIGLET WEIGHT AT BIRTH (lbs.)



(c) INDIVIDUAL PIGLET WEIGHT AT 50 DAYS (lbs.)

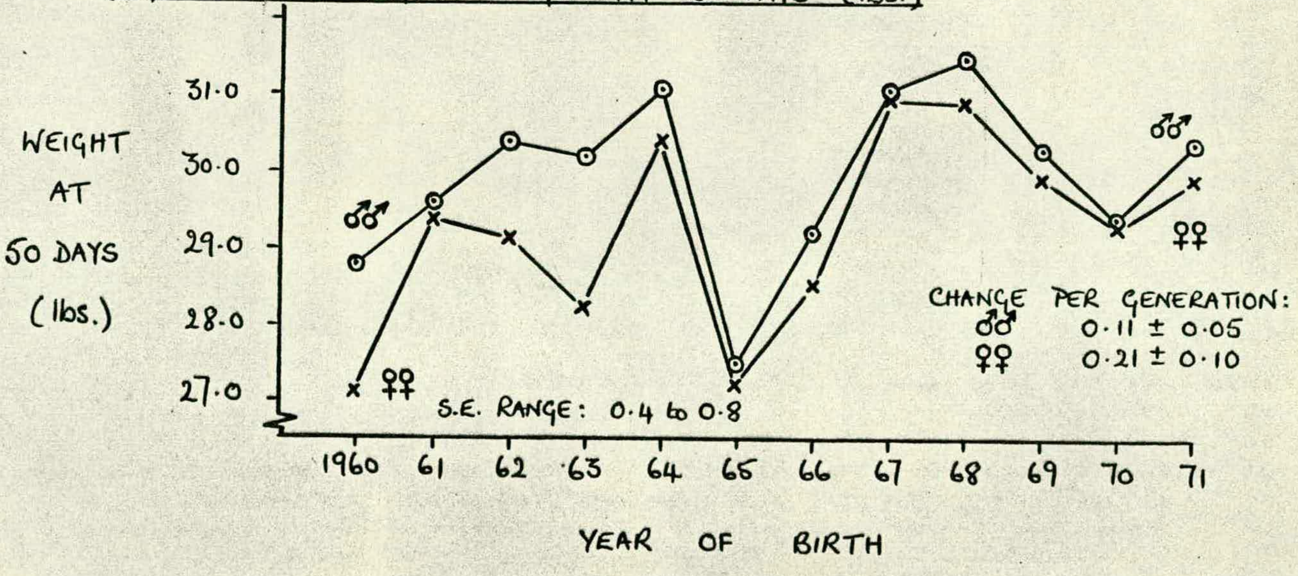
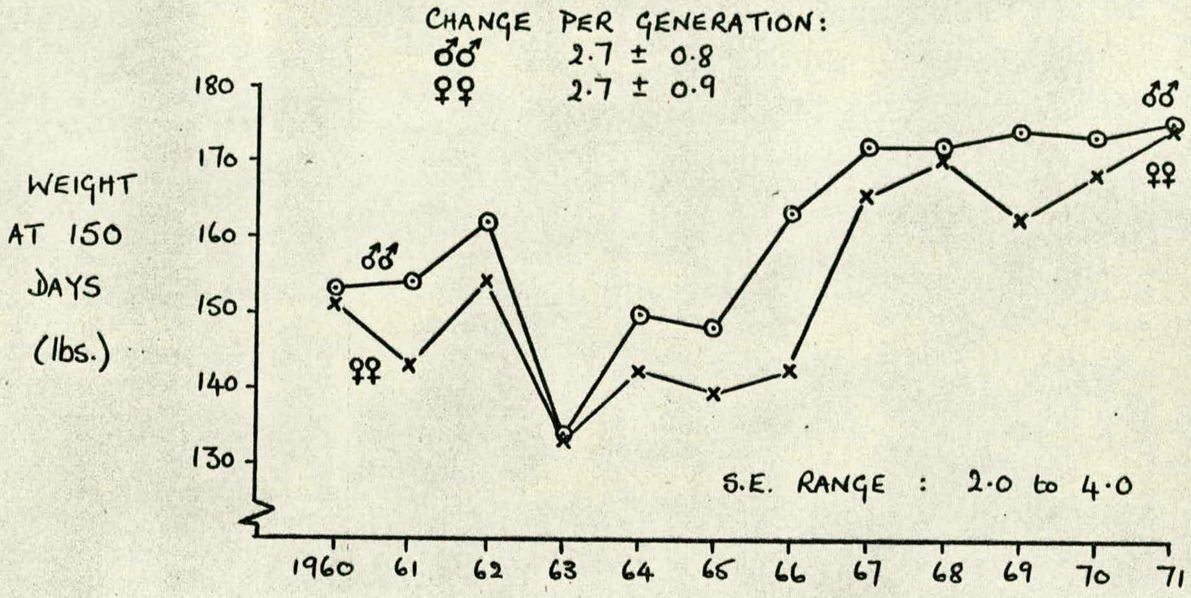


Figure 5.4

Mean Performance of Sire-Line Pigs Reared for Breeding at 150 Days of Age by Years (Generations).

(a) LIVE WEIGHT AT 150 DAYS OF AGE (lbs.)



(b) GROWTH RATE FROM 50 TO 150 DAYS (lbs./day)

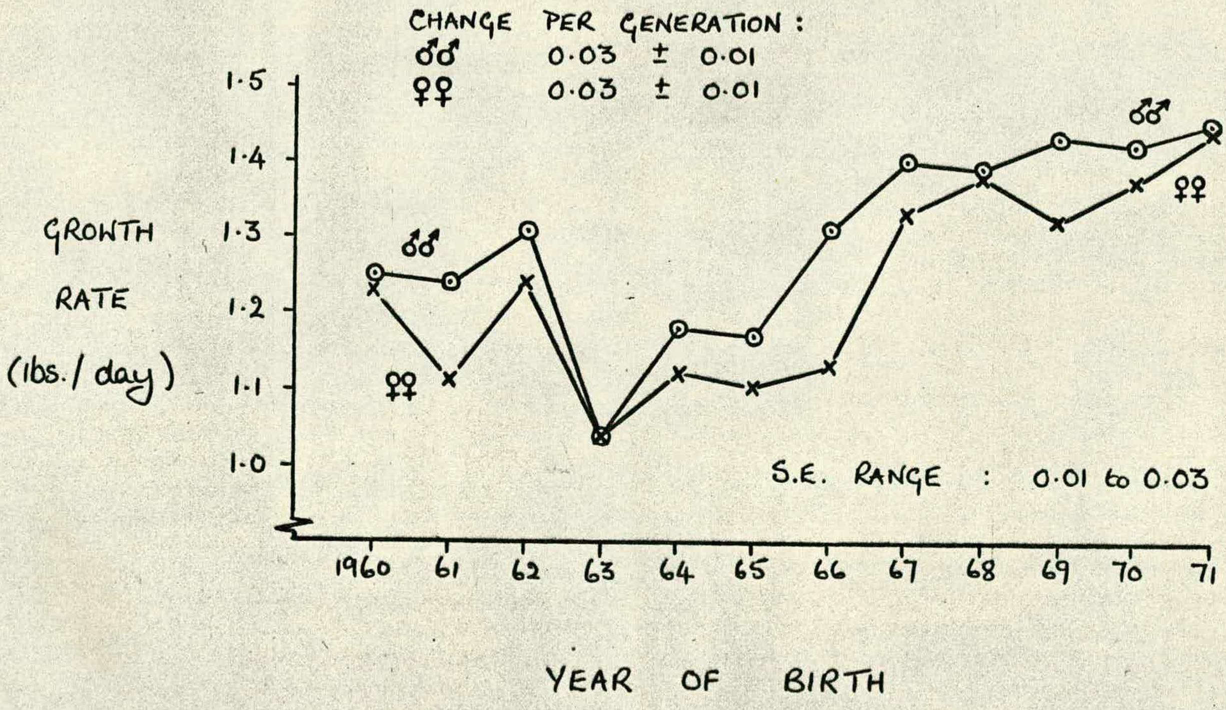
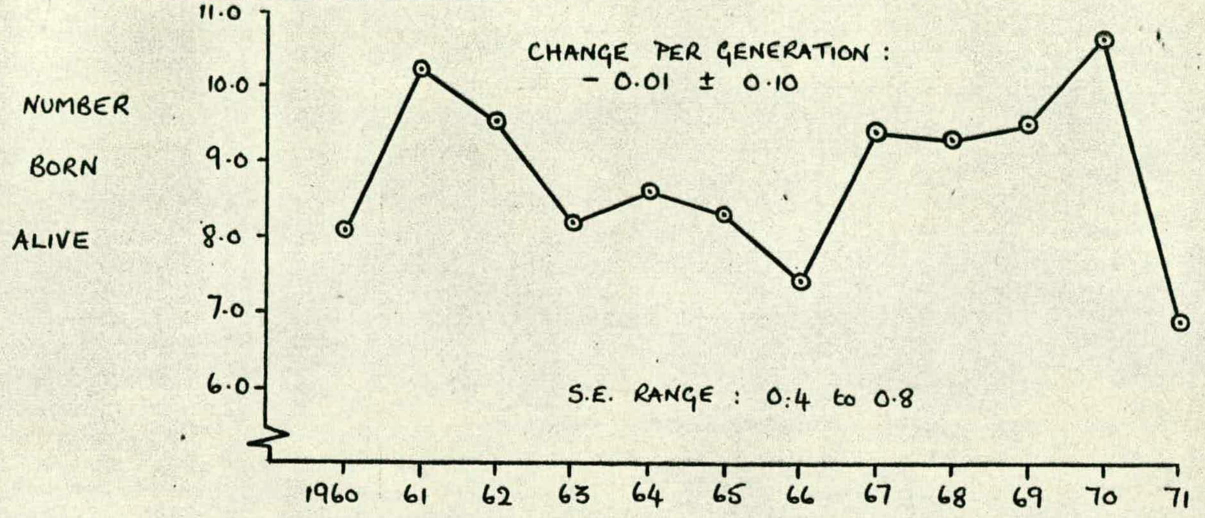


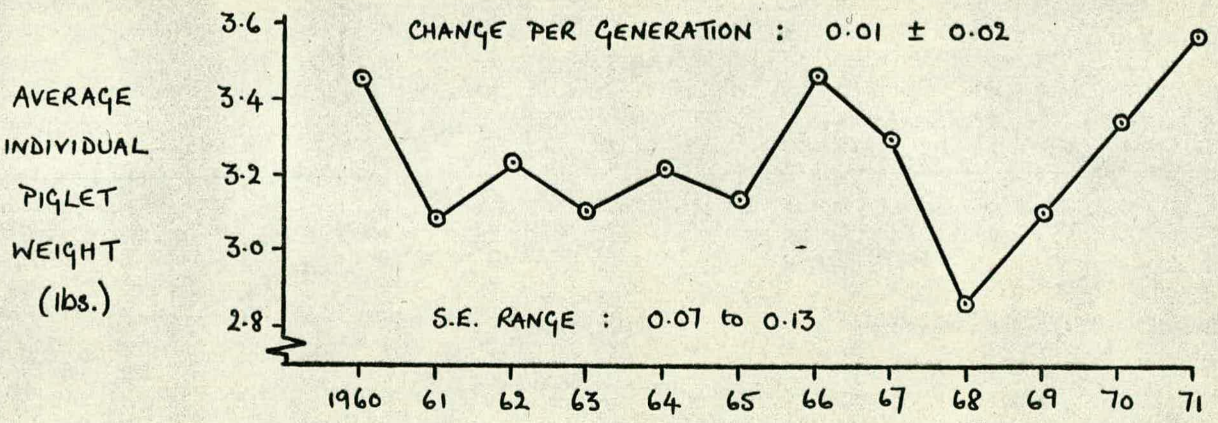
Figure 5.5

Mean Farrowing Performance of Sire-Line Gilts by Years (Generations).

(a) NUMBER BORN ALIVE



(b) AVERAGE INDIVIDUAL PIGLET WEIGHT PER LITTER AT BIRTH (lbs.)



(c) TOTAL LIVE WEIGHT OF LITTER AT BIRTH (lbs.)

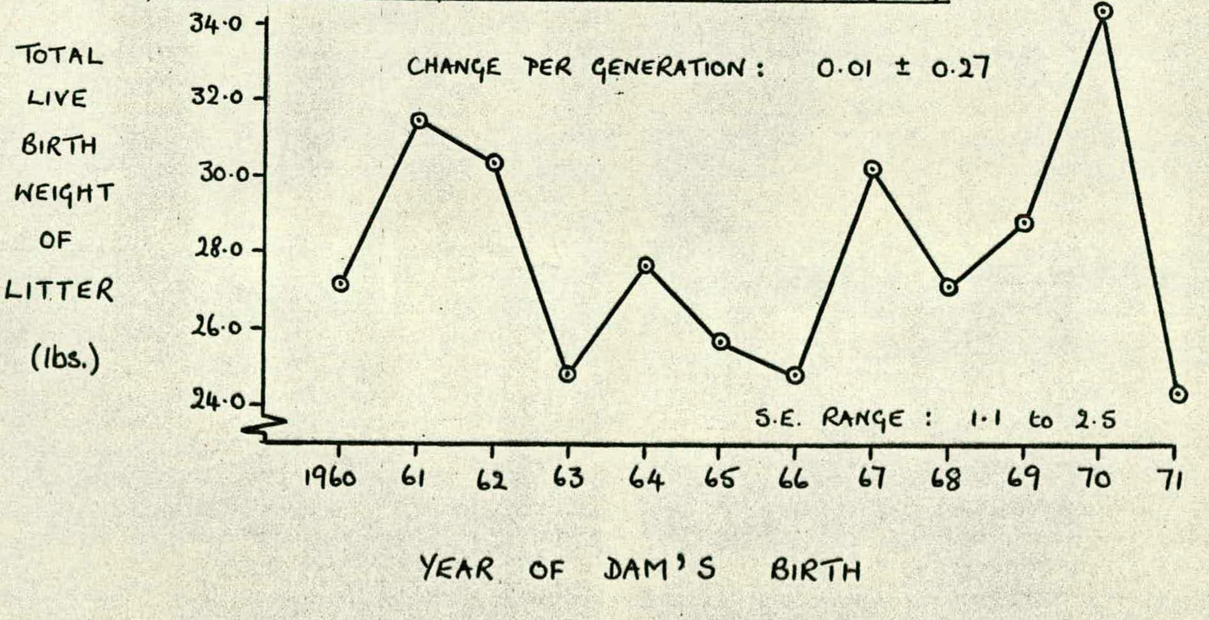
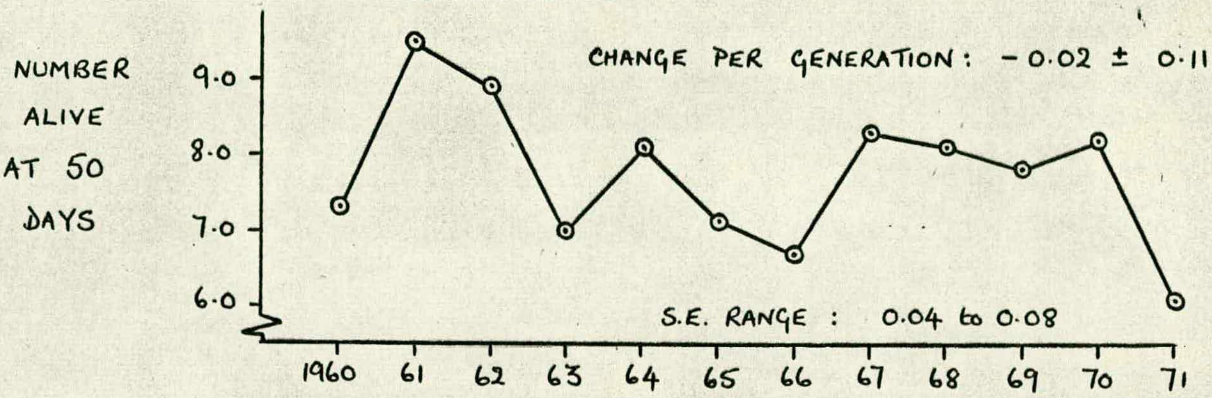


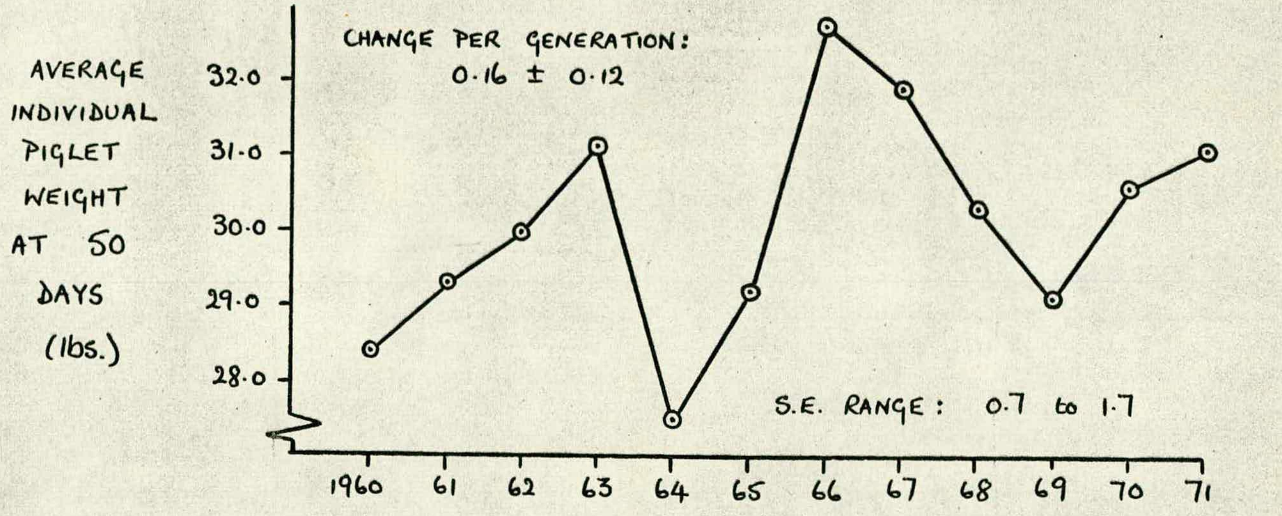
Figure 5.6

Litter Performance of Sire-Line Gilts at 50 Days by Years (Generations).

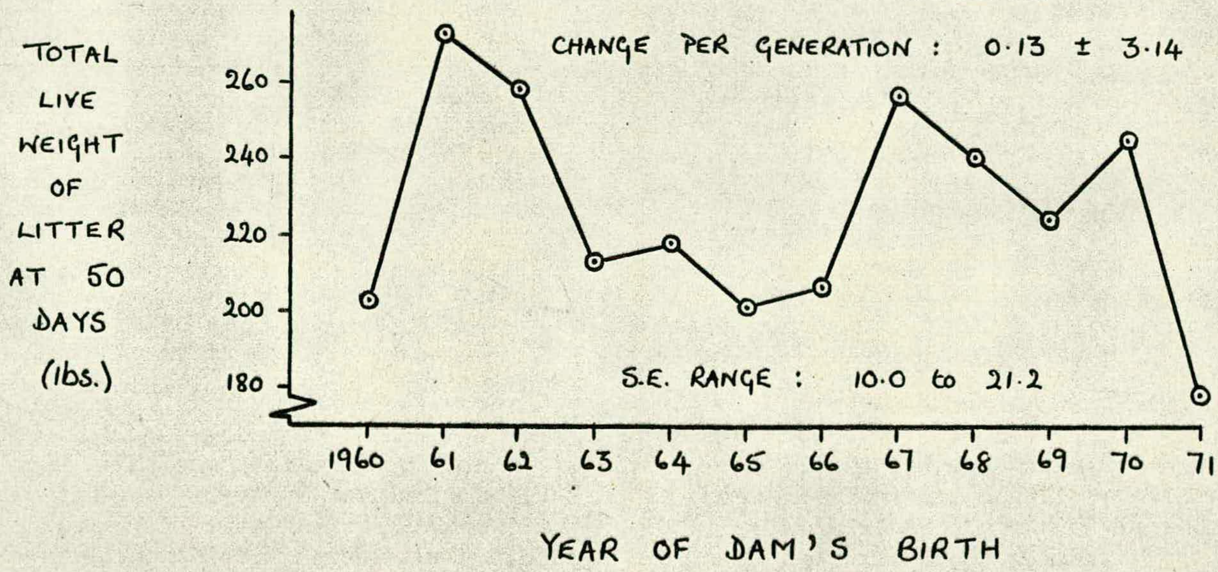
(a) NUMBER ALIVE AT 50 DAYS



(b) AVERAGE INDIVIDUAL PIGLET WEIGHT PER LITTER AT 50 DAYS (lbs.)



(c) TOTAL LIVE WEIGHT OF LITTER AT 50 DAYS (lbs.)



Selected Traits.

Graphs showing mean ultrasonic backfat, growth rate and food conversion are given in Figures 5.1 and 5.2(a) and (b) respectively. Figure 5.1 represents the change in backfat throughout the life of the sire-line. It is clear that the initial decline reported by King (1966) for the first five generations was later followed by a period of little apparent change. The sudden increase following 1970 coincides with a changeover to a proprietary pelleted feed rather than the home-mixed ration (Table 3.5). The sharp increase in boar backfat in 1966 may be the result of a switch to individual boar performance testing in that year. As expected boars were consistently leaner than gilts.

The remaining two traits, first measured in boars on performance test in 1966, are shown in Figure 5.2. Ignoring 1971 when the new ration was introduced, there has been little apparent change in either growth rate or food conversion ratio. Before 1970 boars grew faster and converted better than gilts, but the disappearance of the sex difference in the last two years is difficult to explain.

Without a control line it is impossible to say whether the observed changes were genetic, but the initial conclusion might be that although selection for backfat was very successful in the first years, there was little response to index selection in later years. Reasons for the lack of response might be reduction of selection differential following the introduction of performance testing and a selection index, or alternatively the influx of genes from the Lacombe, Hampshire, Pietrain, and American Yorkshire breeds (Table 3.1). Examination of the selection index will be deferred until Chapter 7, and a discussion of the consequences of immigration will be found in Chapter 8.

Could the steep fall in backfat thickness over the first few generations possibly have been entirely genetic, and if so was it chiefly the result of selection or immigration? No immigrants other than from the foundation breeds were introduced before 1964. Although some 40% of litters were immigrants, the incoming Large White, Landrace and Wessex pigs would have needed to have been considerably better than natives in order to bring about the observed change. Some insight into the potential of selection may be obtained by comparing early response in the sire-line with the response which could be gained by mass selection for backfat alone in a closed randon-mating population. Considering a comparable situation in which 5 boars are selected out of 40 tested, and 30 gilts are selected out of 80 tested, then expected response per generation (R) may be expressed in the usual way:

$$R = h^2 \sigma p \frac{(i_F + i_M)}{2},$$

where h^2, σp and i are the heritability, within-year phenotypic standard deviation and standardised selection differential respectively. Inspection of Table A1 (Appendix A) shows an average within year standard deviation of approximately 3 mm. for ultrasonic backfat thickness. With a conservative maximum value of h^2 of 0.6 (e.g. Smith and Ross, 1965) and setting $i_F = 1.01$ and $i_M = 1.59$ (Becker, 1967), the expected response per generation is 0.23cm./year. This compares with an observed response of 0.21cm./year (Figure 5.1). One could therefore conclude that in a closed population of similar size undergoing selection of a similar intensity, a response of the magnitude observed here could have been entirely due to selection. However, the observed response of 0.21 cm/generation is twice as great as the average change per generation of 0.09 cm. reported by Fredeen (1971) for 3 selection experiments each with control lines. In the same experiments the realised heritability averaged 0.40, which would reduce the response expected above from 0.23 to 0.16 cm./generation. Never-the-less, it is not inconceivable that, after preselection of boars on the basis of X-ray predicted length which is favourably correlated with backfat (Smith and Ross, 1965), and with the introduction of immigrants from population undergoing parallel improvement schenes, the observed phenotypic change in the sire-line between 1960 and 1965 might have been entirely genetic.

Unselected Traits.

Graphs showing the change in traits not directly subject to selection are given in Figures 5.3 and 5.4. Number of teats (Figure 5.3 (a)) showed a marked decline at the rate of 0.1 per generation, and could have been the result of introducing shorter breeds such as the Pietrain and Hampshire into the line. For example a random sample of 10 Hampshire litters at A.B.R.O. in 1970 gave an average teat number of 12.1, while the sire-line average has generally been maintained above 13.0 teats. On the other hand the first exotic breed was not introduced until 1964 and yet the decline had clearly begun in 1963. However, the present average of 13 teats is considered acceptable, particularly since females of the line would not take part in commercial production but would only be required for perpetuation of the line itself. The average number of teats is well in excess of the average number of piglets born alive within the line (see Figure 5.5 (a)).

Individual piglet birth weight (Figure 5.3 (b)) showed no phenotypic change over the life of the sire-line, while individual weight at 50 days (Figure 5.3 (c)) appeared to increase slightly. The sudden dip in 50 day weight in 1965 is difficult to explain, except that an unusually high July-September rainfall of 13.10 inches was recorded, and the effect was apparently not reflected at 150 days.

The graph for liveweight at 150 days of age (Figure 5.4 (a)) is almost exactly mirrored by the graph for growth rate per day over the preceding 100 day period (Figure 5.4 (b)), and both show an apparent increase per generation which is difficult to assess statistically. The two traits "growth rate on test" and "growth rate from 50 to 150 days" would be expected to be closely correlated, and by comparing Figure 5.2 (a) and Figure 5.4 (b) it can be seen that they show a similar pattern of change. However, growth rate to 150 days included the period of weaning and transfer of piglets to a new location, and is more likely to be influenced by maternal and environmental effects than growth rate under controlled test conditions. Boars were heavier than gilts at all ages.

Reproductive Performance.

Changes in reproductive performance are shown graphically in Figures 5.5 and 5.6. Graphs (a) to (c) in Figure 5.5 show no significant trend in numbers of pigs born alive, average birth weight per litter and total litter weight at birth for the first 12 years of the line's development. It is possible that a decline in the additive genotype brought about by the introduction of breeds with lower fertility may have been compensated for by heterosis. The fact that some litters were exhibiting more heterosis than others may partly account for fairly high variation in numbers born alive. (Table A10, Appendix A), for example, although extensive management conditions should not be forgotten in this respect. At 50 days of age while still suckling, graphs (a) to (c) in Figure 5.6 show that a slight drop in the number of pigs born alive and a slight increase in piglet weight, both clearly non-significant, combine to produce no change in total litter weight. As well as heterosis, reproductive performance could have been maintained by an element of "automatic" natural selection whereby larger litters stand a greater chance of contributing progeny to the next generation, as described by Strang and King (1970).

Numbers of congenital defects in each generation are given in Table A12 of Appendix A, together with percentage incidence for all births in the first 12 years. 3.88% of all male births and 1.50% of all female births were recorded as being abnormal, giving an overall figure of 2.69% for the line. Males appear to have the higher incidence simply because females are not subject to scrotal hernias or to the "rig" condition of undescended testes. It is also the result of arbitrarily classifying intersexes as males, and may be partly due to the fact that females suffering from atresia ani or "blind anus" are frequently viable because defaecation takes place through a recto-vaginal fistula (Norrish and Rennie, 1968). In males scrotal hernias showed the highest incidence, followed by rigs and unbilical hernias. It was not possible to obtain the exact incidence of splaylegs, a defect from which newborn pigs may recover. In females hernias constituted the greatest problem.

Clearly there have been no serious outbreaks of any particular defect although there were 21 cases of umbilical hernia in 1971 born pigs. It is concluded that the pooling of breeds did not result in any disastrous uncovering of genetic defects. On the contrary, increased heterozygosity in both the parents and progeny might well serve to mask recessive defects. In view of the fact that by no means all animals born into the line can be tested, and since rigs, intersexes and herniated animals can usually be successfully fattened, the level of congenital abnormalities in the sire-line is considered to be well within the acceptable limit and of no hindrance to selection.

Carcass Data.

Means and variabilities for carcass data obtained from rejected or untested sire-line pigs in some generations are laid out in Appendix B. Time trends have not been plotted out because of differences between factories and small sample sizes. It is of interest to note that carcass length (Table B11) reached a minimum of 787 mm. in 1967 when the percentage of Pietrain plus Hampshire blood in the line reached a maximum (Table 3.1). King (1966a) reported that both the Hampshire and Pietrain reduced length by over 25 mm. in crosses with the Large White. The current length of over 800 mm. is considered adequate for present grading standards. Eye muscle area (Table B4) appears to have increased, although the increase of 7 sq.cms. in 1968 was the result of switching factories and taking the measurement before, rather than after, the curing process. The subsequent increase in eye muscle area could have been the result of the influx of superior Pietrain or Hampshire genes or alternatively a favourable correlated response to selection for feed efficiency and backfat (e.g. Smith and Ross, 1965). Improvements of over 4 sq.cms. were recorded in Pietrain and Hampshire crosses with Large Whites (King, 1966a). The remaining carcass data ~~is~~ are of marginal value but may be used for reference.

M.L.C. Central Test Station Results.

The results from 21 combined groups are summarised separately for boars and sibs in Table 5.2, expressed as deviations from the contemporary Large White mean. A.B.R.O. sire-line pigs were better than Large Whites in all measurements except killing out percentage and shoulder and loin boar backfat depths. Sibs were comparatively leaner than boars at all sites, and this anomaly is difficult to explain. Percentage of lean in the rump and eye muscle area were both significantly better than in Large Whites, indicating a tendency towards meatiness as well as leanness. Both traits would be expected to improve as a result of selection for feed efficiency and backfat (Smith, King and Gilbert, 1962) and as a result of immigration by the Pietrain and Hampshire (King, 1966a). Carcass length was satisfactory at 809 mm. and in agreement with measurements taken at the local bacon factory. No cases of "pale, soft, exudative" eye muscle (P.S.E.) were reported.

Table 5.2

Performance Test Results of 21 "Combined Test" Groups of Sire-Line Pigs at M.L.C. Testing Station, Stirling, Expressed as Deviations from Contemporary Large White Average. (Standard Errors of Differences are Shown in Brackets).

Character	Boars	Sibs
Food Conversion Ratio (lb Food/lb L.W.G.)	-0.07(0.02) B**	-0.05(0.03) B
Daily Liveweight Gain (gms./day)	+27.0(6.0) B***	+23.0(8.0) B**
Days on Test	-2.9(0.6) B***	-2.8(0.8) B**
Conformation Score: 1(bad) - 7(good)	-	+0.2(1.4) B
Fat Depths:		
Shoulder (mm.)	+0.5(0.5) W	-1.1(0.6) B
Mid-Back (mm.)	-0.2(0.3) B	-0.6(0.5) B
Loin "2" (mm.)	+0.4(0.4) W	-2.6(0.4) B***
"C" (mm.)	-0.5(0.4) B	-1.5(0.6) B*
"K" (mm)	-0.2(0.4) B	-2.3(0.8) B**
Streak Score: 1(bad) - 7(good)	-	+0.4(0.1) B**
Eye Muscle *(Longissimus dorsi)* Area (sq.cms.)	-	+1.36(0.44) B**
% Lean in Rump	-	+3.4(1.0) B**
Killing Out %	-	-0.9(0.3) W**
Trimming %	-	+0.3(0.1) B*
% Rump in Hind Quarter	-	+0.6(0.3) B
% Hind Quarter in Side	-	+0.7(0.2) B**
Length† (mm.)	-	809
Points Score for Economy of Production† (Mean =50,S.D.=22)	49	-
Points Score for Carcass Quality†(Mean=50,S.D.=17)	68	-
Total Points Score†(Mean=100 S.D.=35)	117	-
Estimated Difference in Economic Value (P).Per Pig	-	+65

†Expreseed as absolute values and not as deviations.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

B= Better than contemporary mean; W = Worse than comtemporary mean.

The sire-line was barely average on index point score for Economy of Production, but was one standard deviation better for Carcass Quality. The lack of superiority in the economy index was the result of a poorer killing out percentage set against moderate increases in growth rate and food conversion. Since the genetic correlation between backfat and killing out percentage is positive and unfavourable (Smith et al., 1962), a worsening of killing out percentage is perhaps not unexpected. The superiority of the sire-line in carcass quality was principally due to improvements in eye muscle area and % lean in the rump. On total points score the line was 17 better, or one half standard deviation above the contemporary mean. The index points scores should be used with caution, since they represent predicted breeding values calculated on the assumption that the sire-line and Large White populations have the same mean. If this is not the case, some of the real genetic difference between the two populations will have been treated as a phenotypic difference and the predicted difference in breeding values will be incorrect. This problem is discussed at length in a different context in Chapter 8.

The difference in economic value per pig (Table 5.2), treating the sire-line and Large Whites as separate populations, was calculated from the monetary values of improvements in food conversion, daily gain, % lean in the side, killing out %, trimming % and eye muscle area put forward by Cook et al. (1971). % lean in the side was estimated by multiplying % lean in the rump by 0.7. Calculations were made on the sibs' performance only, and indicated a superiority of 65_p per pig in favour of the sire-line, chiefly through improved eye muscle area and % lean in the side. This compares with an estimated superiority of Large White over Landrace of 45_p and of "nucleus" over "commercial" herds of roughly 180_p as given by Cook et al. (1971). When crossed with a Large White dam, for example, the superiority of the commercial progeny of a sire-line boar would be expected to be halved at $32\frac{1}{2}_p$ per pig. Some or all of the loss could be made up by improved viability of the progeny through heterosis.

An idea of the rate of genetic progress in the sire-line may be gained by comparing the 1971 results with those reported by King and Smith in 1968. Their findings for the 1967 generation are summarised in Table 5.3. Relative to Large Whites from nucleus herds the sire-line appears to have improved slightly in food conversion and daily gain, so that the improvements shown in Figure 5.2 (a) and (b) for 1971 might not have been wholly the result of a change of diet. On the other hand the average superiority in fat depths dropped from 3.9 mm. in 1967 to 1.6 mm. in the 1971 sibs, supporting the observed adverse trend in ultrasonic backfat (Figure 5.1). In addition the deficiency in killing out percentage has worsened slightly and some of the superiority in eye muscle area has been lost, while the superiority in percentage lean in the rump back has been maintained.

Cook et al. (1971) reported rates of genetic progress in the M.L.C. pig improvement scheme between 1966 and 1970 of 0.055 units per pig per year for food conversion ratio, 18 gms for daily gain, 0.63 sq.cms. for eye muscle area and 0.29 % for killing out percentage. Bearing in mind possible

Table 5.3

Mean Performance of 20 Sib Groups (1 Hog and 1 Gilt) in 1967 Expressed as Deviations from Contemporary Large White Average (from King and Smith, 1968*).

Trait	Difference	
Daily Gain (gm/day)	-25.0	W
Food conversion Ratio	- 0.01	B
Fat Depth (mm.)	- 3.9	B
Eye Muscle Area (sq.cm.)	+ 3.0	B
Killing Out %	- 0.5	W
% Lean in Rump	+ 3.5	B

B = better than contemporary mean

W = worse than contemporary mean.

* personal communication; abstract only published.

fluctuations in the contemporary mean, one might conclude that some genetic progress has been made in the sire-line maintaining it on a par with Large Whites. However there must be serious doubts as to whether any advance has been made in fat depths or eye muscle area since 1966. Present (1971) performance has been let down by killing out percentage, but any attempt to improve this trait directly would require the slaughtering of sibs which in turn might lead to a reduction of selection differential.

5.4 Conclusions.

Response to selection for ultrasonic backfat thickness in the A.B.R.O. sire-line appears to have fallen off after an initial period of success. In spite of little apparent improvement in backfat or feed efficiency since 1965, the line appears to have held its own in comparison with contemporary Large Whites, showing an economic advantage of 65_p per pig in 1971. There was some evidence from central testing station results that the introduction of performance testing and a selection index in 1966 may have slightly improved growth rate and food conversion. The line was noticeably better than Large Whites in dissected lean and eye muscle area, which could very well be the result of immigration by the Pietrain and Hampshire. The apparent lack of selection response after 1965 is hard to explain. Possible reasons might be that genetic variance was declining or that immigration was in some way working against selection. These two possibilities are examined in Chapters 6 and 8.

Theoretical considerations indicate that reproductive performance may be ignored in a sire-line (Smith, 1964). With the exception of a fall in teat number no adverse changes were recorded for any reproductive traits, and there were no serious outbreaks of congenital abnormalities. It is recognised that a high level of heterozygosity and a certain amount of natural selection may be partly responsible for upholding the litter performance of the line.

At present genetic improvements in the sire-line would be difficult to detect and much of the evidence presented above has been circumstantial. With the development of a line of this sort it is important to be able to monitor genetic changes from generation to generation so that the response to selection and the benefits of the various immigrant contributions can be assessed. There would therefore seem to be a case for maintaining an unselected control line or of using some form of repeat mating design in order to estimate genetic change.

Since the A.B.R.O. sire-line was developed as a "third breed" (see Chapter 2) to act as the sire of crossbred pigs for slaughter, it should strictly be judged in that context. Heterosis from being genetically distinct and lean-meat content from European breeds might well conspire to give greater overall profitability than could be achieved by intense selection for feed efficiency and backfat in the best available British breeds, simply as a result of improved viability of the commercial progeny and better carcass gradings.

Chapter 6 Sources of Variation

6.1 Introduction.

In the previous chapter it was shown that, after a rapid initial decrease in ultrasonic backfat thickness which tailed off in 1965, there has been little further phenotypic change in any of the traits under selection in the A.B.R.O. sire-line. The main purpose of this chapter is to provide information on the amount of additive genetic variation in the line, with particular regard to backfat. An attempt will be made, with rather limited data, to throw light on two distinct possibilities: firstly that the continual pooling of breeds may have substantially increased the proportion of additive genetic variation, and secondly that for some reason the proportion of additive genetic variation may have reached an unusually low level and become a barrier to selection. If the sire-line parameter estimates turned out to be greatly different from those in other pig populations there would be an opportunity to modify the present selection index accordingly.

6.2 Material and Methods.

Heritabilities and genetic correlations were estimated by two methods, paternal half-sib correlation and daughter-dam regression, for seven of the individually recorded traits described in Chapter 3.3 and set out for example in Table 6.1. Food conversion ratio was excluded from the analysis because it was recorded on a variable-sized "group" basis. All pigs born into the sire-line from first parity gilts between 1960 and 1971 were included in the analysis irrespective of their ancestry. Calculations were done separately for various combinations of characters involving different numbers of pigs.

Analysis of Variance.

A standard computer programme was used to perform a hierarchical analysis of variance. As sires were used in one year only and their progeny were all born on one of the two farms, the analysis was carried out within places of birth and within years (or generations) removing a total of 16 degrees of freedom. By means of a built-in facility of the programme separate overall adjustments were made for feeding regime prior to 1967 (ad libitum versus restricted), boar performance test location in 1971 (indoor versus outdoor), and sex. The effects of inequalities of variance among the subgroups and of interactions with genotypes were therefore assumed to be negligible. Smith and Ross (1965), for example, found that although sex by sire interactions were significant for growth rate and backfat they contributed only 4% of the total variation. The same authors were unable to demonstrate significant sex differences in heritability. Results from experiments designed to detect genotype x feeding level interactions, on the other hand, have been rather inconclusive (e.g. King, 1971).

Components of variance were obtained in the normal way by equating observed mean squares with their expectations. The expected composition of the various components is summarised below:

	Expected M.S.	Expected Composition of Components
Between Sires	$\sigma_w^2 + k_1\sigma_d^2 + k_2\sigma_s^2$	$\sigma_s^2 = \frac{1}{4}\sigma_A^2$
Between Dams within Sires	$\sigma_w^2 + k_0\sigma_d^2$	$\sigma_d^2 = \frac{1}{4}\sigma_A^2 + \sigma_M^2$
Within Litters	σ_w^2	$\sigma_w^2 = \frac{1}{2}\sigma_A^2 + \sigma_E^2$

where k-values are the relevant coefficients, and σ_s^2, σ_d^2, and σ_w^2 are the sire, dam and within litter variance respectively. Phenotypic variance ($\hat{\sigma}_P^2$) was calculated within generations as the sum of the sire, dam and within-litter components. Additive genetic variance ($\hat{\sigma}_A^2$) was estimated as four times the sire component, from which an estimate of heritability was obtained Standard errors of heritability estimates were worked out by the method of Woolf (cited by Falconer, 1963). The "maternal" component of variance ($\hat{\sigma}_M^2$) arising from environmental influences common to a single litter was estimated as the difference between dam and sire components, but may also contain non-additive genetic effects mainly due to dominance (e.g. Dickerson, 1969). The residual or "environmental" variance ($\hat{\sigma}_E^2$) was estimated as the within litter component minus twice the sire component, and similarly included a proportion of non-additive genetic variance. Components of covariance were obtained in an exactly analogous manner, genetic correlations being estimated from sire components and phenotypic correlations from the sum of sire, dam and within litter components. Approximate standard errors of the genetic correlations were calculated according to Robertson (1959), and of phenotypic correlations according to Hammond and Nicholas (1972).

No adjustment was made for the effect of positive assortative mating which was practised in the line and which would inflate the covariance of half-sibs, causing an upwards bias in the estimate of heritability. The within-generation phenotypic correlation between mates for backfat was 0.09 ± 0.07, but this figure excludes immigrants on which no measurements were available, with the result that the true value may be somewhat lower. The bias induced on the estimates of heritability was therefore expected to be small.

Intrasire Daughter-Dam Regression.

The daughter-dam regression analysis was carried out within sires eliminating the effects of place and year of birth as well as the effects of assortative mating. The analysis was confined to female progeny in order to avoid the complication of correcting for sex differences or differences in boar performance testing environment after 1967. The records of parents and offspring prior to 1967 were adjusted for feeding regime using separate constants for each year, obtained from a standard least-squares programme. A computer programme was written in order to obtain estimates of heritability using Falconer's (1963) modification of the optimum estimation procedure of Kempthorne and Tandon (1953), weighting sums of squares and products from each dam family according to family size. This procedure has minimum variance and is preferable to giving equal weight to either the dam or the progeny when there is more than one offspring per dam. Intraclass correlations and approximate regression coefficients required for the calculation of weighting factors were obtained from the hierarchical analysis of variance and from a preliminary unweighted regression analysis respectively. Heritability was estimated as the doubled regression coefficient and its standard error as the doubled standard error of the regression proposed by Falconer. In all cases the estimates from the optimum method fell between the values obtained from the two alternative unweighted analyses.

Estimates of genetic correlations were obtained from separate analyses giving equal weight to progeny, as follows:

$$\hat{\gamma}_A = \frac{cov(Y_1X_2) + cov(Y_2X_1)}{2\sqrt{\{cov(Y_1X_1).\,cov(Y_2X_2)\}}}$$ (e.g. Turner and Young, 1969)

where Y and X are observations on the progeny and dam respectively, and subscripts refer to traits 1 and 2. The arithmetic mean of the two cross-covariances was used instead of the geometric mean, so that an estimate of the correlation could still be made when the cross-covariances differed in sign as a result of sampling. Approximate standard errors of the genetic correlation were once again calculated according to Robertson (1959).

The various parameter estimates from both sib and regression analyses were not adjusted for levels of inbreeding or selection, primarily because it was the intention of this study to examine the genetic variability available in the sire-line in its present circumstances. However, it is also recognised that it would be of doubtful value to extrapolate back to a base population in a line subject to regular inbreeding. From Table 3.3 it can be seen that yearly average inbreeding coefficients have never exceeded 6% and have frequently been much lower. Bulmer (1971) demonstrated that although additive genetic variance declines in the first generation of artificial selection for a metric character, it rapidly approaches a limiting value and drops very little ~~a~~ after three or four generations. Selection and inbreeding are not therefore expected to cause a noticeable reduction in additive genetic variance in future generations of the line and their effects will be ignored.

6.3 Results and Discussion.

6.3.1 Heritability.

Heritability estimates from paternal half-sib correlation and intrasire daughter-dam regression are given in Table 6.1. The pattern of the estimates is roughly as expected, the proportion of additive genetic variance declining for characters more closely related to fitness. A slightly different sample of dams was used for the two methods, 34 immigrant dams being omitted from the regression analysis owing to the absence of records. In spite of this, heritabilities from the two methods agree reasonably well bearing in mind fairly large standard errors.

Estimated heritabilities of 0.10 and 0.17 for teat number in the sire-line fall within the range of those reported in the literature. For example Enfield and Rempel (1961) found values of 0.10 ± 0.04 and 0.23 ± 0.20 by offspring-parent regression and half sib correlation respectively in the Minnesota No 1, and Gabris and Stanik (1968) gave values lying between 0.10 and 0.37 for various breeds. Heritabilities of individual birth weight, too, agree broadly with those from other populations. Fahmy and Bernard (1970) reported values of 0.07 ± 0.35 and 0.27 ± 0.06 by sib and regression analysis respectively in Canadian Yorkshires, and Roy et al. (1968) found a half-sib heritability of 0.10 ± 0.15 for the Managra. Sire-line heritability estimates for 50-day weight also agree with other authors' reports for individual weight at and around weaning time. For instance Ward et al. (1964) gave pooled figures of 0.14 ± 0.11 and 0.26 ± 0.07 by sib and regression analysis respectively for weaning weight in the

Table 6.1

Estimates of Heritability from Half-Sib Analysis (h^2_{HS}) and Intrasire Daughter-Dam Regression (h^2_{OP}), together with Estimates of the Within-Year Phenotypic Standard Deviation ($\hat{\sigma}_P$) and the Proportions of Maternal ($\hat{\sigma}^2_M$) and Environmental Variance ($\hat{\sigma}^2_E$) in the A.B.R.O. Sire-Line.

Trait	Number of Pigs	Between Sire D.F.	$\hat{\sigma}_P$	$\hat{h}^2_{HS}$	S.E.*	$\hat{\sigma}^2_M/\hat{\sigma}^2_P$	$\hat{\sigma}^2_E/\hat{\sigma}^2_P$	Number of Dams	$\hat{h}^2_{OP}$	S.E*
Number of Teats	3600	116	1.2	0.10	0.06	0.10	0.80	312	0.17	0.04
Birth Weight (lbs./day)	3600	116	0.63	0.31	0.13	0.28	0.41	312	0.10	0.08
50-Day Weight (lbs.)	2972	115	6.45	0.30	0.15	0.34	0.36	305	0.03	0.09
150-Day Weight (lbs.)	1727	112	20.1	0.14	0.13	0.21	0.65	276	0.17	0.09
Growth Rate From 50 to 150 Days (lbs./day)	1727	112	0.18	0.16	0.12	0.16	0.68	276	0.26	0.09
Corrected Average Ultrasonic Backfat (cms.)	1727	112	0.31	0.63	0.13	-0.04	0.41	271	0.30	0.09
Growth Rate on Test (60-180 lbs) (lbs./day)	1068	71	0.24	0.26	0.13	0.04	0.70	144	0.65	0.11

*approximate standard error

Minnesota No's 1 and 2, while Fahmy and Bernard gave corresponding figures of 0.08 ± 0.27 and 0.19 ± 0.06 for 56-day weight in Yorkshires. The paternal half-sib estimates of 0.31 and 0.30 for birth weight and 50-day weight respectively in the sire-line were perhaps a little greater than values usually encountered for these traits. Sire-line heritabilities of 0.14 and 0.17 for 150-day weight were in rough agreement with Fahmy and Bernard's 140-day weight estimates of 0.16 ± 0.26 and 0.05 ± 0.08 under ad libitum feeding. Growth rate from 50 to 150 days of age spans the weaning period and is therefore a composite of pre and post-weaning growth rate. It appears slightly more heritable than its terminal 150-day weight in the sire-line (Table 6.1). Fahmy and Bernard reported pooled heritabilities of 0.07 and 0.12 for growth rate from 56 to 140 days and growth rate from birth to 56 days respectively.

Of primary interest in this study are the heritabilities of ultrasonic backfat thickness and daily gain on performance test, since these are the objects of selection. The estimates obtained here fall within the range reported in the literature, with the exception of the estimate of 0.65 ± 0.11 for daily gain which is greater than most published values (e.g. see Table 2.1 abridged from Fredeen, 1971). Smith and Ross (1965) found a heritability of 0.74 for average carcass backfat in 2,296 British Landrace pigs, and Smith, King and Gilbert (1962) gave values all greater than 0.60 for four individual carcass backfat depths in 1,976 Large Whites; pigs in both studies being fed to appetite at national testing stations. Stockhausen and Boylan (1966), on the other hand, reported much lower pooled estimates of 0.11 ± 0.04 and 0.09 ± 0.19 from variance and regression analyses of average mechanical ruler probe in the Managra, individual estimates ranging from below zero to

0.56. Roy et al. (1968) later estimated the heritability of carcass backfat in the same line of pigs as 0.35 ± 0.12 from paternal half-sib correlation. Berruecos et al. (1970) indicated an average weighted heritability from various covariances among relatives of 0.38 ± 0.02 for live average ruler probe in the synthetic Red Line, with a corresponding realised estimate of 0.27 ± 0.09 from selection response. For post-weaning daily gain Smith et al. (1962; 1965) reported heritabilities of 0.14 for both Large White and Landrace. Stockhausen and Boylan gave average values of 0.25 ± 0.04 and 0.30 ± 0.11 by regression and sib analysis in the Managra, and Ward et al. (1964) found values of 0.26 ± 0.10 and 0.38 ± 0.09 by variance and intrasire regression analysis for post-weaning gain in the first two Minnesota lines. Total or phenotypic variance of growth rate and backfat (Table 6.1) in the sire-line appears adequate and at least as great as in other well-controlled pig populations. The apparently large differences found here between heritability estimates from the two methods are hard to explain other than by sampling variation. However, in the presence of maternal effects the estimate obtained by daughter-dam regression might be expected to exceed that obtained by half-sib correlation, as was the case for both measures of growth rate.

The estimates of heritability presented in Table 6.1 would seem to indicate that there are no striking differences in the proportions of additive genetic variation between the A.B.R.O. sire-line and other pig populations. With this in mind it would be of interest to know whether heritability has changed within the sire-line during its development. Data for the first twelve years were therefore divided into two roughly equal periods and heritabilities of three traits estimated separately by paternal half-sib correlation for each as shown in Table 6.2. With so few sires the standard errors of heritabilities are large and differences between the two periods clearly non-significant, but the direction of changes will at least provide grounds for speculation.

Only the heritability of average ultrasonic backfat thickness appears to show any change, increasing from 0.54 in the first period, when maximum phenotypic response was obtained (Figure 5.1), to 0.71 in the second period when there was no response at all. On the other hand, the additive genetic variance of backfat suffered a slight decrease over the same period (Table 6.2), so that the improvement in heritability is apparently the result of a decline in environmental variation, possibly associated with the introduction of more well-controlled performance testing in 1966. Unlike backfat the additive genetic variance of 150-day weight appears to have doubled in later years while heritability has remained unchanged. As the change in the estimate of genetic variance was only one half of its standard error the increase cannot be taken too seriously, but the increase in phenotypic variance appears substantial and may be due to within-pen competition between litter-mates when on performance test.

6.3.2 Maternal and Environmental Variance.

The proportions of variance due to "maternal effects" $(\hat{\sigma}^2_M/\hat{\sigma}^2_P)$, which influence all the members of a single litter, show very much the expected pattern for the 7 traits examined in Table 6.1. The proportion of "maternal" variance reached a maximum of 34 per cent for body weight at 50 days, falling

Table 6.2

Genetic and Phenotypic Variability of Three Traits in Early (1960-1966) and Late (1967-1971) Periods During Development of the A.B.R.O. Sire-Line.

Parameter	1960 - 1966			1967 - 1971		
	150-Day Weight (lbs.)	Growth Rate 50-150 days (lbs./day)	Corrected Av. Backfat (cms.)	150-Day Weight (lbs.)	Growth Rate 50-150 days (lbs./day)	Corrected Av. Backfat (cms.)
Between Sire d.f.	47	47	47	65	65	65
Phenotypic Standard Deviation ($\hat{\sigma}_P$)	17.8	0.15	0.33	21.8	0.19	0.29
Heritability ($\hat{h}^2=\hat{\sigma}_A^2/\hat{\sigma}_P^2$) with Standard Error	0.11 (0.21)*	0.16 (0.20)	0.54 (0.20)	0.15 (0.19)	0.15 (0.19)	0.71 (0.18)
Additive Genetic Variance ($\hat{\sigma}_A^2 = 4\hat{\sigma}_S^2$) with Standard Error	33.9 (62.4)*	0.0037 (0.0044)	0.0595 (0.0239)	69.8 (75.3)	0.0056 (0.0054)	0.0573 (0.0164)

*estimated standard error

off to 21 per cent by 150 days of age. "Maternal" effects for traits measured on performance test, backfat and daily gain, were very small as expected since litters were split up after weaning and were no longer influenced by the dam or by an immediate common environment. Smith et al. (1962; 1965) found slightly greater proportions of "maternal" variance of 15 per cent for Large Whites and 11 per cent for Landrace in daily gain at national testing stations, but they found no "maternal" variance for backfat.

Two points of particular interest arise from the observed "maternal" variances. Firstly it is perhaps surprising that there should be a maternal effect on teat number. Since this is fixed at birth one may conclude either that there is an intra-uterine effect on teat numbers, or alternatively that the figure found here does not differ significantly from zero. Secondly, the maternal "carry-over" after weaning to 150-day weight appears to be rather large. Both of these observations could possibly be explained to some extent by the presence of non-additive genetic variation, especially since there might be heterosis in the line following the continuous addition of diverse gentoypes in each generation. The amount of heterosis in backfat thickness would normally be expected to be small (e.g. Sellier, 1970) so that values of zero for proportion of "maternal" variance in backfat might indicate the absence of dominance and epistasis as well as true maternal effects.

The proportions of residual or "environmental" variance are of course complementary to the sum of the other two sources of variation, but for daily gain on test and backfat are higher than those reported by Smith et al. (1962; 1965) under standardised conditions. In the A.B.R.O. sire-line unequal numbers of pigs per pen together with intra-pen competition in later years, and outdoor paddock conditions in earlier years may account for part of the environmental variance. The very high phenotypic standard deviation of 20 lbs. for 150 day weight (Table 6.1) implies that there may be differences of 80 lbs between pigs at that age. All the pigs contributing to this figure were successfully measured ultrasonically for backfat at 180 lbs live weight, and so this gives some idea of the magnitude of environmental effects on the population under test. Disease may unfortunately account for a substantial portion of the environmental variation on performance test in some generations.

6.3.3 Genetic and Phenotypic Correlations.

Estimates of genetic and phenotypic correlations from covariance analysis and of genetic correlations from intrasire regression are shown in Table 6.3. Numbers of pigs associated with each figure are those given in Table 6.1 for the lower of the two traits in each pair. Genetic correlations were subject to large standard errors, and some estimates from sib and regression analysis were in striking disagreement. For this reason they will be discussed only very briefly here. Phenotypic correlations followed more of the expected pattern and had lower standard errors.

Fahmy and Bernard (1970) reported positive and relatively high genetic and phenotypic correlations among body weights at birth, 56 and 140 days and post-weaning growth rate, and this has been the general finding of other authors. Corresponding phenotypic correlations in the A.B.R.O. sire-line were all positive, though genetic correlations were variable.

Table 6.3.

Estimates of Phenotypic Correlations (above the diagonal) and Genetic Correlations (below the diagonal) in the A.B.R.O. Sire-Line with their approximate standard errors (in brackets). Genetic Correlations are presented from Half-Sib (upper) and Daughter-Dam (lower) analyses.

Trait	Teat Number	Birth Weight	50 Day Weight	150 Day Weight	Daily Gain from 50-150 Days	Average Backfat	Daily Gain on Test (60-180 lbs.)
Teat Number		0.12 (0.02)	0.07 (0.03)	0.03 (0.03)	0.02 (0.03)	-0.01 (0.05)	-0.04 (0.04)
Birth Weight	-0.15 (0.37) >1.00		0.51 (0.02)	0.32 (0.03)	0.21 (0.03)	-0.14 (0.03)	0.14 (0.04)
50 Day Weight	0.33 (0.35) >1.00	0.60 (0.21) -*		0.56 (0.02)	0.32 (0.03)	-0.06 (0.03)	0.13 (0.04)
150 Day Weight	-0.62 (0.24) 0.94 (0.04)	0.12 (0.34) -0.34 (0.54)	0.59 (0.24) -0.23 (0.82)		0.96 (0.002)	0.11 (0.03)	0.63 (0.02)

Table 6.3 (cont.)

Trait	Teat Number	Birth Weight	50 Day Weight	150 Day Weight	Daily Gain from 50-150 Days	Average Backfat	Daily Gain on Test (60-180 lbs.)
Daily Gain from 50 to 150 Days	-0.72 (0.18) 0.69 (0.15)	-0.05 (0.32) -0.31 (0.47)	0.36 (0.30) -0.33 (0.65)	0.94 (0.03) 0.99 (0.01)		0.15 (0.03)	0.67 (0.02)
Average Backfat	0.22 (0.24) -0.11 (0.28)	-0.38 (0.18) >1.00	-0.56 (0.18) >1.00	-0.12 (0.23) 0.54 (0.23)	0.08 (0.22) 0.46 (0.22)		0.20 (0.03)
Daily Gain on Test (60-180 lbs.)	-0.68 (0.19) 0.45 (0.19)	-0.08 (0.27) 0.54 (0.21)	0.37 (0.28) -*	0.74 (0.20) >1.00	0.66 (0.20) 0.95 (0.02)	-0.06 (0.21) 0.86 (0.05)	

*Negative daughter-dam covariance estimates.

Some comfort is derived from the expectedly high average figure of 0.97 for the genetic correlation between 150-day weight and preceding growth rate. With the exception of birth and 50-day weights average sire-line genetic correlations with teat number appear close to zero, as do all phenotypic correlations except perhaps birthweight.

Both genetic and phenotypic correlations of backfat with the two measures of growth rate were found to be positive on average in the sire-line (Table 6.3). Smith et al. (1962; 1965) reported values close to zero for both correlations in Large Whites, and a genetic correlation of -0.26 in Landrace. Summarising the results of 8 separate studies they also put forward average values of -0.15 and -0.07 for genetic and phenotypic correlations between carcass backfat and daily gain. Stockhausen and Boylan (1966) indicated a moderate negative correlation of -0.24 for live backfat probe and growth rate in the Managra. It is therefore tempting to conclude that the A.B.R.O. sire-line might be rather unusual in having a positive genetic correlation between growth rate and backfat, and this view would be supported by the relatively high positive phenotypic correlation between the two traits. Smith and Ross (1965), for example, found a correlation of 0.86 between pooled estimates of genetic and phenotypic correlations, and suggested that in the absence of reliable estimates of genetic correlations it might be better to estimate them from the phenotypic correlations.

6.3.4 Maternal and Environmental Correlations.

Estimated "maternal" and "environmental" correlations among 7 traits in the A.B.R.O. sire-line are set out in Table 6.4. "Maternal" correlations, arising from influences of the dam environment which affect more than one character, were positive and high among successive body weights and 50 to 150-day growth rate as expected. "Maternal" correlations involving backfat were predictably low and zero with both measures of growth rate. Pre-weaning and 150-day weight "maternal" effects had a lesser influence on growth rate on test than on growth rate to 150 days. A negative correlation of -0.38 between 50-day weight and growth rate on test is surprising but may represent evidence of compensatory growth on leaving the maternal environment. For example pigs in large litters may have their pre-weaning growth limited by milk supply, while their post-weaning growth on ad libitum feeding would subsequently be expressed to the full, showing a compensatory effect.

"Environmental" correlations, representing residual correlations between environmental deviations as well as various non-additive genetic effects, show the expected pattern. On the whole the "environmental" correlations of all traits with teat number and ultrasonic backfat were positive but low, while correlations among body weights and gains were rather greater.

Table 6.4.

Estimates of Maternal Correlations (above the diagonal) and Environmental Correlations (below the diagonal) among 7 Traits in the A.B.R.O. Sire-Line.

Trait	Teat Number	Birth Weight	50 Day Weight	150 Day Weight	Daily Gain from 50-150 Days	Average Backfat	Daily Gain on Test (60-180 lbs.)
Teat Number		0.34	-0.06	0.40	0.49	-0.01	-0.00
Birth Weight	0.16		0.52	0.65	0.56	-0.00	0.11
50 Day Weight	0.02	0.41		0.73	0.46	0.07	-0.38
150 Day Weight	0.14	0.51	0.58		0.94	0.11	0.26
Daily Gain from 50-150 Days	0.13	0.45	0.39	0.98		0.00	0.51
Average Backfat	-0.07	0.16	0.20	0.20	0.17		0.00
Daily Gain on Test (60-180 lbs.)	0.06	0.31	0.13	0.68	0.72	0.35	

6.4 Conclusions.

The main result from the foregoing analysis is that no great difference was found between the estimated heritability of backfat thickness in the A.B.R.O. sire-line and in other pig populations. There was no suggestion that heritability might be so low as to obstruct the selection programme, or that it might have been significantly raised by the pooling together of many breeds. There was, however, an indication that the heritability of backfat might have increased slightly during development of the line, but this was due to a reduction in environmental variation rather than to an increase in additive genetic variation. There was also evidence of a positive genetic association between growth rate and backfat which may be peculiar to this population. Backfat and daily gain on test were relatively unaffected by the common litter environment.

The question arises of whether any of the parameter values hitherto used in the sire-line selection index, and shown in Table 6.5, should be replaced by their estimates from this study. Cunningham (1972) reviewed the consequences of poor parameter estimation in an index and concluded that, while errors in heritabilities have a relatively small effect, errors in phenotypic and genetic correlations may be more serious. Heritability estimates of backfat and daily gain found here span those previously used in the index, and no change would probably be advisable. The only correlation which could be estimated was that of backfat with daily gain, and the unusual positive estimate of 0.20 could possibly be substituted for the value of 0.00 previously assigned to both

Table 6.5.

Parameter Values Used in the A.B.R.O. Sire-Line Selection Index:

Phenotypic Standard Deviations, Economic Weights, Phenotypic Correlations (above the diagonal), Genetic Correlations (below the diagonal) and Heritabilities (on the diagonal).

Trait	Phenotypic Standard Deviation	Economic "Weight"	Daily Gain on Test	Food Conversion Ratio	Corrected Av. Backfat
Daily Gain on Test (lbs/day)	0.20	1.8	0.30	-0.6	0.0
Food Conversion Ratio (lbs food/lb L.W.G.)	0.40	-4.8	-0.7	0.40	0.4
Corrected Average Backfat (cms. at 180 lbs. L.W.)	0.25	-5.4	0.0	0.5	0.50

phenotypic and genetic correlations. Values of 0.20 lb / day and 0.25 cm previously used for the standard deviations of daily gain and backfat respectively could also be replaced by their estimates of 0.24 lb/day and 0.31 lb/day from this analysis. In addition maternal effects could be disregarded for the two traits.

Chapter 7. The Performance Test.

7.1 Introduction.

The previous two chapters have shown that while there has been little phenotypic improvement in selected traits in the A.B.R.O. sire-line since 1965, genetic variability appears adequate for daily gain and backfat. The beginning of the period during which there was little apparent change in average backfat roughly coincides with the introduction of performance testing and a selection index (Figure 5.1), and the object of this chapter will therefore be to bring certain aspects of the performance test under closer scrutiny.

As explained in Chapter 3 both boars and bilts were performance tested between 60 and 180 lbs. live weight, and then selected on an index combining growth rate, pen food conversion ratio and average weight-corrected ultrasonic backfat. Before 1971 boars were tested either singly or in pairs in outdoor huts, but in 1971 they were tested either outdoors singly or indoors in pairs. Gilts were tested indoors by litter groups. All pigs were preliminarily screened immediately after completing test by means of a simple index consisting of growth rate and food conversion ratio added together, enabling culls to be sold at bacon weight.

Attention will be concentrated on four main areas:

(1) the effect of boar performance test environment,

(2) the accuracy of ultrasonic backfat measurements,

(3) the need for correction for live weights at start and finish of test,

(4) an examination of the preliminary and final selection indices.

In the following analyses an attempt will be made to discover whether one or more of these factors could in some way be responsible for arresting genetic progress, and to see whether any worthwhile improvement could be introduced into the existing selection procedure. Uppermost on the list of possible causes of poor selection response might be genotype by boar test environment interactions, a faulty selection index or errors in ultrasonic backfat measurements. Each topic will now be considered separately, although they are to a certain extent inter-related, and most of the discussion will be postponed until the end of the chapter.

7.2 The Effect of Boar Performance Test Environment.

The consequences of testing boars either singly or in pairs in the outdoor accommodation between 1968 and 1970 were investigated by means of an analysis of variance in order to demonstrate the statistical importance of differences between single and double penning, and hopefully to uncover any immigrant versus native genotype by environment interactions. Breed by pen environment interactions might, for example, be expected if there are differences in social effects such that some breeds respond better to pairing or solitude than others.

In 1971 when boars were penned outdoors singly or indoors in pairs, the effects of number in the pen and test location were confounded. With the intention of separating the effect of single versus double penning from the effect of indoor versus outdoor housing, a trial was set up for the 1972 sire-line generation in which boars were performance tested either singly or in pairs, both indoors and out in a 2 x 2 factorial design.

Unfortunately, owing to an unprecedentedly poor conception rate and farrowing, roughly only one half of the expected number of boars were born. The results are nevertheless presented here.

7.2.1 Material and Methods.

A general least squares computer programme for the analysis of variance (Harvey, 1964) was used for the analysis of boar performance test data between 1968 and 1970, when all the boars were penned outdoors. For the purpose of this analysis only, boars were classified into two rather arbitrary "genotypes": Native and Immigrant. Immigrants were first crosses of pure breeds with the sire-line and Natives were pure sire-line animals, as explained in Chapter 3. Immigrants chiefly consisted of F_1 crosses with Large Whites, Hampshires, Pietrains, Lacombes, Yorkshires and their various inter-crosses in 1968 and 1969, and with Large Whites and Norwegian Landrace in 1970. Several of the Immigrant breed combinations were represented by a single sire and different combinations of breeds were present in each year, and as a result it would have been of little benefit to classify the various breed combinations separately. Pigs in the analysis were the progeny of 14, 10 and 16 sires for the three generations respectively.

"Pen number", referring to single versus double penning, years and "genotypes" were fitted as main effects together with their two-factor interactions. The analysis was repeated for the three performance-recorded traits: daily gain on test, food conversion ratio, and average ultrasonic backfat corrected for liveweight at time of measurement. For boars tested in pairs, the fact that food conversion was measured on a pen basis was ignored, and pen averages were attributed to individual boars. Because pen means were based on only two observations this is expected to cause only a small reduction in the error variance, and consequently a slight over-estimation of variance ratios.

In order to separate the effects of number of boars in the pen and test location, the 1971 method of performance testing boars, described in Chapter 3, was slightly modified the following year. To achieve a 2 x 2 factorial design, double-penning was once again introduced to the outdoor boar huts and single-penning was introduced for the first time to the indoor accommodation. Centre partitions were removed from some of the yards of the outdoor paired huts, making single runs of roughly the same area as the indoor pens. In each new double run the boars were fed together from one ad libitum feeder, and although all pairs had access to two sleeping area they invariably shared the same hut. Similarly, boars were placed on their own in some of the pens in the Danish-type fattening house where normally two boars or up to five gilts would be tested. It was rarely possible for one dam to contribute boars to all four test environments, in which case 6 "testable" boars would have been required. Instead an effort was made to distribute families as widely as possible over environments, keeping the numbers of progeny on each approximately equal. The pelleted ration fed in 1971 (Chapter 3) was fed ad libitum, but with the addition of "Grofas" (trademark for I.C.I. Quindoxin non-antibiotic growth promoter) at 50 gms per ton. Almost all the boars in the Danish-type house suffered from an attack of enteritis towards the end of the test period, and were treated with a variety of wide-spectrum antibiotic preparations. Recovery was complete and there were no losses.

An analysis of variance was again performed with the aid of a standard programme. In this case individuals were classified into 4 genotypes or "breeds", to avoid confusion with the previous analysis, comprising pure sire-line and F_1 sire-line crosses with Large White, Norwegian Landrace and commercial "Harris Hybrid". The first three "breeds" were contributed by 9, 4 and 1 sire respectively, and the "Harris Hybrids" were the progeny of 1 dam only. Young boars taking part in the trial were the progeny of a total of 22 dams. Main effects fitted were "breeds", locations (indoors or out) and "pen number" (one or two boars per pen) with first-order interactions. The analysis was carried out for the three traits as before, treating pen food conversions as individual observations. There were two measurements per pig for each trait, taken at intervals of roughly one week for the purpose of estimating repeatabilities (section 7.3).

7.2.2 Results.

1968 - 1970 Boar Performance Test Results.

Means and numbers of pigs by subclasses for boar performance testing between 1968 and 1970 are given in Table 7.2.1. The corresponding analysis of variance is shown in Table 7.2.2. Differences between years were highly significant for food conversion and significant at a lower level for average

Table 7.2.1.

Least Squares Boar Performance Test Means by Years, "Genotypes" (Natives versus Immigrants), and Pen Number (Single versus Double) between 1968 and 1970 in the A.B.R.O. Sire-Line. Approximate Standard Errors are shown in Brackets.

Number of Boars in Pen	Year (Generation)	1968		1969		1970	
	"Genotype"	Native	Immigrant	Native	Immigrant	Native	Immigrant
Single-Penned	Number of Pigs	22	19	27	13	35	10
	Daily Gain (lbs./day)	1.65(0.04)	1.74(0.04)	1.76(0.04)	1.67(0.05)	1.71(0.03)	1.71(0.06)
	Food Conversion Ratio (lbs. feed/ lb.L.W.G.)	3.23(0.08)	3.20(0.08)	3.20(0.07)	3.45(0.10)	3.58(0.06)	3.32(0.11)
	Corrected average Backfat (cms.)	1.77(0.05)	1.82(0.06)	1.73(0.05)	1.95(0.07)	1.67(0.04)	1.64(0.08)
Double-Penned	Number of Pigs	22	14	32	4	15	13
	Daily Gain (lbs./day)	1.59(0.04)	1.72(0.05)	1.62(0.03)	1.61(0.10)	1.64(0.05)	1.64(0.05)
	Food Conversion Ratio (lbs. feed/ lb. L.W.G.)	3.17(0.06)	2.87(0.08)	3.19(0.05)	3.15(0.15)	3.38(0.08)	3.59(0.08)
	Corrected average Backfat (cms.)	1.62(0.06)	1.77(0.07)	1.70(0.05)	1.89(0.13)	1.57(0.07)	1.82(0.07)

Table 7.2.2.

Analysis of Variance Table for Boars Performance Tested Outdoors Either Individually or in Pairs (Pen Number) Between 1968 and 1970.

Source	d.f.	Mean Square		
		Daily Gain (lbs./day)	Food Conversion Ratio (lbs feed /lb. L.W.G.)	Average Backfat (cms.)
Years	2	0.0052	2.3292***	0.2968
Pen Number	1	0.2455**	0.4435	0.0260
"Genotypes"	1	0.0133	0.0051	0.9326***
Years x Pen Number	2	0.0262	0.0883	0.0692
Years x "Genotypes"	2	0.1117*	0.3460	0.0764
Pen Number x "Genotypes"	1	0.0105	0.0082	0.1967
Remainder	216	0.0349	0.1177	0.0654$^{\$}$

$^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$.

$^{\$}$ 215 d.f. for remainder after adjustment for liveweight.

ultrasonic backfat. Table 7.2.1 indicates that these differences were the result of a steady worsening of food conversion over the three years, and an improvement in backfat in 1970. Part of the difference in food conversion between years may be explained by variation in outdoor conditions, since in wet years feed hoppers tended to become contaminated with mud leading to rejection by the pigs, and any spilled meal was quickly lost underfoot. Growth rate was the only trait significantly affected by the number of boars in the pen, and was consistently lower for double-penned boars compared to singles. A possible explanation for the difference could be the existence of a social effect on two boars in the same pen, resulting either in increased activity and a higher maintenance requirement for energy or alternatively in a reduced degree of boredom leading to a lower food consumption. That there was no significant difference in food conversion between the two types of penning would tend to favour the second explanation, but as the 5% level was only just exceeded it would be unwise to draw a definite conclusion. With double-penning there was a slight non-significant increase in the within-subclass variance of individual growth rate measurements to 0.036 $(\text{lbs.})^2$, compared to 0.034 $(\text{lbs.})^2$ for single boars. A significantly greater variance for double-penned boars could have been taken as evidence of a competition effect, one boar tending to thrive at the expense of its companion so causing a divergence in growth rate. Natives and Immigrants, "genotypes", differed significantly in backfat thickness alone, and with the exception of single-penned boars in 1970

Immigrants were considerably fatter than Natives (Table 7.2.1). A discussion of the consequences of immigration will be postponed until the next chapter.

None of the year by pen number interactions approached significance indicating that any differences between single and double penning were the same in all years. The year by "genotype" interaction was significant only for daily gain, but this was unexpected since the corresponding mean squares for the year and "genotype" main effects were nonsignificant, so that the present result was attributed to chance. The grouping of all immigrant breed combinations together as a single class in the analysis may have contributed to the year by "genotype" interaction, as a result of varying but small differences between immigrants and natives from year to year. This type of interaction would not be expected to interfere with selection which is practised within years and pen types. None of the pen number x "genotype" interactions was significant, and again it is accepted that this may be the result of treating all immigrant crosses as a single genotype. Never-the-less, the classification successfully exposed a "genotype" difference in backfat, yet did not show any interaction. The absence of a "genotype" by pen number interaction would indicate that there is no danger of a serious change in ranking between Immigrants and Natives penned singly or in pairs, and that the selection or rejection of potential immigrants in one environment could be expected to have been duplicated in the other.

1972 Comparison of Boar Performance Test Environments.

The performance and numbers of boars by test environments and "breeds" in the 1972 generation of the sire-line are shown in Table 7.2.3, and the analysis of variance is given in Table 7.2.4. The presence of one missing subclass, "Harris Hybrid" outdoor double-penned boars, did not affect the estimation of two factor interactions. All main effect and interaction mean squares were tested against the between-pig mean square. [redacted] "Breed" differences among pure sire-line boars and sire-line F_1 crosses with three prospective immigrant breeds were detected in daily gain and average ultrasonic backfat. As in earlier generations, immigrants were fatter on average than natives, but pure sire-line boars grew more slowly (Table 7.2.3). There were no significant differences between single- and double-penned boars, and the observed superiority of outdoor single-penned boars between 1968 and 1970 was not confirmed. A significant difference between performances in the outdoor boar huts and in the Danish-type testing house was shown for growth rate and food conversion. The food conversion ratio was consistently greater in the outdoor environment, and the rate of growth was with one exception slower. Both these differences could be explained by lower outdoor temperatures, although the poorer outdoor food conversion might have been partly the result of increased wastage of feed. However, the introduction of a pelleted feed in 1971 was designed to minimise the amount of spillage in both environments. There were no obvious effects

Table 7.2.3.

Least Squares Boar Performance Test Means by "Breeds" and Environments for the 1972 Generation of the A.B.R.O. Sire-Line. (Where Appropriate, Approximate Standard Errors are Shown in Brackets).

Number in Pen	"Breed"	Sire-Line		Large White		Norwegian Landrace		Harris Hybrid	
	Location	IN	OUT	IN	OUT	IN	OUT	IN	OUT
One Pig per Pen (Single)	Number of Pigs*	7	8	3	5	1	1	1	2
	Daily Gain (lbs/day)	1.86 (0.08)	1.63 (0.12)	1.92 (0.12)	1.81 (0.09)	1.86	1.36	2.01	1.54 (0.08)
	Food Conversion Ratio (lbs feed per lb. gain)	3.07 (0.11)	3.48 (0.19)	3.10 (0.15)	3.15 (0.06)	3.22	3.78	2.94	3.12 (0.15)
	Corrected Average (Ultrasonic Backfat (cms.)	2.08 (0.09)	2.05 (0.10)	2.29 (0.13)	2.41 (0.09)	2.43	2.24	2.49	2.38 (0.05)
Two Pigs per Pen (Double)	Number of Pigs*	8	12	4	2	2	2	2	0
	Daily Gain (lbs/day)	1.38 (0.12)	1.42 (0.08)	2.07 (0.13)	1.65 (0.25)	1.79 (0.14)	1.58 (0.08)	1.72 (0.04)	-
	Food Conversion Ratio (lbs feed per lb. gain)	3.31 (0.14)	3.60 (0.13)	2.76 (0.05)	3.07 (0.03)	3.01 (0.07)	3.66 (0.08)	2.98 (0.03)	-
	Corrected Average Ultrasonic Backfat (cms.)	2.03 (0.08)	2.05 (0.10)	2.55 (0.09)	1.89 (0.14)	2.33 (0.21)	2.26 (0.12)	2.71 (0.11)	-

*Two Measurements per Pig (See Text).

Table 7.2.4.

Analysis of Variance Table for Boar Performance Test Data in the 1972 Generation of the A.B.R.O. Sire-Line.

Source	d.f.	Mean Squares		
		Daily Gain (lbs./day)	Food Conversion Ratio (lbs feed /lb. L.W.G.)	Average Backfat (cms.)
"Breeds"	3	0.38738^{*}	0.70926	0.83393^{**}
Pen Number	1	0.15148	0.02306	0.00005
Locations	1	0.76152^{*}	2.07798^{**}	0.17017
"Breeds" x Pen Number	3	0.23665	0.26409	0.02739
"Breeds" x Locations	3	0.10273	0.14161	0.08056
Pen Number x Locations	1	0.00888	0.02110	0.11700
Between Pigs	46	0.13615	0.26784	$0.15560^{\$}$
Within Pigs	60	0.00343	0.00750	0.00717

$^{*}P < 0.05$

$^{**}P < 0.01$

$^{***}P < 0.001$

$^{\$}45$ d.f. after adjustment for liveweight.

on the performance of indoor-housed boars which could be attributed to the outbreak of enteritis.

None of the two factor interactions was significant (Table 7.2.4), the majority of the variance ratios being less than 1.00. [redacted]

The 1972 trial, based on only 60 pigs, has confirmed the finding of the previous analysis that "breed" or "genotype" by pen number (single versus double) interactions involving the sire-line and its potential immigrants are unimportant. In addition the 1972 trial has indicated that the division of boar testing between indoor and outdoor accommodation is unlikely to lead to genotype x environment interactions which would seriously affect the selection of immigrants. However, because of the arbitrary nature of the "genotype" classification in the first analysis and the small numbers of pigs in the second, the degree of certainty that such interactions do not exist is undoubtedly very low.

7.3 The Accuracy of Ultrasonic Backfat Measurements.

Two methods were used to check the accuracy of ultrasonic backfat measurements in the 1972 generation of the A.B.R.O. sire-line. Firstly, repeatabilities were calculated after measuring each pig twice at an interval of roughly one week. Secondly, ultrasonic fat depths were correlated with carcass measurements taken after slaughter at the same sites in a sample of culled pigs. At the same time the opportunity was also taken to obtain the repeatabilities of growth rate and food conversion ratio.

7.3.1 Material and Methods.

Pigs taking part in the investigation were sire-line and F_1 sire-line cross boars and gilts from the 1972 generation on routine performance test. The management of the boars was described in detail in Section 7.2.1, and the gilts were penned in litter-groups of up to 5 in a Danish-type fattening house as in earlier generations (Chapter 3). The pigs were first measured ultrasonically as soon as possible after reaching 180 lbs. live weight, as indicated by weekly weighings. At the same time the self-feeder and its contents in each pen were weighed so that pen food consumption and therefore food conversion could be obtained. When one pig finished test before its pen mates it was credited with the pen food conversion on that day for the purpose of this investigation and for screening on the preliminary selection index. Pen mean food conversion was later taken as the average of pen food conversions at the dates on which each pig in the pen completed test. Ultrasonic backfat and food consumption measurements were repeated after seven days, so that in effect the end of test procedures and calculations were carried out twice for each pig. Owing to a breakdown by the ultrasonic machine roughly halfway through the trial the interval between measurements was extended to 12 days for one batch of pigs only, and thereafter returned to an 8 day interval. The outbreak of enteritis which affected indoor-housed boars (Section 7.2.1) also involved most of the gilts, which were housed in the same building, and although there was a rapid response to antibiotics a handful of pigs lost rather than gained weight between measurements.

The ultrasonic machine was a SONATEST model TE6 of the standard A-scan type operating at 5.0 megacycles per second, with oscilloscope display and calibrated in half-millimetres. Readings were taken at three sites on each side of the back: approximately 6.5 cms off the mid-line as measured by the distance between the tip of the index finger and thumb, slightly behind the shoulder, in the middle of the back and at the loin over the _gluteus medius._ Hair was not clipped at each site, but a spot of motor oil was used to ensure good contact. At all sites ultrasonic reflections were obtained from two distinct interfaces at different depths. The first, referred to here as layer 1, was taken to represent either connective tissue, a thin sheet of muscle in the fat layer or the interface between fat layers of different densities, but was none-the-less recorded. The second reading, always greater than the first and referred to as layer 2, was taken to represent the total depth of subcutaneous fat and was used for selection. Right-hand measurements were taken before left at each position, and measurements were immediately repeated if the two sides differed by more than five half-millimetres. While being measured pigs were totally restrained in a standing position with their heads raised in a specially designed crate. At the out-door boar huts the crate and measuring equipment were moved from run to run in the field, while in the Danish testing house the crate was placed at the end of a race through which the pigs were circulated by pens. The pigs were always weighed at the time of measurement. A single experienced operator, who had measured all the previous sire-line generations, was used throughout. Estimated average backfat was routinely calculated as the mean of the six total (layer 2) ultrasonic readings expressed in centimetres and corrected to 180 lbs. live weight by a linear regression of 0.01 cm./lb.

Repeatabilities of each of the 12 individual ultrasonic backfat readings and the 3 traits routinely measured on performance test were calculated after computing the variance between and within pigs from within subclasses, with the aid of a standard least squares programme (Harvey, 1964). Boar subclasses were "breed"-testing house wing combinations since gilts occupied two separate wings of the same building. All individual ultrasonic readings as well as average backfat were adjusted for live weight at the time of measurement. Repeatabilities and their approximate standard errors were calculated according to the method described by Becker (1967). They were estimated for boars and gilts separately, and then for indoor and outdoor housed boars separately since both the operator's working environment and the pigs' environment were different. A total of 57 boars and 77 gilts contributed to the analysis. Subclasses containing only 1 boar (Table 7.2.3) were omitted from the analysis. Average live weights at the time of the first and second sets of measurements on each pig were 187 and 201 lbs respectively.

The carcass fat depths of boars and gilts which were culled on the basis of the preliminary selection index were measured from one to three hours after slaughter at a local abattoir. The pigs were slaughtered in the usual way by stunning and bleeding, after which carcasses were scalded and flailed, eviscerated, split and hung in a chill-room where the measurements were taken. In order to be able to locate the exact ultrasonic measuring sites on the carcass, the three right-hand sites on the back, at which the second set of live ultrasonic readings were taken, were marked with a tattoo which was clearly recognisable after death. Carcass fat depths off the mid-line were measured by introscope at the three tattooed sites on the right-hand half-carcass and at the corresponding unmarked sites on the left-hand side. Equivalent mid-line measurements at the shoulder, mid-back and loin were made with a steel rule on the split surface of the right side. The introscope, an optical probe which allowed off-the-mid-line measurements to be taken without cutting the carcass into segments, was of the type used routinely for carcass grading by the Meat and Livestock Commission, and was calibrated in millimetres. Carcass weights were not available. Carcass measurements were available on 52 of the 137 sire-line pigs measured alive ultrasonically.

Simple product-moment correlation coefficients of carcass with live ultrasonic fat depths were calculated from within sexes. Off mid-line and mid-line carcass fat depths were correlated with the average of the two total ultrasonic fat depth readings (layer 2) at the same site from the repeatability trial. Individual carcass measurements were adjusted for live weight on the day before slaughter, and first and second ultrasonic measurements at each site were weight-corrected before being averaged. The mean live weight for ultrasonic measurements was 192 lbs., but owing to delays between the second set of ultrasonic measurements and slaughter, mean live weight for the carcass measurements was 243 lbs. The averages of right and left measurements at the shoulder, mid-back and loin, and the average of mid-back and loin averages were included in the analysis as well as the mean of all six off-mid-line total depths used for selection. The pigs in this trial were, of course, a deliberately selected sample consisting of the poorest performing pigs tested, since the remainder were required for breeding.

7.3.2 Results.

Repeatability of Ultrasonic Fat Depths.

Means and within-subclass standard deviations and repeatabilities for boars and gilts are presented in Table 7.3.1. Means and standard deviations of upper-layer (layer 1) fat depths were roughly half those of the total (layer 2) depths at the same sites. Upper-layer fat depths were noticeably less repeatable than total depths only at the loin. All shoulder measurements were very slightly less repeatable than the others in boars, but otherwise no striking pattern emerges. There were no consistent differences in repeatabilities of right- and left-hand side measurements, although the right side was always measured first with the result that there may have been some dependence of left readings on right. Repeatabilities of the three performance test traits, average backfat, daily liveweight gain and food conversion ratio, were all satisfactorily high and marginally greater in boars than in gilts. The lower repeatibility of food conversion in gilts may be partly the result of the outbreak of enteritis in the indoor testing accommodation or alternatively the larger numbers of gilts per pen, but is otherwise difficult to explain.

A similar set of results for indoor versus outdoor housed boars are given in Table 7.3.2. In this case the ultrasonic

Table 7.3.1.

Least Squares Means, Within-Subclass Standard Deviations and Repeatabilities of 12 Ultrasonic Backfat Readings and 3 Traits for Boars and Gilts in the 1972 Generation of the A.B.R.O. Sire-Line.

Measurement		Mean		Standard Deviation		Repeatability	
		Boars	Gilts	Boars	Gilts	Boars	Gilts
Ultrasonic Backfat Readings (in half millimetres):							
Shoulder:	Right 1[*]	32.2	30.4	3.7	4.0	0.79[$]	0.83[$]
	Right 2	65.9	63.1	8.2	8.5	0.78	0.74
	Left 1	32.1	30.4	3.7	4.0	0.78	0.83
	Left 2	66.1	63.3	7.6	8.6	0.80	0.78
Mid-Back:	Right 1	23.4	22.0	2.8	2.9	0.86	0.78
	Right 2	36.3	34.8	5.4	5.7	0.87	0.85
	Left 1	23.4	22.1	2.6	2.9	0.87	0.81
	Left 2	36.5	35.0	4.9	5.6	0.88	0.78
Loin:	Right 1	26.5	26.4	3.8	4.3	0.82	0.81
	Right 2	41.2	42.4	6.2	6.8	0.90	0.86
	Left 1	26.3	26.7	3.8	4.3	0.83	0.84
	Left 2	41.5	42.7	6.2	7.0	0.86	0.89
Performance Test Traits.							
Average Ultrasonic Backfat (cms.)		2.25	2.21	0.27	0.31	0.92	0.91
Daily Gain (lbs/day)		1.69	1.64	0.27	0.28	0.97	0.93
Food Conversion Ratio (lbs feed/lb L.W.G.)		3.22	3.21	0.38	0.26	0.95	0.80

[*] Ultrasonic fat depths '1' and '2' refer to upper-layer and total fat depths respectively as explained in the text.

[$] Approximate standard errors range from 0.01 (for a repeatability of 0.95) to 0.06 (for a repeatability of 0.75).

Between boar d.f.=45; Within boar d.f.=56;
Between gilt d.f.=70; Within gilt d.f.=76.

Table 7.3.2.

A Comparison of the Within-Subclass Repeatabilities of 12 Ultrasonic Backfat Readings and 3 Traits for Indoor and Outdoor Performance Tested Boars in the 1972 Generation of the A.B.R.O. Sire-Line, with Corresponding Least Squares Means and Standard Deviations.

Measurement	Mean		Standard Deviation		Repeatability	
	Indoor	Outdoor	Indoor	Outdoor	Indoor	Outdoor
Ultrasonic Backfat Readings (in half millimetres):						
Shoulder: Right 1[*]	32.3	32.0	3.4	3.9	0.74[$]	0.82[$]
Right 2	67.4	64.3	8.1	8.1	0.71	0.83
Left 1	32.4	31.9	3.5	4.0	0.72	0.84
Left 2	67.1	65.2	7.7	7.6	0.69	0.89
Mid-back Right 1	24.0	22.7	2.4	3.0	0.76	0.91
Right 2	38.7	33.8	4.6	5.9	0.72	0.95
Left 1	24.1	22.8	2.3	2.9	0.80	0.93
Left 2	38.6	34.5	3.7	5.8	0.77	0.93
Loin: Right 1	26.6	26.4	3.4	4.0	0.74	0.86
Right 2	42.4	40.0	5.8	6.4	0.85	0.93
Left 1	26.6	25.9	3.3	4.2	0.70	0.88
Left 2	42.8	40.1	5.5	6.7	0.75	0.92
Performance Test Traits:						
Average Ultrasonic Backfat (cms.)	2.48	2.32	0.24	0.30	0.85	0.96
Daily Gain (lbs/day)	1.79	1.60	0.25	0.28	0.95	0.98
Food Conversion Ratio (lbs feed /lb L.W.G.)	3.04	3.41	0.28	0.44	0.95	0.95

[*] Ultrasonic fat depths '1' and''2' refer to upper-layer and total fat depths respectively as explained in the text.

[$] Approximate standard errors range from 0.04 (for a repeatability of 0.95) to 0.08 (for a repeatability of 0.70).

Between indoor boar d.f.=20; within indoor boar d.f.=25;
Betwwen outdoor boar d.f.=25; within outdoor boar d.f.=30.

repeatabilities of indoor-housed boars were consistently lower than those housed outdoors, to the extent that the estimated average backfat was 11% less repeatable. This is the reverse of what might be expected since the ultrasonic operator's working environment is stationary and more comfortable indoors. However, it is possible that the continuous streaming of pigs to and from the measuring crate indoors placed pressure on the operator to finish each pig more quickly, and therefore resulted in a higher incidence of inaccuracy. Alternatively, the repeatability may have been lowered as a result of the enteritis outbreak in the indoor housing, but this is unlikely because indoor food conversion and growth rate were no less repeatable, and food conversion was 15% more repeatable than for gilts in the same building (Table 7.3.1).

Correlation Between Ultrasonic and Carcass Fat Depths.

Weight-corrected means for culled boars and gilts and pooled within-sex standard deviations of the various ultrasonic and corresponding carcass measurements are shown in Table 7.3.3. In the table "Mid" refers to measurements taken on the split mid-line surface with a ruler, and "Average" refers to the mean of right and left intrascope readings at the same position along the back. Boar and gilt averages for both types of measurement are given in whole millimetres, and it can be seen that the introscope (carcass) readings were consistently lower than the ultrasonic (live) ones, in spite of being measured at a heavier weight. This could have resulted from the shrinkage of subcutaneous fat

Table 7.3.3.

Least Squares Means and Pooled Within-Sex Standard Deviations of Various Introscope Readings and their Corresponding Ultrasonic Measurements on the Live Animal, from the 1972 Generation of the A.B.R.O. Sire-Line.

Character	Ultrasonic (Live Animal). (millimetres)			Introscope (Carcass). (millimetres)		
	Boar Average	Gilt Average	Standard Deviation	Boar Average	Gilt Average	Standard Deviation
Shoulder:						
Mid	---	---	---	42.6	41.4	7.0
Right	34.6	36.4	4.0	30.5	30.7	6.0
Left	34.5	36.4	4.0	29.5	29.0	5.4
Average	34.5	36.3	3.9	30.1	29.9	5.3
Mid-Back:						
Mid	---	---	---	22.0	23.2	4.9
Right	19.5	19.2	3.0	16.8	18.4	4.7
Left	19.7	19.3	3.2	17.4	17.7	4.4
Average	19.1	19.9	3.1	17.1	18.0	4.5
Loin:						
Mid	---	---	---	20.1	22.0	6.0
Right	21.6	24.5	3.7	17.4	17.6	5.2
Left	22.0	24.5	3.7	18.5	19.6	5.7
Average	21.7	24.4	3.7	17.9	18.6	5.4
Average Mid-Back+/						

Table 7.3.3 (cont.)

Character	Ultrasonic (Live Animal). (millimetres)			Introscope (Carcass). (millimetres)		
	Boar Average	Gilt Average	Standard Deviation	Boar Average	Gilt Average	Standard Deviation
Average Mid-Back+ Loin (cms.)	2.04	2.21	0.32	1.75	1.84	0.47
Average Shoulder+ Mid-Back+Loin (cms)	2.51	2.68	0.32	2.17	2.21	0.43

Number of Boars = 28; Number of Gilts = 24.

on chilling after slaughter, and also from the removal or distortion of part of the skin by the flailing process. This type of discrepancy would be expected to be fairly constant and should therefore have little effect on the correlation. Standard deviations of introscope readings were, however, roughly 50% greater. Part of this difference stems from the fact that ultrasonic values were the means of two repeated measurements at the same site, part is undoubtedly due to an inexperienced introscope operator and part the result of measuring carcasses in varying states of chill. Both introscope and ultrasonic mid-backfat depths were less variable than at other sites.

Correlation coefficients of average total (layer 2) ultrasonic fat depths with corresponding carcass measurements at the same sites and at the mid-line are shown in Table 7.3.4. Correlations among off-mid-line fat depths (first column) were greatest at the mid-back, a little less at the loin and very much lower at the shoulder. Correlations of off-mid-line ultrasonic measurements with mid-line carcass depths ((second column) were greatest at the loin, closely followed by the mid-back, but those at the shoulder were once again smallest. The very low shoulder correlations with introscope measurements were not unexpected, since the greatest difficulty was experienced in determining the total fat depth. There were two reasons for this: firstly, the colour of the muscle did not appear to differ sufficiently from the colour of the fat in order to detect the true interface when viewed through the introscope, and secondly there appeared to be one or more layers of muscle or other tissue within the fat layer itself making it difficult to recognise the base of the

Table 7.3.4.

Simple Product-Moment Correlation Coefficients of Ultrasonic with Corresponding and Mid-Line Carcass Fat Depths, Pooled from within Sexes after Adjustment for Live Weight.

Character	Correlation Coefficient	
	Ultrasonic fat depth with corresponding carcass depth	Ultrasonic fat depth with mid-line carcass depth at same site
Shoulder:		
Right	0.27*	0.45*
Left	0.16	0.48
Average	0.22	0.46
Mid-Back:		
Right	0.82	0.63
Left	0.80	0.62
Average	0.85	0.63
Loin:		
Right	0.71	0.68
Left	0.72	0.70
Average	0.73	0.70
Average Mid-Back + Loin (cms.)	0.81	
Average shoulder + Mid-Back + Loin (cms.)	0.72	

*Standard errors range from 0.08 (for a correlation of 0.85) to 0.14 (for a correlation of 0.15), with 49 degrees of freedom.

Number of Boars = 28; Number of Gilts = 24.

subcutaneous fat. A lesser degree of difficulty, reflected by an improvement in the correlations, was experienced in measuring the mid-line carcass fat depths at the shoulder, because fat and muscle layers appeared to gradually merge rather than to show a sharp interface, and shrinkage of the fat often severely distorted the cut surface. Fat-muscle interfaces at the mid-back and loin were relatively clearcut for both types of carcass measurement, although mid-line fat depths were more difficult to determine accurately when carcasses had been untidily split. The correlations of right-hand ultrasonic with carcass fat depths were greater than those on the left only at the shoulder, indicating that incorrect location of the probing site, marked with a tattoo only on the right side of the carcass, may partly account for the poor off-mid-line correlation at the shoulder, but had little effect at other positions.

The reasonably satisfactory correlation of 0.72 between average backfat in the live pig and on the carcass was raised to 0.81 by omitting the shoulder measurements (Table 7.3.4). It is probable that these correlations would have been greater if the pigs could have been slaughtered within one week of the second set of ultrasonic measurements, rather than allowing more than three weeks to elapse.

7.4 The Importance of Correction for Live Weights at Start and Finish of Test.

In past performance-tested generations of the sire-line it has been the practice to adjust only average ultrasonic backfat thickness for live weight at the end of test. For this purpose a linear regression of 0.01 cm./lb was used (Chapter 3), calculated from a between-pig analysis under the implicit assumption that the between- and within-pig regressions do not differ. No correction was made for daily liveweight gain or food conversion ratio and no attention was paid to live weight at the start of test. The validity of the present backfat correction and the case for other possible corrections which might usefully remove variation due to body weights were investigated by linear regression analysis. As only one observation was available on each pig, the analysis was again confined to a between-pig approach and it was recognised that extension of the results to the within-pig situation might be invalid.

7.4.1 Material and Methods.

Data for the analysis were the performance test records of a total of 920 sire-line and F_1 sire-line cross boars and gilts between 1968 and 1971. Management during the test period was described in Chapter 3. In each year or generation the pigs were divided into 3 groups: single-penned males, double-penned males, and females, making a total of 12 year/test-type groups in all. The numbers of pigs in each group are shown below.

Test-Types: Years	Single-Penned Males	Double-Penned Males	Females
1968	43	36	183
1969	40	36	109
1970	45	28	134
1971	58	64	144

A computer programme was written to carry out a linear regression analysis according to the following model:

$Y_{ij} = \alpha_i + \beta_i X_{ij} + e_{ij}$, for $i = 1, \ldots\ldots, 12$ groups;

$j = 1, \ldots. J_i$ pigs in the i^{th} group,

where Y_{ij} is an individual observation on trait Y,

X_{ij} is an individual's live weight,

α_i is the height of the ordinate in group i,

β_i is the regression coefficient of Y_i on X_i in the i^{th} group,

e_{ij} is the deviation of Y_{ij} from the regression line.

Regressions were estimated in two stages. In the first an overall regression coefficient (β) was fitted by pooling sums of squares and cross-products from within each year/test-type group, under the null hypothesis that the slopes for individual groups (β_i) did not differ but that the group means, and therefore the ordinates (α_i), were different. In the second stage the sums of squares remaining after fitting β were used to fit separate slopes (β_i) for each group, providing a statistical test for a difference in slopes between groups. The analysis was performed for three Cases:

(1) regression of performance test traits on live weight at the end of test,

(2) regression of performance test traits on live weight at the start of test,

(3) regression of performance test traits, corrected for live weight at the end of test, on live weight at start of test.

The Case (3) analysis was intended to show the effect of correction for finishing weight on the regressions on starting weight. Traits were corrected to the overall mean live weight at the end of test. The analysis was conducted for growth rate and average backfat, and a reduced analysis based on 186 outdoor single-penned boars was carried out for food conversion. The use of pen mean food conversion was ruled out because all the pigs in a pen did not necessarily complete test on the same date. Mean squares for all effects were tested against the residual mean square. Means and standard deviations of live weights at start and finish of test may be seen in Table A4 of Appendix A.

7.4.2 Results.

Analysis of variance tables for Cases (1) to (3) are given in Table 7.4.1. Terms for the overall mean (α) and the means of year/test-type groups (α_i) were all highly significant, indicating real differences between groups as expected. Dealing first with Case (1), overall within-group regression coefficients (β) were highly significant for daily gain and backfat, but not for food conversion. Mean squares arising from the individual slopes (β_i) were all very low and non-significant, and it was therefore concluded that the common slope (β) would adequately describe the situation.

Table 7.4.1.

Analysis of Variance Tables for Regression of Performance Test Traits on Live Weights at Start and Finish of Test in the A.B.R.O. Sire-Line.

Case (1) Regression of Uncorrected Traits on Weight at End of Test.

Source	Daily Gain (lbs/day)		Food Conversion Ratio		Average Backfat (cms.)	
	d.f.	M.S.	d.f.	M.S.	d.f.	M.S.
Fit single α	1	2616.605***	1	2024.022***	1	4070.062***
Fit α_i after α	11	1.635***	3	1.049***	11	1.827***
Fit β after α_i	1	9.526***	1	0.274	1	21.652***
Fit β_i after β	11	0.065	3	0.047	11	0.070
Residual	896	0.044	178	0.128	896	0.082

Case (2) Regression of Uncorrected Traits on Weight at Start of Test.

Source	Daily Gain (lbs/day)		Food Conversion Ratio		Average Backfat (cms.)	
	d.f.	M.S.	d.f.	M.S.	d.f.	M.S.
Fit single α	1	2616.605***	1	2024.022***	1	4070.062***
Fit α_i after α	11	1.635***	3	1.049***	11	1.827***
Fit β after α_i	1	2.408***	1	0.003	1	2.576***
Fit β_i after β	11	0.067	3	0.095	11	0.062
Residual	896	0.052	178	0.129	896	0.103

Case (3) Regression of Traits, Corrected for Weight at End of Test, on Weight at Start of Test.

Source	Daily Gain (lbs/day)		Food Conversion Ratio		Average Backfat (cms.)	
	d.f.	M.S.	d.f.	M.S.	d.f.	M.S.
Fit single α	1	2622.511***	1	2090.971***	1	3448.403***
Fit α_i after α	11	1.611***	3	0.912***	11	2.357***
Fit β after α_i	1	0.655***	1	0.003	1	0.297
Fit β_i after β	11	0.034	3	0.058	11	0.028
Residual	895	0.044	177	0.128	895	0.082

$^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$.

Estimates of the resulting pooled overall regression coefficients may be found in Table 7.4.2. The estimate of 0.01 cm./lb. for backfat was exactly equal to the value actually applied to all previous sire-line generations. The estimated regression of food conversion on live weight, though non-significant, was negative implying that heavier pigs were more efficient. This was the opposite of what might normally be expected, and was explained by the fact that pigs which exceed the minimum finishing weight (180 lbs.) by the greatest amount must necessarily on average have grown the fastest and, again on average, have been more efficient since a phenotypic correlation of -0.6 (e.g. Smith, King and Gilbert, 1962) may be expected between the two characters. In this situation live weight at the end of test is not strictly an independent variable because it contains an element of weight for age.

Overall regressions (β) of daily gain and backfat on live weight at the start of test (Case 2) were highly significant, and the individual slopes (β_i) did not differ significantly from the common slope. Once again there was no significant regression of food conversion on live weight. After applying the corrections for weight at the end of test (Case 3), the regression of daily gain on weight at the start of test diminished in significance while the regression for backfat became non-significant. Regression coefficients were markedly lower after adjustment for weight at the end of test (Table 7.4.2), which means that the covariance with starting weight was reduced by correction for finishing weight. This could be explained either by a decrease in the variance of the

Table 7.4.2.

Pooled Regression Coefficients (β) of Performance Test Traits on Live Weights at Start and Finish of Test with their Standard Errors (SE(β)), Estimated from Within Year/Test-Type Groups and Expressed as Units of Each Trait per lb Change in Live Body Weight.

CASE	Daily Gain (lbs/day)		Food Conversion Ratio		Average Backfat (cms.)	
	β	S.E.(β)	β	S.E.(β)	β	S.E.(β)
(1) Uncorrected Traits on Weight at End of Test	0.0070	0.0005	-0.0024	0.0016	0.0105	0.0006
(2) Uncorrected Traits on Weight at Start of Test	0.0054	0.0008	0.0006	0.0037	0.0056	0.0011
(3) Traits Corrected For Weight at End, on Weight at Start	0.0028	0.0007	0.0006	0.0037	0.0019	0.0010

traits after correction, or by a correlation between start and finish weights. A priori, no association would be expected between start and finish weights since, although the pigs in a pen commenced test together, they finished test independently. On the other hand, if the smallest pigs in a group are the slowest growing at the start, they might pass the finishing weight of 180 lbs. more slowly and stand a greater chance of finishing test at a relatively lower weight. This explanation will not however be pursued since the operational usefulness of the corrections is of prime interest here. The usual procedure would be to correct for weight at the end of test, and then apply any necessary adjustments for weight at the start of test to the corrected data.

7.4.3 Application.

To assess the relevance of the various possible weight corrections in the sire-line it will be necessary to obtain the expected ranges of weights at the start and finish of test. From Table A4 (Appendix A) the average standard deviations at start and finish were roughly 9 and 13 lbs. respectively. Approximately 95% of pigs would therefore be expected to weigh within 18 and 26 lbs. of the mean weight at the beginning and end of test. Taking 1970 as a sample generation, starting weights ranged from 57 to 101 lbs. and finishing weights from 165 to 237 lbs. at the extremes.

Adjustment of the growth rate of a pig whose finishing weight is 2 standard deviations from the mean, using the regression coefficient from Table 7.4.2, would produce a change (Δy) of:

$$\begin{aligned}\Delta y &= \beta_{yx} \cdot \Delta x\\ &= 0.0070 \times 26\\ &= 0.18 \text{ lb./day}\\ &= 0.18/0.24\,\sigma_y\\ &= 0.75\,\sigma_y\end{aligned}$$

where $\sigma_y = 0.24$ for daily gain (Table 6.1). Correction for finishing weight would therefore almost certainly produce changes in the ranking of daily gain. Further correction for two standard deviations difference from the mean starting weight would similarly result in a change of:

$$\begin{aligned}\Delta y &= 0.0028 \times 18\\ &= 0.05 \text{ lb./day}\\ &= 0.21\,\sigma_y\end{aligned}$$

assuming no change in σ_y following prior correction, which may have a small effect on ranking. Applying equivalent corrections (Table 7.4.2) for the same liveweight deviations to average backfat, the primary adjustment for finishing weight would be 0.27 cms. ($0.87\,\sigma_y$, for $\sigma_y = 0.31$) and the secondary adjustment, though nonsignificant, would be 0.03 cms. ($0.10\,\sigma_y$ assuming no change in σ_y). Again, only the adjustment for end of test weight would be expected to seriously affect ranking.

The importance of liveweight corrections would clearly diminish if the variation in the weights themselves could be reduced. This might be achieved by better management in placing pigs on test at a strict pen average of 60 or 65 lbs. and by more frequent ultrasonic measuring sessions to narrow the range of end of test weights. This analysis has verified the existing weight correction for backfat, and shown that correction of daily gain for live weight at the end of test is expected to have nearly as much relative effect on the ranking for the trait as does the backfat correction. On the other hand, live weight itself may to a certain extent be dependent on daily gain, which receives considerably less emphasis in the selection index than backfat. Further discussion will therefore be postponed until the more general discussion at the end of this chapter (section 7.6).

7.5 An Examination of the Selection Index.

In view of the apparent absence of selection response since its introduction, it was considered prudent to carry out a re-appraisal of the selection index. This will now be conducted by examining various parameters relating to efficiency, and evaluating the relative contributions of each item of individual or family information to genetic progress. In 1972 the index was modified to include half-sib records, and the efficiency of the resulting new index will be compared with that of the existing one. In addition, a check will be made on the validity of the preliminary index for screening out the worst pigs at bacon weight.

7.5.1 Material and Methods.

A description of the set-up and method of calculation of the A.B.R.O. sire-line selection index will be found in Appendix C. The investigations were all carried out with the aid of a specialised selection index computer programme, "SELIND" (Cunningham, 1969), designed to give various indicators of comparative efficiency. Elements of the phenotypic (P) and genetic (G) variance-covariance matrices were obtained from the sire-line's own selection index programme and input as data to the SELIND programme. The following quantities were given by the programme for each index calculated:

(1) relative index coefficients or "weights" (b_i),

(2) percent reduction in the rate of genetic progress on aggregate genotype which would result if each variate in turn was omitted,

(3) genetic regression of each trait in the aggregate genotype on the index ($\beta_x I$),

(4) percent of the total gain in aggregate genotype accounted for by each trait,

(5) correlation of the index and aggregate genotype (γ_{IM}),

(6) standard deviation of the index (σ_I),

(7) standard deviation of the aggregate genotype (σ_M).

The definition of the aggregate genotype (M), comprising an individual's breeding value for growth rate, food conversion and backfat, and therefore its standard deviation (σ_M) were constant throughout.

In the first part of the investigation four separate indices were compared. The first (Index 1) was the full index used for the selection of single-penned boars between 1966 and 1971, when family information from male and female full sibs was included. The second index (Index 2) was similar to the first except that the boar's individual food conversion was omitted, so that it was equivalent to the index for a double-penned boar. The third and fourth indices

(Indices 3 and 4) were analogous to the first two, but contained male and female half-sib in addition to full-sib family records. A full-sib family size of 2 boars and 3 gilts, and a half-sib structure of 2 dams per sire were assumed, since these approximated average family sizes in past generations. Information from related double-penned boars was not used in computing the selection indices of single-penned boars, and vice versa.

The second part of the investigation was concerned with the preliminary selection index, which simply consisted of the sum of corrected average backfat and individual or pen food conversion as available. Individuals with the lowest values were retained, and re-selected on the full index after all the pigs in the generation had completed test. Two simple selection indices were calculated with the SELIND programme. The first (Index 5) consisted of individual daily gain and corrected average backfat together with individual or pen food conversion. The second (Index 6) resembled the first except that individual daily gain was omitted. Both indices were re-calculated for full-sib pen sizes of one to five pigs.

All index calculations were carried out for the single set of genetic and economic parameter values currently in use in the sire-line and set out in Table 6.5. The effects of varying the values of different parameters were not investigated.

7.5.2 Results.

The Full Selection Index.

Parameters from Indices 1 - 4 containing different combinations of full- and half-sib family information are shown in Table 7.5.1. The presence of index weights (b_i) indicates that a particular variate has been included in the index. At the bottom of the table the relative efficiencies of the indices may be compared, either directly from their correlations with the aggregate genotype (γ_{IM}) on a scale in which a 100% efficient index would have $\gamma_{IM} = 1.00$, or alternatively from the ratios of their standard deviations, since $\gamma_{IM} = cov_{IM}/\sigma_I . \sigma_M = \sigma_I/\sigma_M$, where $cov_{IM} = \sigma_I^2$ for scaling and σ_M is constant. Taking 100 γ_{IM} as the universal measure of efficiency, loss of individual food conversion caused a reduction of only 1% in both Index 1 (full-sib records) and Index 3 (full- and half-sib records). With larger family sizes this reduction in efficiency is expected to be even lower, because family means based on greater numbers are better predictors of genotype. With or without individual food conversion ratio, the inclusion of half-sib family means improved efficiency by a meagre 3%.

Index weights (b_i) were positive with respect to merit for all variates in Index 1, but in Index 2, after dropping individual food conversion, the weights on full-sib (FS) male means unexpectedly turned negative. However, the sums of Individual and FS male weights were exactly equal for all three traits in Indices 1 and 2, while the weightings on

Table 7.5.1.

A Comparison of Four Selection Indices Utilising Different Combinations of Full-Sib (FS) and/or Half-Sib (HS) Family Information. Table shows Index Weights (b_i), % Reduction in Overall Genetic Gain if Variate is Dropped, Regression of Each Trait on Index ($\beta_x I$), % of Gain Accounted for by Each Trait, Correlation of Index and Aggregate Genotype (γ_{IM}) and Standard Deviation of Index (σ_I).

Variate (x 100 for Index Calculation)	Index 1		Index 2		Index 3		Index 4	
	b_i	% Reduction	b_i	% Reduction	b_i	% Reduction	b_i	% Reduction
Daily Gain (lbs/day):								
Individual	0.37	0.03	1.92	1.46	0.36	0.03	1.92	1.34
FS Male Mean	0.18	0.00	-1.37	0.32	-0.13	0.00	-1.68	0.25
FS Female Mean	0.30	0.02	0.29	0.02	0.41	0.02	0.40	0.01
HS Male Mean	-	-	-	-	0.56	0.02	0.56	0.02
HS Female Mean	-	-	-	-	-0.10	0.00	-0.08	0.00
Food Conversion Ratio:								
Individual	-1.39	1.47	-	-	-1.39	1.37	-	-
FS Male Mean	-0.49	0.10	-1.88	3.67	0.71	0.12	-0.67	0.15
FS Female Mean	-0.73	0.42	-0.73	0.43	-1.38	0.52	-1.39	0.54
HS Male Mean	-	-	-	-	-1.83	0.69	-1.84	0.72
HS Female Mean	-	-	-	-	0.57	0.05	0.59	0.06
Corrected Average Backfat (cms.):								
Individual	-2.55	2.72	-3.40	6.35	-2.55	2.51	-3.40	5.85
FS Male Mean	-0.49	0.06	0.36	0.04	1.77	0.31	2.62	0.74
FS Female Mean	-0.73	0.25	-0.73	0.26	-2.36	0.62	-2.36	0.64
HS Male Mean	-	-	-	-	-2.99	0.87	-3.00	0.89
HS Female Mean	-	-	-	-	1.59	0.20	1.59	0.21

Trait	$\beta_x I$	% of Gain	$\beta_x I$	% of Gain	$\beta_x I$	% of Gain	$\beta_x I$	% of Gain
Daily Gain (lbs/day)	0.025	4.49	0.025	4.43	0.025	4.56	0.025	4.50
Food Conversion Ratio	-0.113	54.23	-0.111	53.36	-0.113	54.41	-0.112	53.61
Corrected Average Backfat (cms.)	-0.076	41.28	-0.078	42.20	-0.076	41.03	-0.078	41.88

Parameter	Index 1	Index 2	Index 3	Index 4
Correlation of Index and M (γ_{IM})	0.7075	0.6971	0.7354	0.7254
Standard Deviation of Index (σ_I)	140	138	146	144

Standard Deviation of Aggregate Genotype (σ_M) = 198.

female variates remained identical. The two indices therefore put equal weight on the three characters, but placed different emphasis on the various items of family information within each character. A similar pattern was observed in the weights of the two half-sib indices (Indices 3 and 4).

A surprising feature of these results was that in all four indices the percentage reductions in the rate of genetic progress, which would result on deletion of a single variate, were very low. In all cases individual backfat was the most important variate, but the maximum loss that could be incurred by dropping it was only 6% (Index 4). As expected the removal of individual food conversion ratio caused its FS male mean to rise in importance, but also caused individual daily gain and backfat to become more critical. The apparent robustness of these indices to the loss of single variates, and the way in which the importance of variates alters as a result, is explained by the generally favourable genetic and phenotypic correlation structures among the three traits (Table 6.5). The percentages of genetic gain in aggregate genotype attributable to each trait, shown in the centre portion of Table 7.5.1, were very similar in the four indices. In spite of its greater economic weighting and heritability, backfat did not contribute the most to genetic gain. Instead food conversion, through its higher genetic correlations with daily gain and backfat and greater variability, made the greatest contribution to genetic advance.

As the γ_{IM} values indicate the expected gain, in standard deviations of aggregate genotype (σ_M), from one standard deviation of selection on the index, it is clear that positive genetic gains would be expected from Indices 1 - 4 (Table 7.5.1). Values for the genetic regressions of the traits on the index ($\beta_x I$), in the centre of Table 7.5.1, permit calculation of the expected advance in each of the three characters from selection on the index. The expected genetic change in the jth trait, Δx_j , is as follows (e.g. Turner and Young, 1969):

$$\Delta x_j = \beta_{x_j} I \cdot \Delta I = \beta_{x_j} I \cdot \sigma_I \cdot i \quad ,$$

where i is the standardised selection differential. It will be useful to briefly consider the magnitude of advances in daily gain, food conversion and backfat expected from one generation of selection on index in the A.B.R.O. sire-line. For simplicity suppose that the sire-line is a closed population, that all selection is practised on males and that 10 out of 100 individually-penned males are selected on Index 1. Then i = 1.73, σ_I = 140 and, removing the scaling factor of 100, $i\sigma_I$ = 2.42, so that for daily gain, for example:

$$\Delta x_1 = 2.42 \times 0.025 = 0.061 \text{ lb/day},$$

and similar Δx_j for food conversion and backfat are - 0.274 lb feed /lb L.W.G. and - 0.184 cm. respectively. With selection on males only, one half of this improvement would be passed on so that the population would be advancing at 0.03 lb/day, -0.14 lb feed/lb L.W.G. and -0.09 cm. per generation for the three traits respectively. Reference to Figures 5.1 and 5.2 shows that, disregarding 1971 when the ration changed, average improvements per generation of this order were certainly not realised for food conversion and backfat in the sire-line between 1966 and 1970. The expected rate of advance in the aggregate genotype, equal to $i\sigma_I$ since the regression of aggregate genotype on index is 1.00, would be 121 points per generation for the hypothetical population considered above. From the introduction of the index until 1970, the average yearly change in aggregate genotype of the sire-line was +12 points, although this figure also contains mean annual environmental fluctuations. Similar calculations show that the effect of subdivision of the male population into outdoor single- and indoor double-penned subgroups, coupled with independent selection of 5 out of 50 boars on each of Indices 1 and 2, produces a negligible reduction in the gains expected in each of the traits (Δx_j).

In the 1971 sire-line generation simple standard deviations of boar selection indices were computed from observed sums of squares for comparison with the theoretical value calculated as $\sigma_I = \sqrt{b' P b}$, where P is the phenotypic variance-covariance matrix and b is the vector of index weights. The observed standard deviation was only 100 index points, while the average of the expected standard deviations was roughly 140 index points. A possible explanation is that many of the individuals in the population were full-sibs of one another, whereas the variance according to $b' P b$ implicitly assumes individuals to be unrelated (Hill, personal communication). With σ_I = 100 rather than 140 points the rates of progress given above are reduced to 0.02 lb/day, -0.10 lbfeed/lb L.W.G. and -0.07 cm per generation for daily gain, food conversion and backfat. Recognisable genetic improvements would therefore still be expected in food conversion and backfat after 5 generations of selection.

The Preliminary Selection Index.

Results for the two simple selection indices (Indices 5 and 6) for one to five pigs per pen are shown in Table 7.5.2. Index 5 utilises pen food conversion and individual daily gain and backfat, and Index 6 resembles Index 5 except that daily gain is omitted. Index 6 therefore uses the same information as the preliminary index applied to the sire-line. Clearly the difference in the efficiency (γ_{IM}) of the two indices as a result of dropping daily gain is minimal, although it widens as the number of pigs in the pen increases. As expected the use of pen mean rather than individual pig food conversion initially causes a slight fall-off in efficiency which then passes through a minimum and begins to rise with increasing numbers of pigs per pen. Indices 5 and 6 with two pigs per pen are, of course, special cases of Index 2 (Table 7.5.1) in which all full sib data except for male pen average food conversion has been omitted. Thus it can be seen that, for the family sizes considered in Table 7.5.1, full-sib family information adds only two per cent to the efficiency of selection. This figure would, however, increase for larger family sizes. The remaining parameters in Table 7.5.2 follow the expected pattern and the $\beta_{x}I$, especially, are changed very little from Index 1.

The main reason for calculating these indices has been to compare the 1:1 ratio of index weights presently used for backfat and food conversion with the theoretically optimum value. However, when working out the preliminary index in practice as each pig completes test, the variates could not be expressed as deviations from the population mean which at

Table 7.5.2.

A Comparison of Two Simple Selection Indices for Rapid Selection in the A.B.R.O. Sire-Line. Table Shows Index Weights (b_i), Relative Weightings (b_i/b_j), % Reduction in Rate of Genetic Gain by Dropping Each Variable, Regression of Each Trait on Index (βxI), % of Genetic Gain Accounted for by Each Trait, Correlation of Index with Aggregate Genotype (γ_{MI}), and Standard Deviation of Index (σ_I). Note that different numbers of pigs were involved in each calculation.

Number of Pigs in Pen	Index 5: Individual Daily Gain (DG), Corrected Average Backfat (BF) and Pen Food Conversion Ratio (FCR).							
	Trait	b_i	b_i/b_j	% Reduction	βxI	% of Genetic Gain	γ_{MI}	σ_I
1	DG	0.56	1.00	0.19	0.024	4.3	0.6841	135
	FCR	-1.93	-3.45	8.12	-0.112	53.7		
	BF	-3.18	-5.68	13.91	-0.078	42.0		
2	DG	1.30	1.00	1.37	0.025	4.4	0.6815	135
	FCR	-2.01	-1.55	7.77	-0.110	52.9		
	BF	-3.53	-2.72	20.15	-0.079	42.7		
3	DG	1.47	1.00	1.86	0.025	4.5	0.6842	135
	FCR	-2.18	-1.48	8.13	-0.110	52.8		
	BF	-3.60	-2.45	21.54	-0.079	42.7		
4	DG	1.54	1.00	2.11	0.025	4.5	0.6866	136
	FCR	-2.32	-1.51	8.46	-0.110	52.9		
	BF	-3.62	-2.35	22.05	-0.079	42.6		
5	DG	1.58	1.00	2.25	0.025	4.6	0.6886	136
	FCR	-2.43	-1.54	8.72	-0.110	53.0		
	BF	-3.63	-2.30	22.25	-0.079	42.4		

Table 7.5.2 (cont).

Number of Pigs in Pen	Index 6: Pen Food Conversion Ratio (FCR) and Individual Corrected Average Backfat (BF).							
	Trait	b_i	b_i/b_j	% Reduction	$\beta x I$	% of Genetic Gain	γ_{MI}	σ_I
1	DG				0.023	4.1	0.6828	135
	FCR	-2.13	1.00	18.31	-0.112	53.7		
	BF	-3.05	1.43	14.46	10.078	42.2		
2	DG				0.020	3.6	0.6722	133
	FCR	-2.45	1.00	17.02	-0.108	52.1		
	BF	-3.33	1.36	19.16	-0.082	44.3		
3	DG				0.020	3.5	0.6715	133
	FCR	-2.68	1.00	16.49	-0.108	51.7		
	BF	-3.41	1.27	20.59	-0.083	44.8		
4	DG				0.019	3.5	0.6722	133
	FCR	-2.83	1.00	17.02	-0.107	51.6		
	BF	-3.45	1.22	21.20	-0.083	44.9		
5	DG				0.019	3.5	0.6731	133
	FCR	-2.95	1.00	17.14	-0.107	51.5		
	BF	-3.46	1.17	21.49	-0.083	45.0		

Standard Deviation of Aggregate Genotype (σ_M) = 198 that stage was unknown. As Henderson (1963) pointed out, unknown means only leave the ranking unaffected when the family sizes of each individual are equal, since when

$$I = b_1(y_1 - \mu_1) + b_2(y_2 - \mu_2),$$

and $$I' = b_1(y_1' - \mu_1) + b_2(y_2' - \mu_2), \quad I \neq I', \; y_i \neq y_i',$$

then $$I - I' = b_1(y_1 - y_1') + b_2(y_2 - y_2'),$$

and $-(b_1\mu_1 + b_2\mu_2)$ is common to all indices. If food conversion is based on varying numbers of pigs per pen, the b_i for indices involving different numbers are not equivalent (e.g. Index 6), and:

$$I - I' = -(b_1\mu_1 - b_1'\mu_1) + b_1(y_1 - y_1') + b_2(y_2 - y_2') - (b_2\mu_2 - b_2'\mu_2),$$
$$I \neq I', \; y_i \neq y_i', \; b_i \neq b_i'$$

when $b_i\mu_i \neq b_i'\mu_i$ so that terms in μ_i no longer cancel. Henderson indicated that this difficulty could be overcome by maximising γ_{IM} subject to the condition $E(I) = 0$, but this will not be pursued here.

The problem of unknown population means will therefore not affect the preliminary selection of boars in the sire-line because they are already selected from within single-penned and double-penned groups, with the same amount of information available on every individual in the group. Past relative weightings of 1.00 on food conversion and backfat may be compared with the optium weightings in Table 7.5.2 where weights are expressed as ratios of one another (b_i/b_j). For single-penned boars the optimum weighting is 1.00:1.43 for food conversion: backfat (Index 6), while for double-penned boars it is 1.00:1.36. It is doubtful whether anything was actually lost by departure from the optimum weighting in past generations, since preliminary culling levels were pitched well below actual culling levels on the full index. It is nevertheless of interest to note that backfat was the underweighted trait. The b_i/b_j values in Index 5 show what the relative weightings would be if daily gain was included in the preliminary index.

The question of unknown population means arises when initially selecting gilts, because pen sizes may vary from one to five pigs per pen all selected as a single population. However the optimum b_i/b_j values (Index 6) approach the 1:1 ratio used in practice as numbers per pen increase, and optimum relative weightings are all very similar for 3,4 or 5 gilts per pen so that $b_i\mu_i \simeq b_i'\mu_i$ and terms involving the mean will have little effect on ranking. Possible solutions might be to select gilts from within sub-populations according to pen group size, or alternatively to select pen group sizes of 3,4 or 5 gilts as a single population when an overall weighting of 1.20:1.00 for backfat: food conversion should suffice. The use of a rolling or accumulating contemporary mean is ruled out, owing to small numbers of pigs tested and the fact that index theory assumes the mean to be known without error (e.g. Henderson, 1963).

The final selection of each pig on Index 6 as it completes test at first appears to be an attractive proposition, since only 2% would be lost in terms of genetic progress compared to the full-sib index (Indices 1 and 2, Table 7.5.1) and a considerable saving in feed costs would be made by earlier culling. However, experience has shown that pigs finishing test first invariably include a higher proportion of those finally selected on the full index. Putting this another way, the proportions which should be selected from each batch of pigs finishing test will undoubtedly fall off, and in order to set a suitable culling level on the index the breeder is forced to anticipate the performance of the pigs still on test. Witholding decisions on borderline pigs awaiting the performances of others would simply throw away the advantages of the reduced preliminary index in allowing culls to be marketed at bacon weight. The argument would therefore be in favour of retaining the full index, with the maximum available amount of family information, for use when all the pigs in a generation have completed test. Worst animals would still be culled on the optimum (Index 6) preliminary index immediately after completing test.

Finally it is emphasized that the findings reported here for Indices 1 - 6 should not be generalised beyond the practical situation to which they apply, since the effects of varying economic and genetic parameters, of varying family sizes and structures, or of varying selection objectives were not investigated.

7.6 Discussion and Recommendations.

The findings from the foregoing investigations into various aspects of the performance testing procedure in the A.B.R.O. sire-line indicate that a positive response to selection on the index would be expected, and that no single factor could be responsible for the apparent lack of progress since 1966. The results will, however, serve to show whether the performance test can usefully be improved upon in any way.

Although no genotype by boar test environment interactions were demonstrated in two very crude analyses with low numbers, these could by no means be entirely ruled out and it would therefore be more satisfactory if all boars could be tested in one environment. The index studies show that, at worst, only 1% would be lost in the rate of genetic progress by penning boars in pairs and using joint rather than individual food conversion. To avoid the risk of sex by environment interaction and the hazards of variable midwinter weather conditions, the better policy would probably be to house all the boars indoors in the same building as the gilts. In the existing Danish-type testing house penning boars in pairs would be wasteful in terms of space, because all pens hold up to five pigs. An alternative would therefore be to increase the boar test group size to four full-sibs. This may at first seem unacceptable since food conversion is expected to contribute the most to genetic progress, but in practice when fewer than a dozen boars are required in each generation one is frequently obliged to select only unrelated boars to avoid inbreeding, with the consequence that family selection takes place. This in itself would tend to lower the selection differential but is preferable to a rise in inbreeding. Under these circumstances the penning of boars in full-sib groups would have no effect on selection of the best families, but would place all the emphasis of within-group selection on daily gain and backfat. Individuals' breeding values for food conversion would then, in effect, be predicted from genetic correlations with the other two traits as deviation from the group mean, resulting in only a small loss of accuracy. A definite case could therefore be made for testing boars and gilts in full-sib groups, all under the same roof.

A relatively sophisticated selection index procedure of the sort applied to the sire-line cannot be expected to lead to rapid improvement unless the characters involved are measured with a fair degree of accuracy. Daily gain, the easiest to obtain and probably least subject to measurement errors of the three characters, contributed the least to genetic progress. For food conversion ratio, errors of measurement are particularly likely in food consumption since not all the food recorded as "used" may actually have been "consumed" due to spillage. That the repeatabilities of food conversion were high signifies only that the final weighings and calculations were accurate and gives little indication of inaccuracy from wastage. A consoling factor is that wastage may be fairly constant for each pig in a given environment.

The repeatabilities of ultrasonic fat depths and their correlations with carcass measurements in the sire-line were in accord with those reported in the literature and recently reviewed for example by Sundgren (1973). Correlations of live and dead measurements at the shoulder were a little lower than those usually reported for most sites, and a definite anomaly exists in the sire-line results in that while the correlation between ultrasonic and carcass measurements was reduced from 0.80 to 0.22 at the shoulder compared with other sites, the repeatability at the shoulder was only very slightly smaller. The ultrasonic method may therefore be able to constantly pick out a particular muscle-fat interface which it is difficult to distinguish by eye. Are there any grounds for omitting ultrasonic shoulder measurements from average backfat because of the low correlation with carcass depths? Clearly only a fractional increase in the repeatability of estimated backfat, already greater than 0.90, would result, and there is evidence that shoulder fat is as good a predictor of lean percentage in the carcass as loin fat, and a better predictor than mid-back fat (Hazel and Kline, 1953). What increase in the accuracy of selection for backfat would result if ultrasonic measurements were routinely repeated after one week, and pigs selected on the mean of the two estimates? Phenotypic variance would be reduced and heritability increased according to the formula:

$$h^{2'} = h^2 \left[\frac{n}{1 + (n-1)R} \right] ,$$

where $h^{2'}$ is the improved heritability and R the repeatability on n records per pig (e.g. Becker, 1967). With the repeatability of roughly 0.90 found here heritability would be increased by a factor of 1.05, or 2.5% with an original value of 50% as used in the index (Table 6.5). The expense and effort involved in measuring pigs a second time would therefore seem unjustified under research or commercial conditions.

Having established that performance test traits can be measured with a fair degree of accuracy it is important that variation due to live weight should be removed so that selection takes place at a constant weight. The accuracy of corrections will obviously become more important as the range of live weights increases, so that keeping the ranges of finishing weights to a minimum is a simple means of avoiding errors. The regression analysis carried out earlier (section 7.4) has verified the present between-pig correction of 0.01 cm./lb. for backfat at the end of test, and indicated that a correction of 0.007 lb/day per lb. might be applied to daily gain. If, as already suggested, live weight at the end of test contains an element of weight for age and is not purely an independent variable, then some over-correction of daily gain may result through the high positive correlation between daily gain and weight for age (e.g. Table 6.3). In other words, pigs may tend to have high weight deviations because they have a higher growth rate, whereas they do not have high weight deviations because they are fatter. Great care must therefore be exercised in applying corrections to growth rate, and in view of the fact that daily gain receives a relatively low weighting (b_i) in the selection index (Tables 7.5.1 and 7.5.2) so that small changes in its ranking will have little effect on the indices of individual pigs, the correction may probably be safely ignored.

Corrections of backfat for live weight in the sire-line have so far been based on regressions estimated from between pigs. Minkema (1972) pointed out that such regressions would be better estimated from repeated observations within pigs. He showed that within-pig regressions of ultrasonic backfat on weight were slightly lower than when estimated from between pigs, and demonstrated a sex difference in the within-pig estimates. Minkema also developed a procedure which would take account of the fact that the regression of backfat on liveweight within pigs may be dependent on the pig's own fatness. This approach would clearly warrant investigation for the sire-line, but three or four repeated observations per pig would be desirable in order to have some idea of the error attaching to individual within-pig regressions. A rough estimate of the within-pig regression for backfat from the average slope $(y_2 - y_1)/(x_2 - x_1)$ in the 1972 ultrasonic repeatability trial was 0.0074 cm./lb which is slightly less than the usual between-pig regression of 0.01 cm./lb.

Given that reliable measurements of the separate characters were available, and the variation due to live-weight had been removed, it was shown that genetic progress would have been expected from selection on the index used in the sire-line between 1966 and 1971. The further addition of half-sib family information was shown to contribute an extra 3% to the rate of genetic progress, bringing the total contribution of all sib information up to 5%. These figures would be increased if all boars could be tested in a single environment and male full-sib family size effectively raised. This would overcome the deficiency of the past procedure in failing to acknowledge that there were really 3 "sexes": single-penned males, doubled-penned males, and females, when male sib information from the second environment was not included. Alternatively information from the third "sex" could be included in the index as a further 6 measured variates, but computation would then prove laborious and expensive. Similarly, within-sex-family pen effects could be taken into account by breaking family structure down one stage further into half-sib, full-sib and pen averages. The value of this addition would depend on the magnitude of the between-pen within-family variance. Refinements such as these are, however, time-consuming to initiate and generally yield only small improvements in efficiency.

In summary, possible improvements to the existing selection procedure in the sire-line might include the performance testing of all boars by litter groups of two or more in a single environment, the use of optimum weightings for the preliminary selection index and a narrowing of liveweight ranges at the start and finish of test. Calculation of preliminary and final indices, and of the traits themselves, might be greatly facilitated by total computerisation of the test results. Then, for example, optimum preliminary index weightings and liveweight corrections could be applied quickly and accurately.

Discussion of possible modifications of a more longterm nature, such as alterations to the objectives of selection or to the ad libitum feeding regime, has deliberately been postponed until Chapter 9. The object here has been to show that genetic progress would be expected in a closed population under A.B.R.O. sire-line conditions. Apart from looking for possible genotype by test environment interactions, no attempt has yet been made to investigate the effects of immigration on the sire-line improvement programme and this will be the subject of the next chapter.

Chapter 8 Immigration

8.1 Introduction.

The most novel aspect of the A.B.R.O. sire-line has been that, in addition to intense selection, new genes have been introduced each year without regard to breed. This policy was adopted with the intention of bringing about a faster rate of genetic improvement than would have been possible by selection alone in a closed line of the same size. In so doing it was intended to make full use of small samples of newly imported breeds such as the Lacombe and Pietrain, as well as boars of exceptionally high merit at British central testing stations. It has already been pointed out (Chapter 5) that, in the absence of reliable estimates of the rate of genetic progress, the current performance of the sire-line in comparison with highly selected contemporary Large Whites at national testing stations is the best guide to the success of the whole enterprise. The emphasis of this chapter will therefore be on the accuracy of the procedure for selecting immigrants into the line, rather than on aspects of comparative performance.

The examination of the immigration procedure will be divided into two parts. The first will take the form of a study of possible sources of bias in the past method of selecting immigrants, and the second part will attempt to relate the findings of the first to some simple practical observations from past generations. The objective will be to provide a critical appraisal of the concept of immigration, using all the available information.

8.2 Sources of Bias in the Selection of Immigrants.

The procedure for testing immigrants for admission to the sire-line has already been described in Chapters 2 and 3. Potential immigrant animals of any breed and from any country of origin were simply mated to sire-line pigs of the opposite sex and their "cross-bred" progeny allowed to compete directly for selection as parents of the next generation. As indicated in Chapter 2, the comparison of immigrant and native progeny is open to bias from two sources. Firstly, the F_1 immigrant x sire-line progeny (hereafter referred to only as "immigrant progeny") may exhibit heterosis on performance test, causing an upwards bias in their selection indices and erroneously increasing their chances of being selected. In 1973 a small trial was set-up to measure heterosis in immigrant x sire-line crosses in order to assess the importance of this bias, and some results will be presented here. The second bias arises from the fact that native and immigrant progeny have been treated as members of a single population, leading to incorrect estimates of immigrant breeding values relative to those of natives. This bias is less straightforward and will now be considered first.

8.2.1 Differences in Population Means.

Treating immigrant and native progeny as members of a single population may result in bias simply because immigrant breeding values are then expressed as deviations from the sire-line rather than their own population mean. The way in which the bias could arise may be demonstrated by treating the native sire-line and each potential immigrant breed, for example Landrace or Large White, as separate populations. In fact, this is an over-simplification because the native sire-line population is itself a collection of sub-populations as a result of immigration in previous generations. However a single native population will serve here for illustration, and may be a reasonable approximation for practical purposes.

Selection for One Character.

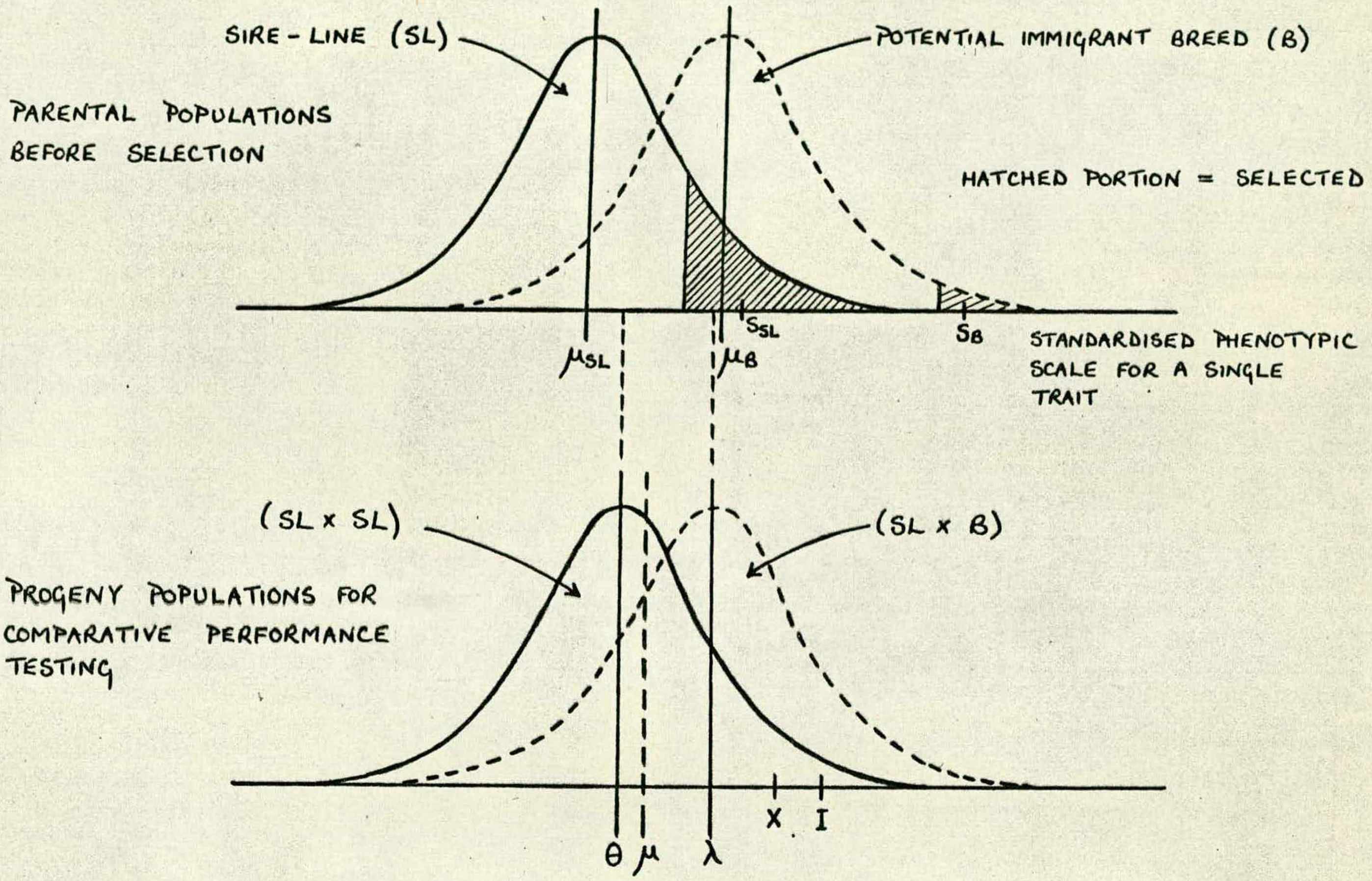
Suppose that individuals of conventional breed "B", with contemporary breed mean μ_B, are to be tested in the usual way as immigrants to the sire-line (SL), with mean μ_{SL}, for a single trait which does not exhibit heterosis: backfat thickness, for example. Assume also that mass selection is practised on males only, that immigrant and native parents are assigned to mates at random and that the heritabilities (h^2) and phenotypic variances of immigrant and native populations are equal. The parental and resulting progeny distributions are depicted diagrammatically in Figure 8.1. Selected sire-line boars of average superiority ($S_{sl} - \mu_{sl}$) are mated to unselected gilts to give "pure" native progeny of mean θ, where:

$$\theta - \mu_{sl} = \frac{h^2 (S_{sl} - \mu_{sl})}{2}$$

In the same way selected potential immigrant sires with superiority ($S_b - \mu_b$) over their breed "B" mean are mated to unselected sire-line gilts, producing a sub-population of "cross-bred" prospective immigrant progeny with mean λ,

Figure 8.1

Native Sire-Line and Immigrant Population Means and Distributions Before and After the Mating of Selected Parents (Not Drawn to Scale).



Explanation of Symbols

μ_{sl} = mean of sire-line parental population

θ = mean of 'pure' sire-line progeny after selection and mating of parents

S_{sl} = mean of selected sire-line parents

μ_b = contemporary mean of whole immigrant population

S_b = mean of immigrants chosen to be mated to the sire-line

μ = overall mean of all progeny measured in any one generation

λ = mean of F_1 immigrant x sire-line progeny

I = phenotypic observation on one immigrant x sire-line individual

X = phenotypic observation on one sire-line individual where:

$$\lambda - \mu_{sl} = \frac{(\mu_b - \mu_{sl}) + h^2 (S_b - \mu_b)}{2}$$

In practice μ_{sl} may be estimated, but μ_b and S_b are generally unknown. However, native (θ) and immigrant (λ) progeny means may be estimated directly as each generation completes performance. Assume for the present that θ and λ, and the overall mean of all progeny tested (μ) are known without error.

According to the past method of evaluation, treating immigrants and natives as a single population (Method 1), the predicted breeding values of native (A_{sl}) and immigrant (A_I) individuals for comparison are as follows:

$$A_{sl(1)} = h^2 (X - \mu),$$
$$A_{I(1)} = h^2 (I - \mu).$$

The predicted difference in breeding value between an immigrant and a native is then:

$$A_{I(1)} - A_{sl(1)} = h^2 (I - X) \ldots\ldots\ldots\ldots\ldots\ldots \quad (1)$$

Now treating immigrants and natives as separate populations (Method 2), these quantities become:

$$A_{sl(2)} = h^2 (X - \theta),$$

$$A_{I(2)} = h^2 (I - \lambda) + (\lambda - \theta),$$

and $$A_{I(2)} - A_{sl(2)} = \left[h^2 (I - \lambda) + (\lambda - \theta)\right] - \left[h^2 (X - \theta)\right] \ldots (2)$$

The difference in the estimated genetic superiority of an immigrant over a native by the two methods is then a convenient measure of the bias which results from treating the two progeny populations as one. Subtracting equation (2) from equation (1) the estimate of bias, Q , becomes :

$$Q = h^2(\lambda - \theta) - (\lambda - \theta) \ldots\ldots\ldots\ldots\ldots (3)$$

$$= (\lambda - \theta)(h^2 - 1)$$

The bias is therefore negative when the immigrant population is on average superior to the native population ($\lambda > \theta$: $h^2 < 1.0$), and positive when the immigrant population is inferior ($\lambda < \theta$; $h^2 < 1.0$). This implies that in the past prospective immigrants which were on average better than the sire-line have been under-rated, while those which were poorer in performance were over-rated. The ability to discriminate among native and immigrant sub-populations was therefore reduced. Equation (3) demonstrates that the bias stems from treating the average difference between immigrants and natives ($\lambda - \theta$) as a phenotypic difference when in fact it is genetic.

Example

For the sake of example, the true values of the sub-population means will be replaced by their estimates for ultrasonic backfat in the sire-line in the 1970 generation when Norwegian Landrace and Large Whites were tried as immigrants. The following were the year means for both sexes in all environments:

Genotype	Mean ± Standard error	No. Pigs	No.Sire
"Pure" native sire-line ($\hat{\theta}$)	1.80 ± 0.02cms.	140	12
F_1 sire-line x Norwegian Landrace ($\hat{\lambda}_{nl}$)	1.59 ± 0.04cms.	31	2
F_1 sire-line x Large White ($\hat{\lambda}_{lw}$)	2.21 ± 0.06cms.	22	2

Assuming the phenotypic variance of the three sub-populations to be equal, $h^2 = 0.5$ and zero heterosis, the bias ($\hat{Q}$) from using Method 1 as opposed to Method 2 may be calculated from equation (3):

Norwegian Landrace: $\hat{Q}_{nl} = 0.5\ (1.59 - 1.80) - (1.59 - 1.80)$

$= + 0.105$ cm. or $+ 0.34\ \sigma_p$

Large White: $\hat{Q}_{lw} = 0.5\ (2.21 - 1.80) - (2.21 - 1.80)$

$= - 0.205$ cm. or $- 0.66\ \sigma_p$

where $\sigma_p = 0.31$ cm. (Table 6.1). According to these calculations, treatment of all progeny as a single population would have under-rated Norwegian Landrace crosses by 0.105 cm. and over-rated Large Whites by 0.205 cm. in a mass selection programme for backfat alone. Clearly detrimental biases of this magnitude could hamper genetic progress.

The above example has helped to illustrate two properties of the bias: that it is reduced as heritability increases, and more obviously that it depends on the degree of superiority or inferiority of the immigrant sub-population. It is noteworthy that, if only one individual immigrant offspring is tested in any generation, according to Method 2 $I = \lambda$ and the prediction of breeding value (A_I) reduces to:

$$A_{I(2)} = (\lambda - \theta) = (I - \theta)$$

so that under these circumstances the animal's phenotype (I) is the best indicator of its breeding value, and the measure of bias, Q, is unchanged.

Selection For More than One Character.

The problem may now be directly extended to the situation where individuals are selected on an index combining several traits. Selection in the A.B.R.O. sire-line has been on an index comprising daily gain, food conversion ratio and average backfat since 1966. The detailed form of the index is described in Appendix C, but takes the general form

$$I = \sum_i b_i (y_i - \mu_i) \quad \text{for } i = 1,\ldots\ldots, m \text{ variates,}$$

where y_i is the measured variate, μ_i the appropriate population sex mean and b_i the index coefficient. Similarly, the aggregate genotype takes the general form

$$M = \sum_j a_j x_j \quad \text{for } j = 1,\ldots, n \text{ traits,}$$

where x_j is an individual's true breeding value and a_j is the economic partial regression coefficient. The mean aggregate genotype (M) for a group of individuals may be estimated as

$$\bar{M} = \sum_j a_j \mu_j \ ,$$

where μ_j, the observed mean phenotypic value, is assumed equivalent to the mean genotypic value.

Assume for simplicity that an equal amount of family information is available on each individual so that the same index weights (b_i) apply to all pigs. Let μ_i be a trait-sex mean for the whole population of progeny on test, and let θ_i and λ_i represent means for "pure" native and separate immigrant crossbred populations, assumed to be known without error as before. Treating natives and immigrants as members of a single population (Method 1), the individual selection criteria or index values for a native (I_{sl}) and an immigrant (I_I) are:

$$I_{sl(1)} = \sum_i b_i (y_i - \mu_i)$$

and
$$I_{I(1)} = \sum_i b_i (z_i - \mu_i),$$

where z_i distinguishes observations taken on immigrants from those taken on natives (y_i). The estimated superiority of an immigrant is then:

$$I_{I(1)} - I_{sl(1)} = \sum_i b_i (z_i - y_i) \ldots\ldots \quad (4)$$

Acknowledging the fact that immigrant and native population means are different (Method 2), native and immigrant index values are calculated as:

$$I_{sl(2)} = \sum_i b_i (y_i - \theta_i)$$

and
$$I_{I(2)} = \sum_i b_i (z_i - \lambda_i) + \sum_j a_j (\lambda_j - \theta_j).$$

In estimating the index value of an immigrant the second term is an adjustment for the difference in mean aggregate genotype between immigrant and native populations, obtained simply as follows:

$$\bar{M}_I = \sum_j a_j \lambda_j$$

$$\bar{M}_{sl} = \sum_j a_j \theta_j$$

$$\bar{M}_I - \bar{M}_{sl} = \sum_j a_j (\lambda_j - \theta_j).$$

For the purpose of selection Method 2 index values of immigrants may be directly compared with those of natives, since (e.g. Henderson, 1963) for an immigrant: $E(M_I \mid I_o) = \mu_{M(I)} + I_o$,

and for a native : $E(M_{sl} \mid I_o) = \mu_{M(sl)} + I_o$,

where I_o is an observed index value and μ_M is the appropriate true mean aggregate genotype. The estimated superiority of an immigrant over a native by Method 2 is therefore:

$$I_{I(2)} - I_{sl(2)} = \left\{\sum_i b_i(z_i - \lambda_i) + \sum_j a_j(\lambda_j - \theta_j)\right\} - \left\{\sum_i b_i(y_i - \theta_i)\right\} \quad (5)$$

The bias (Q) which results from using Method 1 rather than Method 2 is then obtained by subtracting equation (5) from equation (4) as before:

$$Q = \sum_i b_i(\lambda_i - \theta_i) - \sum_j a_j(\lambda_j - \theta_j) \ \ldots\ldots \qquad (6)$$

which is analogous to equation (3) in the case of a single character.

Example.

Returning to the earlier example of the 1970 generation, the necessary sub-population means with standard errors are:

Genotype	Daily Gain (lbs/day)	F.C.R.	Average Backfat (cms.)
"Pure" native sire-line ($\hat{\theta}_i$)	1.69 ± 0.02	3.52 ± 0.03	1.80 ± 0.02
F_1 sire-line x Norwegian Landrace ($\hat{\lambda}_{(NL)i}$)	1.69 ± 0.04	3.45 ± 0.05	1.59 ± 0.04
F_1 sire-line x Large White ($\hat{\lambda}_{(LW)i}$)	1.62 ± 0.04	3.53 ± 0.05	2.21 ± 0.06

Assume now that pigs are selected on a simple index consisting of records taken only on themselves so that i = j. The necessary index weights (b_i), taken from Table 7.5.2, the economic weights (a_j), taken from Table 6.5, and some intermediate stages in calculating Q are set out in Table 8.1. Summation of the third column for each breed shows that the mean difference in aggregate genotype between immigrants and natives was + 148 points (better) for Norwegian Landrace and - 239 points (worse) for Large Whites. The estimate of bias (Q) from using Method 1 as opposed to Method 2 is obtained by subtracting the sum of the third column from the sum of the second, when:

$$\hat{Q}_{nl} = 80 - 148 = - 67 \text{ points or } 0.50\,\sigma_I$$

$$\hat{Q}_{lw} = -136 + 239 = +103 \text{ points or } 0.76\,\sigma_I\ ,$$

where σ_I = 135 points (Table 7.5.2). Treating immigrants and natives as members of a single population would therefore have caused Norwegian Landrace to be under-rated by 67 index points and Large Whites to be over-rated by 103 points. There can be little doubt that differences of this magnitude would affect the selection of immigrants.

So far an attempt has only been made to demonstrate that the bias occurs. In principle the simplest way to avoid the bias in future generations would be to adopt Method 2 and estimate native and immigrant sub-population means from the data separately, making the adjustment for differences in aggregate genotype. Unequal amounts of family information on each pig would not affect the method of estimating an immigrant's index value ($I_{I(2)}$), but the bias (Q) would differ from pig to pig since the b_i would no longer cancel. The main drawback to the practical application of the new

Table 8.1.

Sample Calculations of Various Quantities Required for Estimating Selection Bias in Comparisons of Immigrants and Natives in the A.B.R.O. Sire-Line.

Trait i	b_i[*]	a_j	Norwegian Landrace			Large White		
			$(\lambda_i-\theta_i)$[$]	$b_i(\lambda_i-\theta_i)$	$a_i(\lambda_j-\theta_j)$	$(\lambda_i-\theta_i)$[$]	$b_i(\lambda_i-\theta_i)$	$a_j(\lambda_j-\theta_j)$
Daily Gain (lbs/day)	+0.56	+1.80	0	0.0	0.0	-7	-3.9	-12.6
Food Conversion Ratio	-1.93	-4.80	-7	+13.5	+33.6	+1	-1.9	-4.8
Average Backfat (cms.)	-3.18	-5.40	-21	+66.8	+133.4	+41	-130.4	-221.4
				+80.3	+148.0		-136.2	-238.8

---

[*] For explanation of symbols see text.

[$] Multiplied by 100.

estimation procedure (Method 2) is the assumption that the sub-population means are known without error. Clearly, there will be occasions when only a very limited number of immigrant parents of a particular breed are available, with the result that the immigrant progeny population will be very small. This might be the case where small samples of newly imported foreign breeds or individuals of exceptionally high merit are the candidates for immigration. If it is accepted that breeds are "fixed" effects, or that they do not represent random samples from a wider population, it is difficult to see how the problem may be resolved since individual breed means cannot then be regressed to the overall mean. In the unlikely event that an argument could be made out for treating breeds as "random" effects, the genetic variance could be partitioned into between- and within-breed components in the manner described by James (James, 1966; Jackson and James, 1970) and handled in the same way as between- and within-family variation. The question of how best to utilise "fixed" effects means of low precision will therefore be a subject for future statistical investigation. Usual selection index theory assumes that the population means are known without error, and is widely used in practice for large population sizes. In order to usefully apply Method 2 in favour of Method 1 it would be desirable to have as large an immigrant progeny population as possible, with numbers approaching those of the native population. With small groups of immigrants on test Method 2 may be as much in error as Method 1. A practical way of maximising the size of the immigrant population, where there are sufficient parents, would be to test only one immigrant "breed" in each generation. The preliminary selection index

(Chapter 3 and Chapter 7), to which Method 2 cannot be applied because the means are unknown, would also need to be used with caution to avoid culling under-rated immigrants prematurely.

Finally it should be pointed out that if an F_1 immigrant x sire-line individual is successful in being selected as a parent of the next generation, the bias will still be present in the backcross progeny but will be reduced since the quantity $(\lambda_j - \theta_j)$ will be roughly halved in each successive generation. The native population is therefore an aggregate of such sub-populations all of which are slightly genetically different from one another. The first trial of an individual from outside the line as an immigrant is however the most critical, since erroneous rejection is absolute or alternatively, once incorrectly selected, it will be much more difficult to remove the relatively large numbers of progeny by subsequent selection.

8.2.2 Heterosis.

The occurence of heterosis in the cross-bred F_1 progeny of potential immigrants may increase their chances of selection relative to native sire-line progeny in which the amount of heterosis would be expected when the sire-line and immigrant populations are genetically dissimilar. From the 1972 breed composition of the sire-line (Table 3.1) it can be seen that at least half the genes of any native pig would be expected to differ in origin from those of any existing breed which has already contributed to the line, and would of course differ totally from those of a new breed being introduced for the first time. Genetic diversity between immigrants and natives would therefore usually be greater than genetic diversity among natives, and bias in selection would result from the relative increase in heterosis levels in immigrants compared to natives.

It will be useful to briefly consider the circumstances under which the bias due to heterosis is likely to have the greatest effect. Suppose that heterosis is shown by the cross-bred immigrant progeny but not by the native progeny. Suppose further that mass selection on phenotype for a single trait is practised at an intensity (p_{sl}) of 0.10 among native sire-line boars, and that truncation selection to the same cut-off point (T) is applied to the immigrant progeny population. The distributions of native and immigrant progeny (solid lines) are drawn diagrammatically in Figure 8.2. The presence of heterosis in the immigrant progeny, assumed to affect all pigs equally, would cause an upwards shift in the immigrant distribution (dotted line) equal to the amount of heterosis (H/σ). The effect of heterosis would then be to inflate the proportion of the immigrant distribution from which immigrants could be selected, as determined by the cut-off point (T) at which 10% of natives are selected. The net result of heterosis is therefore to lower the selection intensity applied to the immigrant test population , and to cause the selection of a proportion of animals whose "heterosis-free" value would be below the level of acceptance (T) for immigration into the sire-line. This model is somewhat simplified because in practice the truncation point (T) would be determined by the joint performances of immigrants and natives. Where small numbers of immigrants are tested however, T would be largely determined by the performance of the natives.

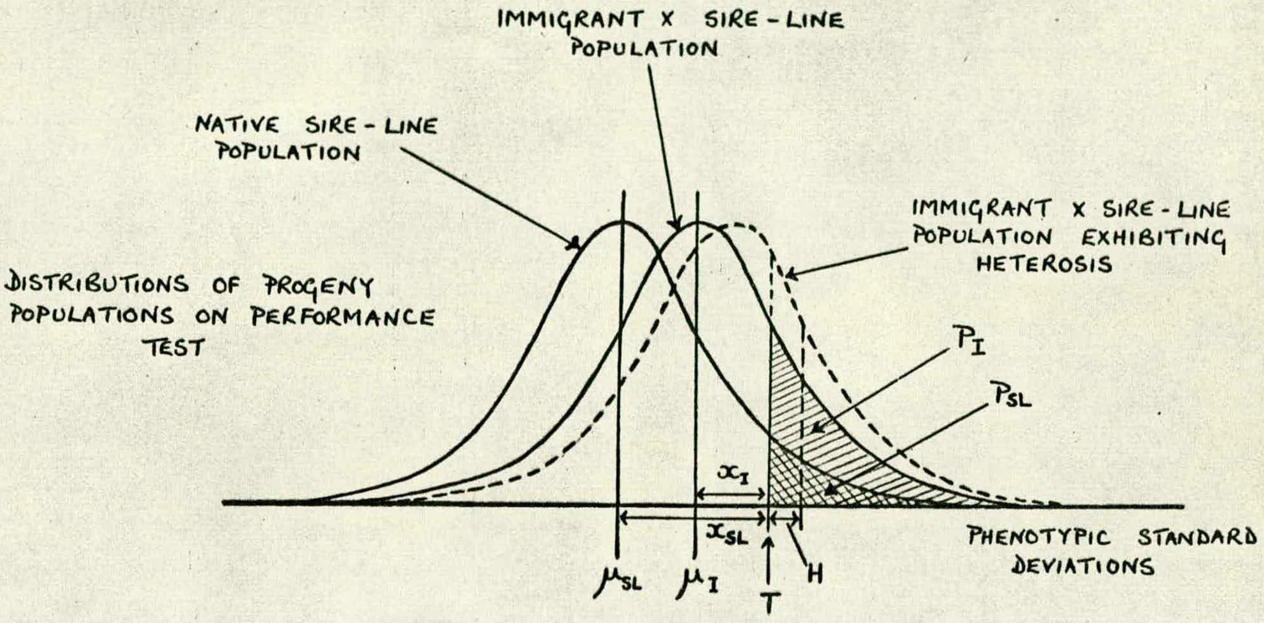
For a given difference between immigrant (μ_I) and native (μ_{sl}) true progeny population means, and with equality of variances (σ), the distance (x_I) between μ_I and T can be deduced as:

$$x_I = x_{sl} - (\mu_I - \mu_{sl}),$$

where x_{sl} is known ($p_{sl} = 0.10$). The proportion of tested immigrants which could be selected (p_I) may then be obtained from tables. H standard deviations of heterosis would reduce the true x_I to (x_I - H), increasing p_I to p_I'. A proportion ($p_I' - p_I$) of all would-be immigrants tested would therefore have a chance of being erroneously selected solely as a result of heterosis. Consequently a proportion R = $(p_I' - p_I)/p_I'$ of immigrants actually selected in the presence of heterosis might have been selected in error. R could then be interpreted as the probability that an individual's heterosis-free value lies below the truncation point (T), given that it has already been selected. Again this may be an over-simplification since not all the individuals lying within the selected portion of the immigrant distribution may be required as parents and there must be a gradation of probabilities inside the truncated area. Nevertheless the value of R will be sufficient to compare the relative seriousness of the bias under different conditions.

Figure 8.2

Diagrammatic Representation of Quantities Required for Calculating the Probability of Incorrect Selection of Potential Immigrants for Entry to the A.B.R.O.Sire-Line.



Explanation of Symbols

μ_I = true mean of immigrant x sire-line population.

μ_{sl} = true mean of sire-line population.

x_I = distance between cut-off point and μ_I, in standard deviations.

x_{sl} = distance between cut-off point and μ_{sl}, in standard deviations.

p_I = proportion of immigrant x sire-line population selected.

p_{sl} = proportion of sire-line population selected.

H = amount of heterosis occurring in immigrant x sire-line population, in standard deviations.

T = cut-off (truncation) point.

$$\mu_I - \mu_{SL} = x_{SL} - x_I$$

Example

Suppose the true means of immigrant and native progeny populations on test differ by $(\mu_I - \mu_{s1})/\sigma = 0.2$, and that heterosis in the immigrant population amounts to $H/\sigma = 0.5$. If 10% of natives are selected, $p_{s1} = 0.1$ and $x_{s1} = 1.28$ (Table II1 of Fisher and Yates, 1963). Then $x_I = 1.28 - 0.20 = 1.08$ for the heterosis-free immigrant distribution so that $p_I = 0.14$. Taking account of heterosis x_I is reduced to $x_I' = 1.08 - 0.50 = 0.58$ and p_I is increased to $p_I' = 0.28$. The probability that an immigrant has been incorrectly selected due to heterosis is therefore:

$$R = 0.14/0.28 = 0.50 \text{ or } 50\%.$$

Results of sample calculations of R for differences in population means ranging from $+ 1.5\sigma$ to $- 1.0\sigma$ and heterosis levels ranging from 0.2σ to 1.5σ are given in Table 8.2. The Table includes the values of the standardised selection differentials (i_I and i_I') corresponding to p_I and p_I', obtained from tables for a population size of 100 (Becker, 1967), giving an indication of the loss of selection differential on immigrant boars due to heterosis. For a given situation the superiority of the selected immigrants over the native population mean could then be evaluated as $(\mu_I - \mu_{s1})/\sigma + i_I'$ for direct comparison with i_{s1}.

The pattern of R values in Table 8.2 confirms what is intuitively obvious: namely that the probability of selecting

Table 8.2.

Sample Calculations to Show the Relative Effects of Varying Levels of Heterosis in the Performance of Potential Immigrants and Varying Differences Between Immigrant and Native Populations on the Selection of Immigrants. (A full explanation of symbols is given in the text in conjunction with Figure 8.2).

Mean Difference $\frac{(\mu_I - \mu_{SL})}{\sigma}$	Heterosis $\frac{H}{\sigma}$	Distance from to cut-off x_I	Proportion without Heterosis p_I	Proportion with Heterosis p_I'	Selection Differential without Heterosis i_I	Selection Differential with Heterosis i_I'	R = $\frac{p_I' - p_I}{p_I'}$
1.5	0.2	-0.22	0.59	0.66	0.65	0.55	0.11
	0.5			0.76		0.41	0.22
	1.0			0.89		0.21	0.34
	1.5			0.96		0.09	0.39
1.0	0.2	0.28	0.39	0.47	0.98	0.84	0.17
	0.5			0.59		0.65	0.34
	1.0			0.76		0.41	0.49
	1.5			0.89		0.21	0.56
0.5	0.2	0.78	0.22	0.28	1.33	1.19	0.21
	0.5			0.39		0.98	0.44
	1.0			0.59		0.65	0.63
	1.5			0.76		0.41	0.71
0.2	0.2	1.08	0.14	0.19	1.57	1.41	0.26
	0.5			0.28		1.19	0.50
	1.0			0.47		0.84	0.70
	1.5			0.66		0.55	0.79

Table 8.2 (cont).

$\frac{(\mu_I - \mu_{sL})}{\sigma}$	$\frac{H}{\sigma}$	x_I	p_I	p_I'	i_I	i_I'	$\frac{p_I' - p_I}{p_I'}$
0.0	0.2	1.28	0.10	0.14	1.73	1.57	0.29
	0.5			0.22		1.33	0.55
	1.0			0.39		0.98	0.74
	1.5			0.51		0.65	0.83
-0.2	0.2	1.48	0.07	0.10	1.88	1.73	0.30
	0.5			0.16		1.50	0.56
	1.0			0.32		1.11	0.78
	1.5			0.51		0.78	0.86
-0.5	0.2	1.78	0.04	0.06	2.10	1.95	0.33
	0.5			0.10		1.73	0.60
	1.0			0.22		1.33	0.82
	1.5			0.39		0.98	0.90
-1.0	0.2	2.28	0.011	0.019	2.51	2.33	0.39
	0.5			0.04		2.10	0.75
	1.0			0.10		1.73	0.90
	1.5			0.22		1.33	0.95

an immigrant whose heterosis-free value lies below the acceptance limit (T) increases with the amount of heterosis, and with decreasing levels of real superiority of immigrants over natives. For example, with heterosis at 0.5σ, or 5% in a character whose coefficient of variation (σ/μ_I) is 10%, R ranges from 0.22 where the immigrants are 1.5σ better, to 0.55 where there is no difference between immigrants and natives, down to 0.75 where immigrants are 1.0σ worse. For higher amounts of heterosis the values of R are correspondingly greater. At the extremes R = 0 ($p_I = p'_I = 1.00$) when immigrants are very much better than natives, and R = 1.00 ($p_I = 0$; $p'_I > 0$) when immigrants are very much worse.

In the A.B.R.O. sire-line performance test, heterosis might be expected in daily gain and food conversion ratio but not in ultrasonic backfat (e.g. Sellier, 1970). 5% heterosis in daily gain and food conversion, for example, would bias the mean difference in aggregate genotype between immigrant and native progeny, $\sum_j a_j(\lambda_j - \theta_j)$ (from section 8.2.1), by $\sum_j a_j H_j \simeq 70$ index points or $0.52\sigma_I$, where H_j is the amount of heterosis in units of the j^th trait and σ_I = 135 points. As there is little reason to suspect that presently available pure breeds are greatly superior to the sire-line on aggregate, and since any real superiority would be halved in the "cross-bred" candidate immigrant population on test, it is likely that heterosis, if present, might have quite a large effect on the accuracy of selection decisions on immigrants (Table 8.2). If heterosis levels are known they could be taken into account by modifying Method 2 of the previous section for calculating the index values of immigrants, so that:

$$I_{I(2)} = \sum_i b_i (Z_i - \lambda_i) + \sum_j a_j \left\{ (\lambda_j - \theta_j) - H_j \right\} .$$

As already discussed, this solution to the problem of bias has questionable utility with small population sizes since the means are assumed to be known without error. Note that, when calculated from actual performance test results, the observed immigrant subpopulation means (λ_i) contain average heterosis effects, but the first term $\sum_i b_i (Z_i - \lambda_i)$ is unbiased when heterosis is assumed to affect all individuals equally.

In order to obtain estimates of the levels of heterosis present in potential immigrants on performance test, an experiment has been set up to measure heterosis in crosses of the sire-line with Large Whites. The results will now be presented.

8.2.2.1 Estimation of Heterosis in Large White x Sire-Line Crosses.

Design and Analysis.

The experiment to measure heterosis on performance test was designed as a 2 x 2 reciprocal mating of a sample of the sire-line with some outbred Large Whites (e.g. Robertson, 1949). The sire-line parents were randomly chosen 1971-born boars and gilts. The Large White parents were made up of pigs from a small herd of outbred Large Whites maintained at A.B.R.O. together with stock purchased from the University of Newcastle. Both sire-line and Large White females were of mixed, first and second, parities. In setting up the trial the object was to maximise the number of sires rather than to test a large number of progeny per sire. 8 sire-line (SL) boars and 9 Large White (LW) boars were each mated to both sire-line and Large White females, giving 4 classes of progeny: SL xSL, SL x LW, LW x SL and LW x LW. Pigs were born contemporaneously on A.B.R.O.'s two pig farms (see Chapter 3), those farrowed at Skedsbush being transported soon after weaning to Mountmarle for testing.

The trial was intended to imitate as closely as possible the conditions under which sire-line and potential immigrant progeny are performance-tested in each new generation, described in Chapter 3. To avoid the possibility of genotype or sex by environment interactions boars and gilts were all tested indoors in the Danish-type fattening house, and therefore in order to economise on testing accommodation all the boars were penned in pairs. The two heaviest, most well-matched boars and up to 5 of the heaviest gilts in each litter were placed in two equally sized pens. In this way each dam contributed two pens of tested progeny: one containing a pair of boars and the other a group of gilts. Where a subclass of the 2 x 2 table was poorly represented, two pairs of boars were exceptionally tested in separate pens. The layout of the experiment, the number of dams contributing offspring from each sire and the number of progeny tested from each sire are shown in Table 8.3. Due to poor reproductive performance by the LW females, two of the SL boars failed to contribute SL x LW progeny, and two of the LW boars failed to contribute LW x LW progeny. Only one of the dams shown in the Table failed to contribute at least one offspring of both sexes.

Table 8.3.

Numbers and Distribution of Pigs Tested by Subclasses in Experiment to Measure Heterosis in Sire-Line x Large White Crosses.

			BREED OF DAM			
			Sire-Line (SL)		Large White (LW)	
		Boar Identity	Number of Dams	Number of Progeny (Boars+ Gilts)	Number of Dams	Number of Progeny (Boars+ Gilts)
BREED OF SIRE	Sire-Line (SL)	1	1	7	1	4
		2	2	10	1	7
		3	1	5	1	6
		4	2	10	0	0
		5	2	8	1	9
		6	2	11	0	0
		7	2	12	1	8
		8	1	6	1	6
		Total:	13	69	6	40
	Large-White (LW)	1	2	11	1	7
		2	1	5	1	7
		3	2	12	0	0
		4	1	4	2	11
		5	2	12	0	0
		6	1	6	1	9
		7	2	11	1	7
		8	2	13	1	7
		9	2	14	1	7
		Total:	15	88	8	55

The testing procedure was carried out as normal, and pigs were fed ad libitum on a proprietary pelleted ration containing approximately 2.99 Mcals. M.E. per kg. of dry matter and 14.5% crude protein (fresh weight), and supplemented by "Grofas" (trademark for I.C.I. Quindoxin non-antibiotic growth promoter) at 50 gms. per ton. Growth rate, pen food conversion ratio and average ultrasonic backfat thickness were recorded as each individual pig attained 180 lbs. liveweight. There were no recognisable outbreaks of disease during the trial.

The analysis was performed with the aid of a general least squares computer programme able to handle unequal or missing subclasses (Harvey, 1960), according to the following model:

$$Y_{ijklm} = a_i + b_j + c_k + (ab)_{ij} + (ac)_{ik} + (bc)_{jk} + S_{l(j)} + (CS)_{kl(j)} + e_{m(ijkl)},$$

where

a_i = effect of sex i
b_j = effect of j^{th} sire breed
c_k = effect of k^{th} dam breed
$S_{l(j)}$ = effect of l^{th} boar (sire) with sire breed j

$e_{m(ijkl)}$ = within-subclass residual effect.

Paired main effects denote first order interactions, and a_i, b_j and c_k are assumed to be fixed while $S_{l(j)}$ and $e_{m(ijkl)}$ are assumed to be random effects. Sex was treated as an overall main effect as described by Johnson, Omtvedt and Walters (1973), but interactions of sex with breed of sire and dam effects were included to remove breed differences. Parity effects of the dam were removed by partial regression, although significance levels of all main effects were unchanged by removing this source of variation. Since all the progeny of a given sire were born on one of the two farms, any difference between farms was confounded with sire differences. Removal of the between-farm sum of squares, calculated via a linear contrast, from the between-boar sum of squares resulted in a negligible reduction in the mean square for boars, so that farm effects were subsequently ignored. For growth rate and average backfat the analysis was conducted on individual pig records, but for food conversion it was conducted on un-weighted pen means.

Results.

The analysis of variance for performance test records on 252 purebred and crossbred pigs, consisting of 92 boars and 160 gilts in a total of 90 pens, is given in Table 8.4. The three mean squares involving sex were tested against the remainder. As expected the overall sex effect was significant for all three traits, but none of the sex x breed interactions was significant indicating a similar sex difference in the four types of progeny. The breed of sire mean squares were tested against the mean squares for boars within breed of sire, while the breed of dam and breed of sire x breed of dam interaction mean squares were tested against the breed of dam x boars within breed of sire interaction mean squares (e.g. Bereskin, Shelby and Hazel, 1971). 4 degrees of freedom were lost from the breed of dam x boars within

Table 8.4.

Analysis of Variance Table for Trial to Measure Heterosis in Sire-Line x Large White Crossbred Progeny on Performance Test.

Source	d.f.	Mean Squares		
		Growth Rate (lbs/day)	Food Conversion Ratio (lbs feed/lb gain)	Average Backfat (cms.)
Sex	1	1.047^{***}	0.574^{***}	0.093^{*}
Sex x Breed of Sire	1	0.124 NS	0.084 NS	0.001 NS
Sex x Breed of Dam	1	0.112 NS	0.011 NS	0.002 NS
Breed of Sire	1	0.294 NS	0.022 NS	1.063^{**}
Boars/Breed of Sire	15	0.236	0.093	0.109
Breed of Dam	1	0.891^{*}	0.284^{*}	0.520^{*}
Breed of Sire x Breed of Dam	1	0.516 NS	0.143 NS	0.024 NS
Breed of Dam x Boars/ Breed of Sire	11	0.179	0.056	0.049
Remainder	218	0.050	$0.042^{\$}$	0.019

NS = non-significant. $^{*} = P < 0.05$; $^{**} = P < 0.01$; $^{***} = P < 0.001$.

$^{\$}$56 degrees of freedom for the remainder - analysis carried out on pen means.

breed of sire mean squares owing to the presence of 4 missing subclasses (Table 8.3). Only the breed of sire mean square for backfat was significant, whereas the breed of dam mean squares were significant for all three traits suggesting the presence of maternal effects for growth rate and food conversion. The breed of sire x breed of dam interaction mean squares, providing a statistical test for heterosis, were non-significant for the three traits. Although significance levels are not shown, the two error terms for the breed effects were significantly different from the remainder mean squares except in the case of the breed of dam x boars within breed of sire mean square for food conversion. However the interaction or heterosis mean square for food conversion remained non-significant even after pooling to give a new error term with 67 degrees of freedom.

Least squares means and constant estimates are shown in Table 8.5. Standard errors of progeny class means and sex differences are based on the total variance of each trait, whereas standard errors of the three linear contrasts were calculated approximately from the appropriate error terms in the analysis of variance table. Significance levels are therefore those shown in Table 8.4. The estimates of breed of sire effects indicate that the sire-line were 0.08 lb/day and 0.03 lb. feed /lb.gain worse than Large White in daily gain and food conversion ratio respectively, and 0.15 cm. better than Large Whites in average backfat. The corresponding effects of the dam breed for growth rate and food conversion were much larger, and the difference between sire and dam breed effects may be taken as a measure of maternal influence.

Table 8.5.

Least Squares Means and Constant Estimates with Approximate Standard Errors from Trial to Measure Heterosis in Sire-Line x Large White Crossbred Progeny on Performance Test.

Effect	Growth Rate (lbs/day)	Food Conversion Ratio[$] (lbs feed/lb gain)	Average Backfat (cms.)
Progeny cross means:			
SL x SL	1.606±0.030	3.161±0.042	2.013±0.019
SL x LW	1.861±0.040	2.931±0.057	2.148±0.025
LW x SL	1.792±0.027	3.032±0.038	2.184±0.017
LW x LW	1.830±0.034	2.992±0.052	2.273±0.021
Constant estimates:			
Breed of Sire (SL-LW)	-0.078±0.070	0.034±0.068	-0.148±0.048
Breed of Dam (SL-LW)	-0.147±0.066	0.135±0.058	-0.112±0.035
Heterosis (crossbreds - purebreds)	0.108±0.064	-0.095±0.057	0.023±0.034
Sex (boars - gilts)	0.141±0.031	-0.170±0.044	-0.042±0.019

[$] Analysis based on pen means.

The linear contrast for estimating heterosis was defined as:

$$H = \tfrac{1}{2}(SL \times LW) + \tfrac{1}{2}(LW \times SL) - \tfrac{1}{2}(SL \times SL) - \tfrac{1}{2}(LW \times LW),$$

which was free from maternal and sire effects. The estimated values indicate an advantage of crossbreds over purebreds of 0.11 lb./day in growth rate and 0.10 lb. feed/lb. gain in food conversion. In addition there was an adverse heterotic effect of 0.02 cm. in average backfat. None of the heterosis estimates was significantly different from zero.

Discussion.

For the purpose of estimating the bias affecting selection decisions on the incorporation of potential immigrant crossbred progeny into the sire-line, the magnitude of the observed heterosis is of more interest than its statistical significance. Taking the heterosis estimates (Table 8.5) as percentages of the mid-value of the "pure" breeds, they amount to 6%, 3% and 1% for daily gain, food conversion and backfat respectively. The values for the first two traits were in exact agreement with the mean figures for a two-way cross put forward by Sellier (1970) in his review (Table 2.2), and this might be taken as evidence that the sire-line and Large Whites are as genetically distinct from one another as any other two breeds which might normally be used in a crossing programme. Although relatively small, positive heterosis in average ultrasonic backfat thickness was unexpected, and may well be due to chance. However, Bereskin et al. (1971) detected significant positive heterosis for carcass backfat in crosses of Durocs and Yorkshires, and suggested physiological conflicts between parental strains as a possible cause.

From the values for heterosis found here, the bias in the mean difference between the aggregate genotypes of sire-line and sire-line x Large White progeny on performance test would be $\sum_j a_j H_j \simeq 53$ index points or $0.4\,\sigma_I$ where $\sigma_I = 135$ points. Returning to the worked example of the bias on index selection arising from unknown population means on page 151, the mean difference between sire-line and Large White progeny, $\sum_j a_j\,(\lambda_j - \theta_j) = -239$ points, could be adjusted by $\sum_j a_j H_j$ to $\sum_j a_j \{(\lambda_j - \theta_j) - H_j\} = -292$ points. Remembering that the observed value for the mean of the immigrant subpopulation (λ_i) will contain any heterosis, the "total" bias taking into account both heterosis and differences between native and immigrant population means then becomes:

$$Q_{lw} = \sum_i b_i(\lambda_i - \theta_i) - \sum_j a_j\,(\lambda_j - \theta_j - H_j)$$

which is equal to + 156 points or $1.16\sigma_I$. If Norwegian Landrace crosses with the sire-line showed an equal amount of heterosis, the two sources of bias in the example would oppose one another and $\hat{Q}_{nl}$ would be reduced from -67 points to a trivial - 15 points. There would therefore appear to have been a greater risk of over-rating inferior immigrants in the past than of under-rating superior ones.

Before taking practical steps to combat the possible heterosis bias it will be important to establish that the levels found in this experiment were not simply due to chance, and to determine whether similar levels apply to crosses with other potential immigrant breeds. For this reason plans are now in hand for a second larger trial crossing the sire-line with Norwegian Landrace. Because of the magnitude of apparent maternal effects (Table 8.5) it may be wise to avoid the use of female immigrant parents whenever possible, since a bias similar to that arising from heterosis may result.

8.3 Past Immigration.

In the preceding section it was shown that, on the present method of performance testing crossbred immigrants alongside natives, immigrant progeny which are poorer in performance than the sire-line would tend to be over-rated as a result, firstly, of treating the sire-line and immigrant populations as one and, secondly, of ignoring the effects of heterosis. On the other hand, crossbred potential immigrants which are truly superior to the sire-line would tend to be under-rated due to the first source of bias and over-rated due to the second. Incorrect selection decisions on immigrants would therefore have been more likely in the case of inferior immigrant individuals than of superior ones. In this section the available evidence relating to past immigration will be reviewed. From now on it will be convenient to refer to unselected potential immigrant x native crossbred progeny simply as "immigrants".

The numbers of male and female parents of each genotype that has contributed progeny for testing as potential immigrants to the A.B.R.O. sire-line are shown in Table 8.6. The first 5 genotypes listed as contributing all

Table 8.6.

Numbers and Genotypes of Male (M) and Female (F) Immigrant Parents Contributing Progeny for Testing as Potential Immigrants to the A.B.R.O. Sire-Line, by Years.

Genotype	1960		1961		1962		1963		1964		1965		1966		1967		1968		1969		1970		1971		1972	
	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F
Native Sire-Line	0	0	7	21	6	23	4	16	7	24	6	16	5	19	5	28	8	41	8	37	12	43	13	44	9	23
Immigrant:																										
Tamworth x Wessex Saddleback	1	2																								
Tamworth x British Landrace	2	10																								
Large White x Wessex Saddleback	2	10						1																		
British Landrace		1	1	4	1	1	1				1				1	1										
Large White		2	1	2	2	1	1		1	8		1	1		3		1				2		2		4	
Wessex Saddleback			1	2	1		1					1														
Lacombe									1								1									
Hampshire									1			2	1		1		1									
Pietrain											1		2		1											
Hampshire x Pietrain														3												
Lacombe x Pietrain														2					1							
Lacombe x Hampshire														1												
Welsh															1											
Yorkshire																	3		1							
Large White x Hampshire																	1									
Large White x Pietrain																		3								
Pietrain x (Large White x B.L.)																			1							
Commercial Hybrid*																					1					1
Norwegian Landrace																					2		2		1	
Total Immigrants	5	25	3	8	4	2	3	1	3	8	2	4	4	6	7	1	7	3	3	0	5	0	4	0	5	1
Total Number of Parents	5	25	10	29	10	25	7	17	10	32	8	16	9	25	12	29	15	44	11	37	17	43	17	44	14	24

*The two commercial hybrid immigrants were not from the same company.

the measured offspring in 1960 were regarded as the founders of the sire-line, so that their progeny were the native parents of the 1961 generation. The pure Large White breed was most frequently tried as an immigrant, whereas only one representative of the Welsh breed and some of the crosses was tried. All the founder parents containing Tamworth genes were the progeny of a single boar, which was given no further opportunity to contribute.

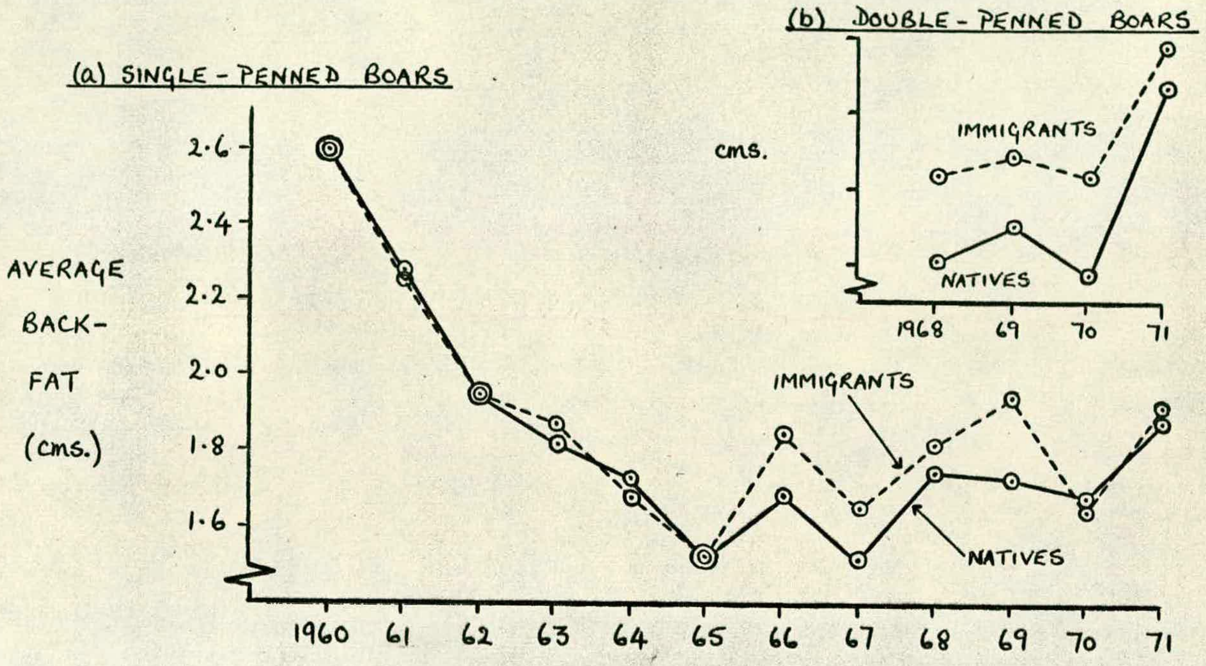
8.3.1 Performance of Immigrants Versus Natives.

To compare the performances of the 19 immigrant genotypes with the "native" sire-line in each year would be of little value since there were very few progeny from any one genotype in a given year. However the mean performance of all immigrant breeds together in relation to natives would give an indication of the average superiority of the immigrants in each generation. This is shown graphically for the three performance testing traits in Figures 8.3 - 8.5, and the corresponding means with standard errors are given in Tables 8.7 - 8.9. Referring to Figure 8.3 for example, the broken line represents a trend line of the mean performance of all immigrants, irrespective of breed, in each generation. The solid line joins the generation means of natives, and the weighted mean of the two lines would reduce to the graphs shown in Figures 5.1 and 5.2.

Figure 8.3 shows that before 1966, when there was a strong phenotypic decline in backfat, the immigrants were no better or worse than the natives, but between 1965 and 1970 immigrants appeared to lag some way behind. This is best

Figure 8.3

Graphs to show Mean Average Ultrasonic Backfat of Native Sire-Line Progeny (Solid Line) by Generations with Trend Line (Broken Line) Indicating Whether Potential Immigrant Progeny were Better or Worse on Average than Natives



(a) SINGLE-PENNED BOARS

(b) DOUBLE-PENNED BOARS

(c) GILTS

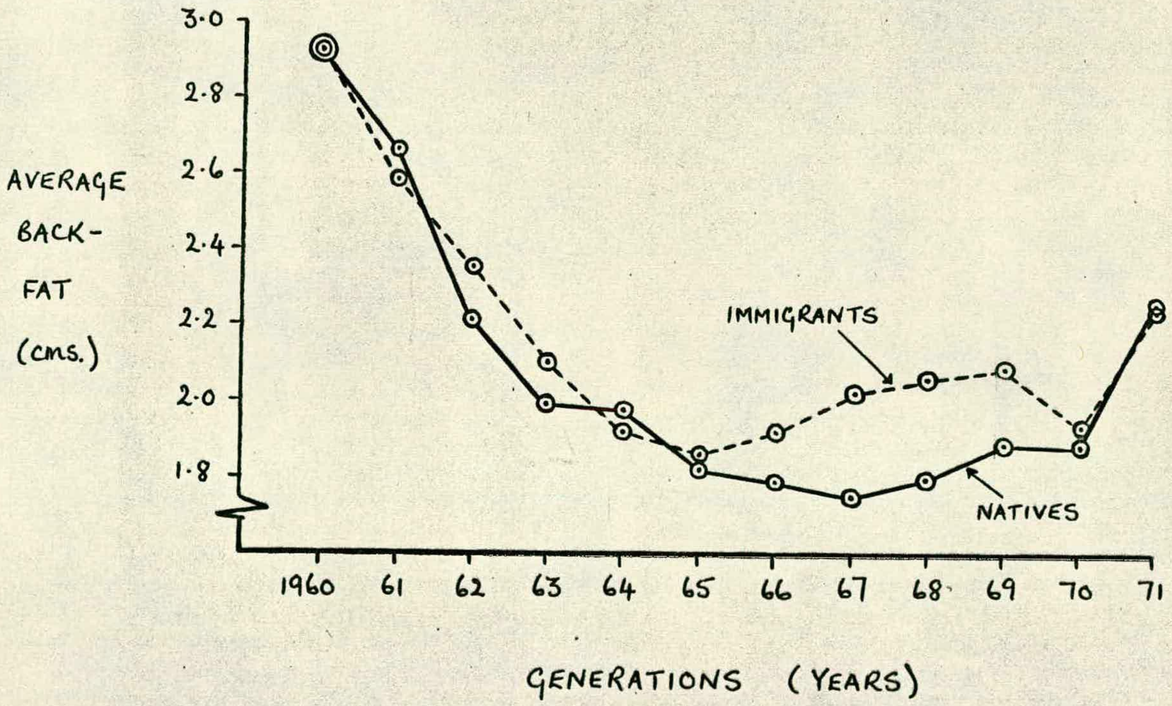
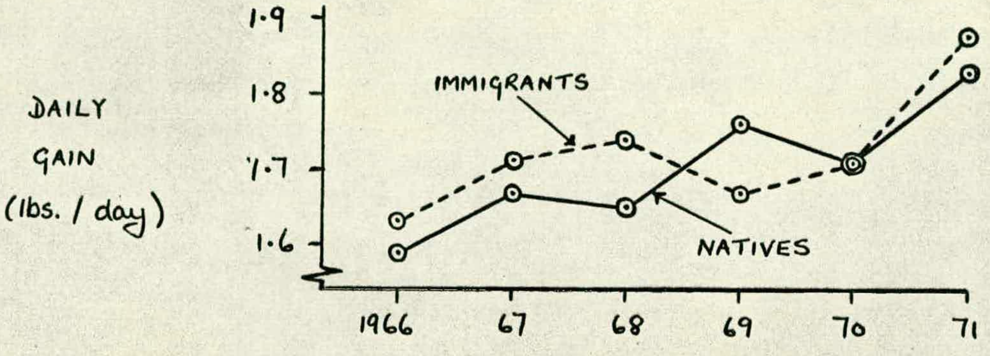


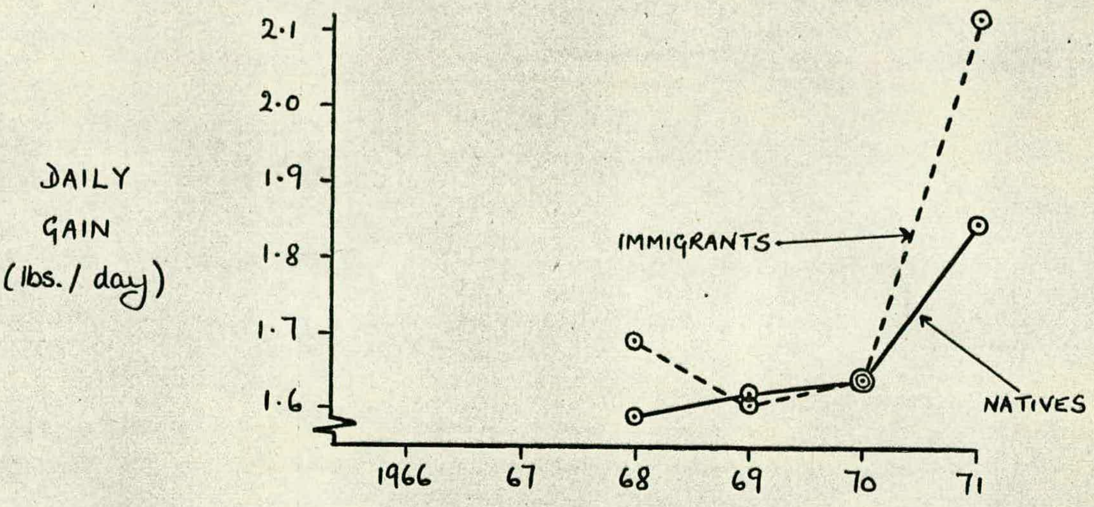
Figure 8.4

Graphs to show Mean Daily Gain of Native Sire-Line Progeny (Solid Line) by Generations with Trend Line (Broken Line) Indicating whether Potential Immigrant Progeny were Better or Worse on Average than Natives.

(a) SINGLE - PENNED BOARS



(b) DOUBLE - PENNED BOARS



(c) GILTS

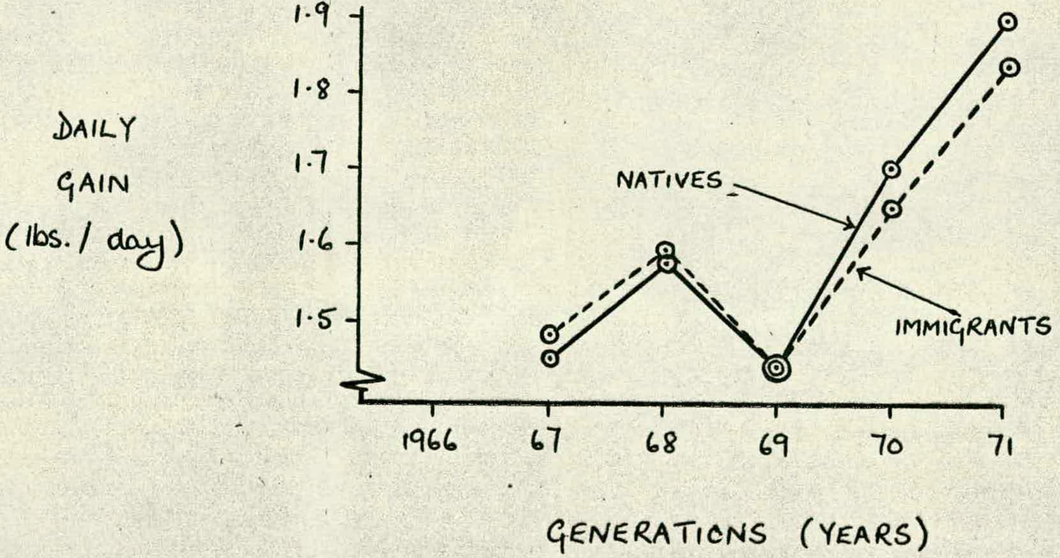
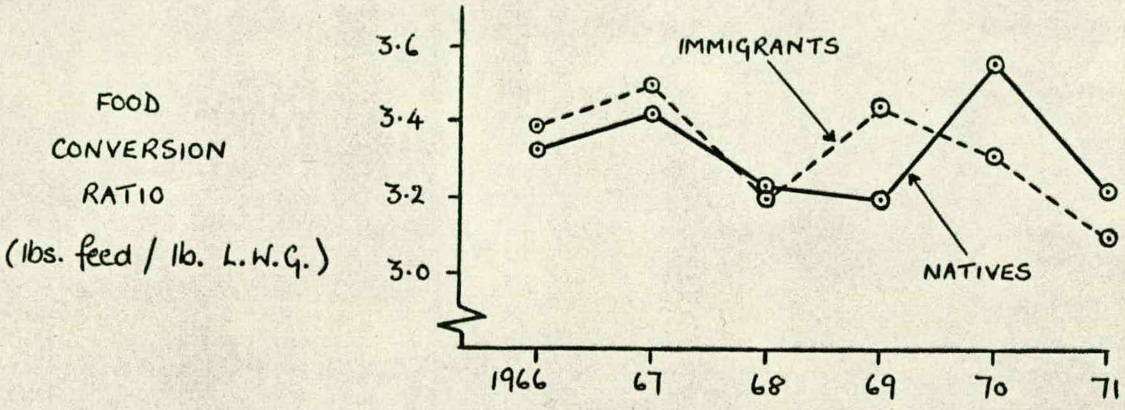


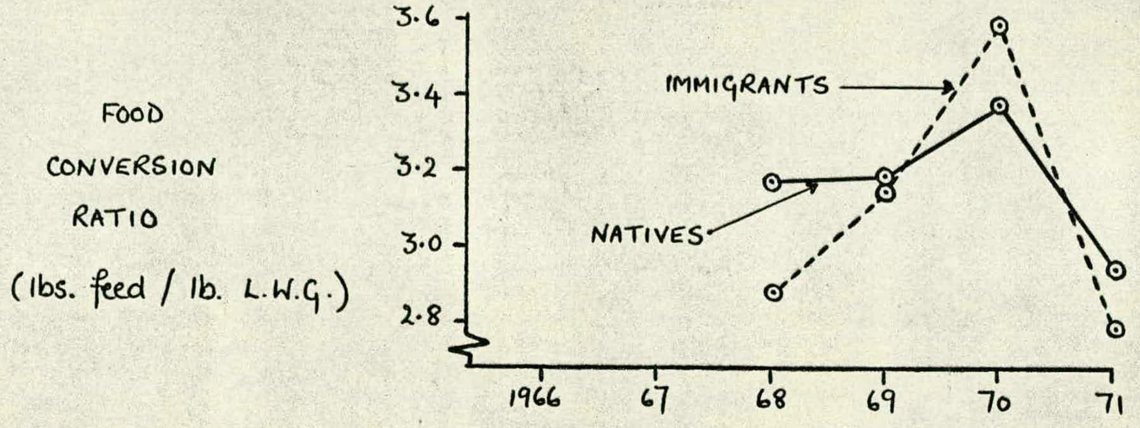
Figure 8.5

Graphs to show Mean Food Conversion Ratio of Native Sire-Line Progeny (Solid Line) by Generations, with Trend Line (Broken Line) Indicating whether Potential Immigrant Progeny were Better or Worse on Average than Natives.

(a) SINGLE-PENNED BOARS



(b) DOUBLE-PENNED BOARS



(c) GILTS

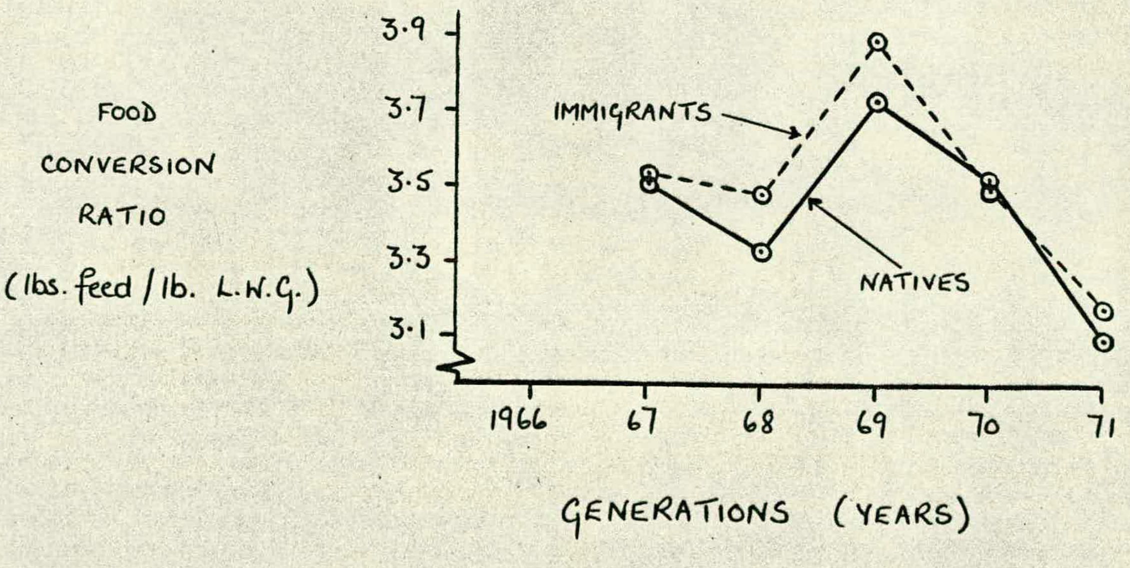


Table 8.7.

Average Weight-Corrected Ultrasonic Backfat Thickness (cms.) of Natives and Immigrants in the A.B.R.O. Sire-Line by Test Environments* and Years. Table Shows the Number of Pigs Tested, Subclass Mean and its Standard Error (S.E.).

	Single-Penned or Paddocked Boars						Double-Penned Boars						Gilts					
	Natives			Immigrants			Natives			Immigrants			Natives			Immigrants		
Year	No.	Mean	S.E.	No.	Mean	S.E.	No.	Mean	S.E.	No.	Mean	S.E.	No.	Mean	S.E.	No.	Mean	S.E.
1960	33	2.61	0.07										62	2.92	0.05			
1961	19	2.28	0.06	20	2.26	0.06							29	2.66	0.06	44	2.58	0.03
1962	18	1.95	0.05	15	1.95	0.07							50	2.21	0.03	37	2.35	0.04
1963	18	1.82	0.07	20	1.87	0.08							27	1.99	0.05	36	2.10	0.05
1964	31	1.73	0.07	10	1.68	0.08							60	1.98	0.04	15	1.92	0.05
1965	24	1.52	0.05	11	1.52	0.09							47	1.82	0.04	18	1.86	0.08
1966	14	1.69	0.06	17	1.85	0.06							26	1.79	0.06	21	1.92	0.07
1967	24	1.51	0.05	34	1.65	0.04							39	1.75	0.04	49	2.02	0.04
1968	24	1.75	0.04	19	1.82	0.06	24	1.61	0.04	12	1.84	0.08	86	1.80	0.03	87	2.06	0.03
1969	27	1.73	0.04	13	1.95	0.05	32	1.70	0.05	4	1.89	0.15	73	1.89	0.03	36	2.09	0.05
1970	35	1.67	0.04	10	1.64	0.13	15	1.57	0.07	13	1.83	0.07	90	1.88	0.03	44	1.93	0.06
1971	45	1.88	0.05	11	1.92	0.08	56	2.07	0.03	8	2.18	0.10	114	2.24	0.03	27	2.25	0.05

* see Section 3.1

Table 8.8.

Average Daily Liveweight Gain (lbs/day) of Natives and Immigrants in the A.B.R.O. Sire-Line by Test Environments and Years. Table Shows the Number of Pigs Tested, Subclass Mean and its Standard Error (S.E.)

	SINGLE-PENNED BOARS						DOUBLE-PENNED BOARS						GILTS					
	NATIVES			IMMIGRANTS			NATIVES			IMMIGRANTS			NATIVES			IMMIGRANTS		
Year	No.	Mean	S.E.	No.	Mean	S.E.	No.	Mean	S.E.	No.	Mean	S.E.	No.	Mean	S.E.	No.	Mean	S.E.
1966	14	1.59	0.04	17	1.63	0.02												
1967	24	1.67	0.05	34	1.71	0.04							39	1.45	0.03	49	1.48	0.04
1968	22	1.65	0.04	19	1.74	0.04	22	1.59	0.05	12	1.69	0.04	86	1.58	0.02	86	1.59	0.02
1969	27	1.76	0.03	13	1.67	0.05	32	1.62	0.03	4	1.61	0.08	73	1.44	0.02	36	1.44	0.03
1970	35	1.71	0.03	10	1.71	0.08	15	1.64	0.06	13	1.64	0.05	90	1.70	0.03	44	1.65	0.03
1971	45	1.83	0.05	11	1.88	0.06	56	1.85	0.04	8	2.12	0.06	114	1.90	0.03	27	1.84	0.04

Table 8.9.

Average Food Conversion Ratio (lbs feed/lb. liveweight gain) of Natives and Immigrants in the A.B.R.O. Sire-Line by Test Environments and Years. Table Shows the Number of Pigs Tested, Subclass Mean and its Standard Error (S.E.)

	SINGLE-PENNED BOARS						DOUBLE-PENNED BOARS						GILTS					
	NATIVES			IMMIGRANTS			NATIVES			IMMIGRANTS			NATIVES			IMMIGRANTS		
Year	No.	Mean	S.E.	No.	Mean	S.E.	No.	Mean	S.E.	No.	Mean	S.E.	No.	Mean	S.E.	No.	Mean	S.E.
1966	14	3.33	0.06	17	3.39	0.07												
1967	24	3.42	0.06	34	3.50	0.06							39	3.52	0.06	49	3.53	0.10
1968	22	3.23	0.09	19	3.20	0.07	22	3.17	0.07	12	2.88	0.11	86	3.33	0.04	86	3.48	0.05
1969	27	3.20	0.08	13	3.45	0.09	32	3.19	0.05	4	3.15	0.15	73	3.73	0.04	36	3.89	0.07
1970	35	3.58	0.06	10	3.32	0.08	15	3.38	0.07	13	3.59	0.04	90	3.52	0.04	44	3.50	0.04
1971	45	3.22	0.05	11	3.10	0.06	56	2.94	0.04	8	2.79	0.06	114	3.10	0.02	27	3.18	0.03

explained by the fact that before 1966 most of the potential immigrants were British Landrace, Large White or Wessex Saddleback sire-line crosses: three out of the four foundation breeds. Either parallel improvement programmes in these breeds had kept pace with progress in the sire-line, or they had been subject to the same environmental influences as the sire-line. After 1965 immigrants contained a large proportion of Lacombe, Hampshire, Pietrain and Yorkshire genes (Table 8.6), and were fatter on average than natives. With the trial of Norwegian Landrace as immigrants in 1970 the gap once again began to close. No such clearcut differences between immigrants and natives were visible for daily gain or food conversion (Figures 8.4 and 8.5).

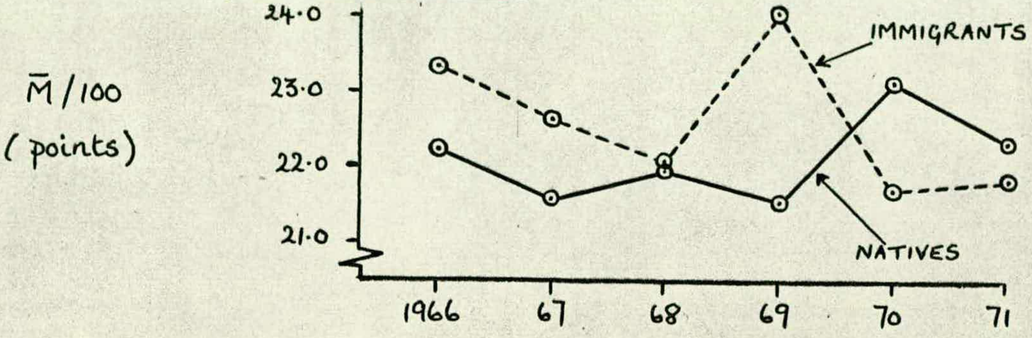
Ignoring the two other traits for the time being, the graphs of the average backfat of immigrants and natives (Figure 8.3) will serve to illustrate an important point. Considering all the immigrants in any one year together, any gene flow between immigrants and natives during the period from 1966 to 1969 would on average clearly be expected to be harmful. Picking out the few superior immigrants which could contribute "useful" genes to the sire-line will therefore heavily depend on accurate breeding value estimation, and this is by no means guaranteed as shown in the previous section. Thus it is possible that the apparent termination or reversal of selection response for backfat after 1966 could be the result of the erroneous incorporation of immigrants, rather than the introduction of 3-trait performance testing or other environmental factors. On this hypothesis immigration could "hold-back" rather than enhance genetic progress in the Line. In addition the situation where a pure-bred immigrant population is considerably worse on average than the sire-line would also seem to be the least predisposing to correct decisions on the incorporation of individual immigrants.

From the graphs in Figure 8.3 there is no indication that immigration could have held back genetic improvement prior to 1966 when selection was solely for backfat thickness after X-rayed body length. To ascertain whether immigration could have slowed genetic progress from 1966 onwards when selection was based on an index, the mean aggregate genotype, calculated as $\overline{M} = \sum_j a_j \overline{X}_j$ where $\overline{X}_j$ is the observed mean, by years has been plotted in Figure 8.6. A low value of M is favourable reflecting the predominance of backfat and food conversion, and the graphs indicate that before 1970 immigrants tended to be poorer on average than natives. This is not altogether unexpected since by 1968 the line contained Welsh, Yorkshire Pietrain, Lacombe and Hampshire blood as well as the 4 Foundation breeds (see Table 3.1). It is therefore a definite possibility that between 1965 and 1970 genetic progress in the line could have been held back as a result of incorrect selection decisions taken on immigrants, whose overall merit was over-rated.

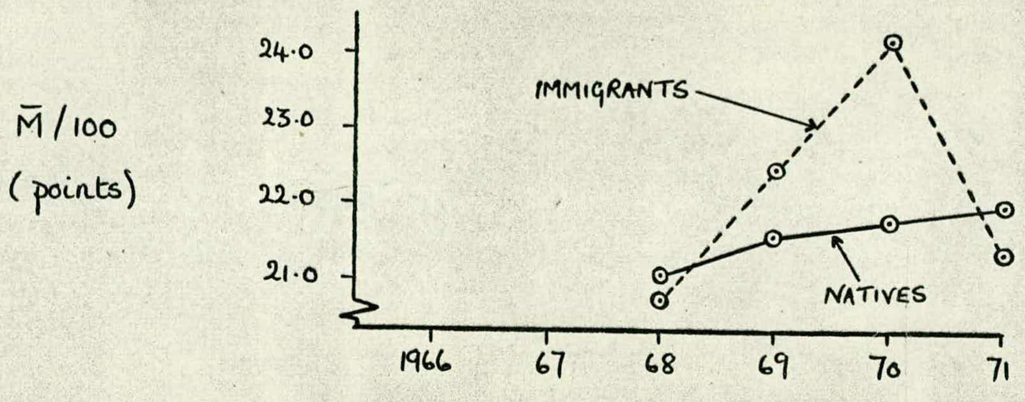
Figure 8.6

Graphs to show Mean Aggregate Genotype ($\bar{M}$) of Native Sire-Line Progeny (Solid Line) by Generations, with Trend Line (Broken Line) Indicating whether Potential Immigrant Progeny were Better or Worse on Average than Natives (Note that $\bar{M}$ has been scaled down by a factor of 1/100, and that low values are favourable).

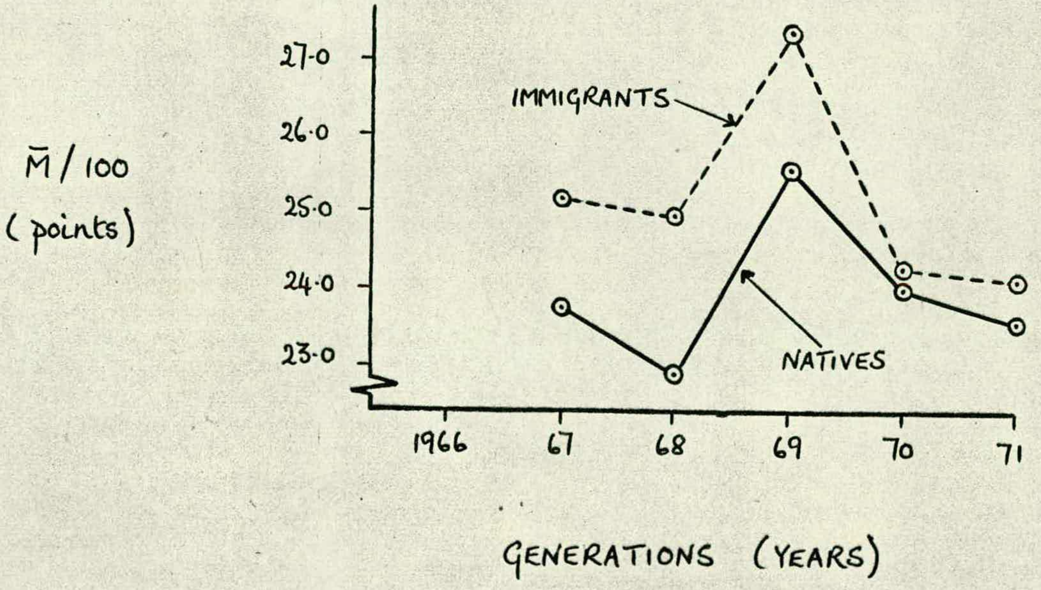
(a) SINGLE-PENNED BOARS



(b) DOUBLE-PENNED BOARS



(c) GILTS



8.3.2 Success of Immigrant Breeds.

Indirect evidence as to the success of past immigration may alternatively be obtained from the changes in the breed composition of the sire-line over time, since an immigrant's estimated breeding value ultimately determined whether or not it was selected. In each generation the native sire-line may be regarded as a "tester" against which the best available contemporary stock have been evaluated. The observed or "actual" (A) percentage contribution of a particular breed in any one year may therefore be compared with its "possible" (P) contribution under conditions of random mating. If the actual contributions of each breed to the line do not differ from their possible values under random mating, then it could be concluded that the selection procedure has failed to discriminate between breeds of high and low relative merit and breeds have been incorporated at random. If, on the other hand, some breeds show a much greater contribution and some a much lesser contribution than would have occurred from random mating, this could be interpreted as evidence that the selection procedure was successful in discriminating between breeds. As a method of assessing immigration, the ratio A/P takes into account the generations of selection which follow the initial introduction of a breed, and the fact that if immigrant progeny are incorrectly selected in one generation the opportunity exists for them to be selected out again in later generations.

The"actual"(A) and "possible" (P) percentage breed compositions and the A/P ratio for the A.B.R.O. sire-line are shown in Table 8.10 by years. A was taken to be the

Table 8.10.

Success of Breeds Contributing to the A.B.R.O. Sire-Line: "Actual" Observed (A) and "Possible" Under Random Mating (P) Breed Compositions* (%) of Parents Leaving Progeny by Years, Together With Ratio of Actual/Possible (A/P) Compositions.

Breed	1960			1961			1962			1963			1964		
	A	P	A/P	A	P	A/P	A	P	A/P	A	P	A/P	A	P	A/P
Wessex Saddleback	26.0	26.0	1.00	26.3	26.2	1.00	20.7	24.9	0.83	19.5	26.4	0.74	10.5	21.1	0.50
Tamworth	27.0	27.0	1.00	20.3	20.0	1.01	13.8	16.0	0.86	9.9	12.7	0.78	7.4	10.1	0.73
Large White	24.0	24.0	1.00	26.3	28.1	0.94	29.3	32.5	0.90	35.7	33.9	1.05	42.8	41.1	1.04
British Landrace	23.0	23.0	1.00	27.1	25.7	1.06	36.2	26.6	1.37	34.9	27.0	1.30	33.1	21.5	1.54
Lacombe													3.1	3.1	1.00
Hampshire													3.1	3.1	1.00
Pietrain															
Welsh															
American Yorkshire															
Norwegian Landrace															
Commercial Hybrid 1															
Commercial Hybrid 2															

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*Compositions were evaluated to more decimal places than shown, and, due to rounding, do not always total 100%.

Table 8.10 (cont).

Breed	1965			1966			1967			1968			1969		
	A	P	A/P	A	P	A/P	A	P	A/P	A	P	A/P	A	P	A/P
Wessex Saddleback	11.4	20.0	0.57	5.6	15.6	0.36	3.5	11.0	0.32	2.9	8.5	0.34	2.4	7.5	0.32
Tamworth	6.6	8.5	0.78	4.7	6.6	0.70	3.0	4.7	0.64	2.5	3.6	0.68	2.1	3.2	0.66
Large White	36.4	36.8	1.00	40.6	32.7	1.24	40.5	31.7	1.28	42.6	29.1	1.47	35.7	26.9	1.33
British Landrace	32.0	20.3	1.57	25.1	15.9	1.58	22.8	16.4	1.39	20.2	12.7	1.59	24.1	12.5	1.93
Lacombe	3.4	2.6	1.30	4.0	5.1	0.79	2.6	3.6	0.73	4.9	6.2	0.79	4.4	8.1	0.54
Hampshire	5.7	7.2	0.79	6.0	11.6	0.52	6.5	11.6	0.56	7.7	13.0	0.59	5.2	11.4	0.46
Pietrain	4.5	4.5	1.00	14.0	12.5	1.12	16.0	15.8	1.01	9.7	13.9	0.70	14.6	17.6	0.83
Welsh							5.2	5.2	1.00	0.6	4.0	0.14	0	3.5	0
American Yorkshire										9.1	9.1	1.00	11.49	9.3	1.23
Norwegian Landrace															
Commercial Hybrid 1															
Commercial Hybrid 2															

Table 8.10 (cont).

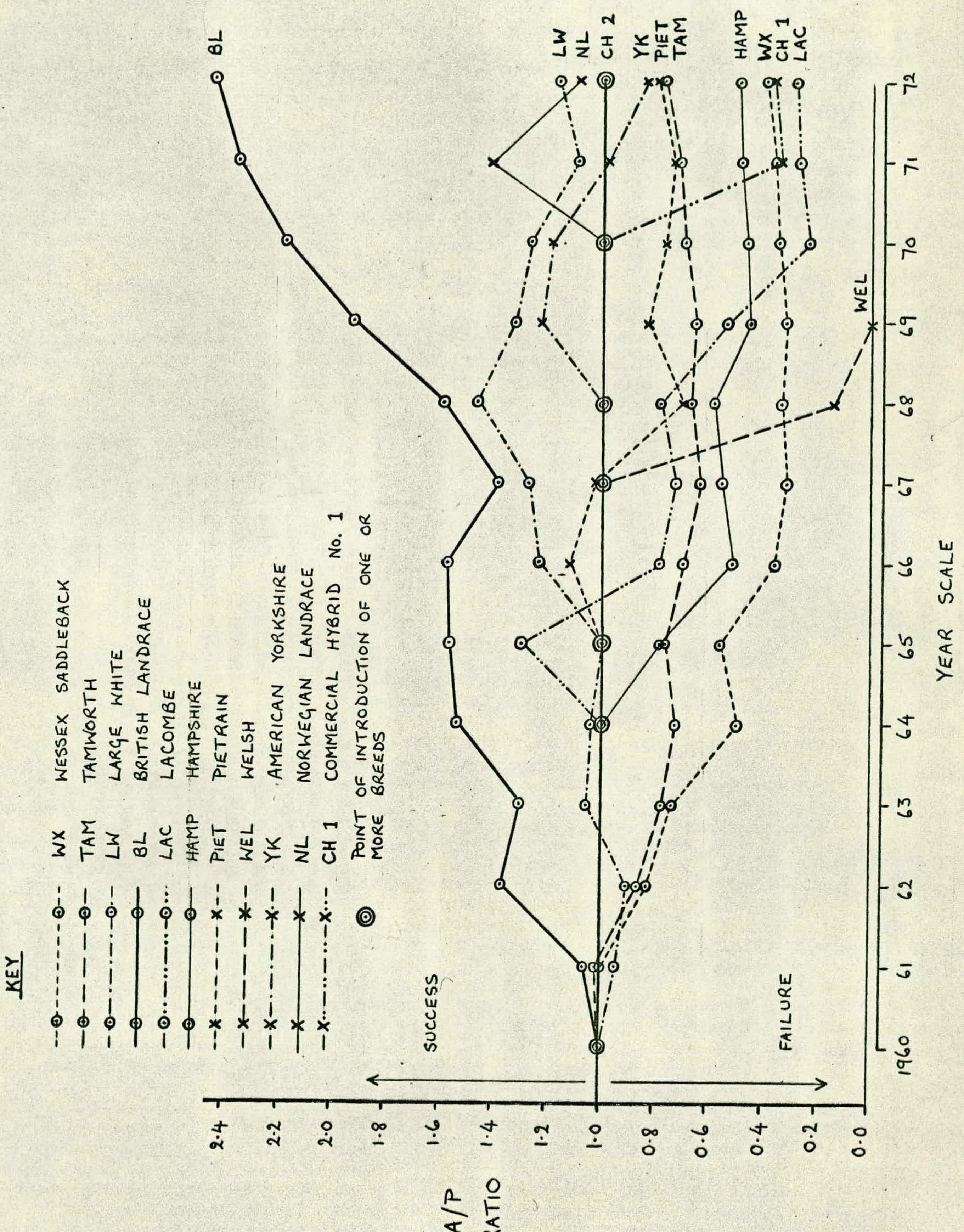
Breed	1970			1971			1972		
	A	P	A/P	A	P	A/P	A	P	A/P
Wessex Saddleback	2.2	6.3	0.35	2.1	5.7	0.36	2.0	5.0	0.40
Tamworth	1.9	2.7	0.70	1.7	2.4	0.72	1.7	2.1	0.78
Large White	34.6	27.2	1.27	29.8	27.0	1.10	37.2	31.9	1.17
British Landrace	22.9	10.4	2.19	22.4	9.5	2.36	20.4	8.3	2.45
Lacombe	1.7	6.8	0.24	1.7	6.2	0.28	1.6	5.4	0.29
Hampshire	4.5	9.6	0.47	4.3	8.7	0.49	3.8	7.6	0.50
Pietrain	11.4	14.7	0.77	9.8	13.4	0.73	9.4	11.8	0.80
Welsh	0	2.9	0	0	2.7	0	0	2.3	0
American Yorkshire	9.3	7.8	1.19	7.1	7.1	0.99	5.2	6.2	0.84
Norwegian Landrace	8.1	8.1	1.00	20.0	14.1	1.42	15.6	14.4	1.09
Commercial Hybrid 1	3.5	3.5	1.00	1.1	3.2	0.35	1.0	2.8	0.37
Commercial Hybrid 2							2.1	2.1	1.00

unweighted average breed composition of parents, both immigrant and native, leaving progeny in the line. P was calculated as the expected average composition of the progeny of the parents in the previous generation assuming they had been mated at random and left equal numbers of offspring from which parents were randomly chosen. For the P values the parents of a given generation were therefore assumed to have the same average composition as the grandparents, whereas for the A values their composition was assumed to have been determined only by selection. In practice, of course, there will be an effect of relative fertility which could raise or lower a breed's contribution purely by chance. For ease of interpretation over the whole 12 year period the A/P values have been graphed in Figure 8.7. On the graph A/P values of greater than unity represent observed contributions in excess of those expected under random mating, and infer that the immigrant has something to offer in terms of improved performance. The converse applies to A/P values of less than one, which approach zero as a breed nears total elimination from the line (A = 0).

Figure 8.7 indicates that the British Landrace consistently had the highest A/P ratio and appeared to be more successful than even the Large White, which continually made the greatest "actual" contribution after 1963. The explanation for the apparently inordinate success of the Landrace is that, compared to Large Whites, few Landrace immigrants were tried. Consequently the "possible" contribution of the Landrace was always smaller than that of the Large Whites (Table 8.10), and pigs with a high proportion of Landrace genes were selected in spite of low amounts of fresh immigration. Table 8.6, for

Figure 8.7

Success of Breeds Contributing to the A.B.R.O. Sire-Line: Graph to show the Ratio of "Actual" Observed Breed Composition of Parents Leaving Progeny to the "Possible" Composition Expected Under Random Mating (A/P) by Years.



example, shows that a total of 32 pure Large Whites were tried as immigrants compared to only 12 British Landrace. After 1967 when the last pure Landrace immigrant was tested, the graph of "success" (A/P) clearly breaks away. In view of its increased number of opportunities to contribute to the line, it could be argued that the Large White breed has enjoyed comparatively mediocre success.

The graph (Figure 8.7) shows that only one breed, the Welsh, has been eliminated from the sire-line, and this was the result of reproductive failure. The Wessex Saddleback was the least successful of the foundation breeds, since unlike the Tamworth it was re-tried as an immigrant in later generations. Three separate breeds, the Lacombe in 1964, the Pietrain in 1965 and the American Yorkshire in 1968, had A/P ratios greater than unity in the first generation after their introduction, but these fell off rapidly to become less than unity in the next two or three generations. It appears therefore that subsequent immigration attempts were for some reason proportionately less successful than the first.

It is concluded that the graphical representation in Figure 8.7 provides evidence that the past selection procedure for immigrants to the A.B.R.O. sire-line was at least to some extent successful in discriminating between "useful" and "non-useful" breeds. The ranking of A/P, "success", values for the various breeds is roughly as expected from their recognised characteristics. For example the three most successful breeds in 1972 were the British Landrace, Large White and Norwegian Landrace, while the least successful breeds were the Lacombe, a Commercial Hybrid and the Wessex Saddleback. However a disturbing feature of these findings is that no breed has failed to contribute to the line or been eliminated from it purely on the grounds of performance as one might expect. This could indicate either that all the breeds truly contained individuals of sufficient merit for incorporation or alternatively that a certain proportion of selection decisions regarding immigrants were incorrect.

Finally it should be emphasised that the A/P values given here refer not to the relative performance of immigrant breeds, but to their contribution to the line relative to the number of opportunities to contribute. If every breed had had an equal opportunity to contribute, the ranking on A/P would more nearly reflect the ranking on performance. Further complicating factors are that some breeds have been tried as crossbreds, that some breeds have been placed at a disadvantage because they have been tested in company with a second superior immigrant breed, that native population size and therefore immigrant acceptance levels have fluctuated, and that some immigrant genes may be "masked" from selection by exceptionally good native genes. However, the A/P ratio provides a better measure of the "historical" success of breeds than the current "actual" composition which is directly influenced by recent immigration.

8.4 Discussion and Conclusions.

Evidence has been presented that selection decisions on past immigrants to the A.B.R.O. sire-line could have been biased firstly as a result of treating immigrant and native populations as one, and secondly by the occurrence of heterosis. In the case of an immigrant population which is superior to the sire-line the two sources of bias tend to cancel one another out, whereas if the immigrant population is inferior they are added together. For example, if heterosis amounts to +50 index points and the breeding values of members of two immigrant populations, one superior and the other inferior, are each under- and overestimated by -100 and +100 points respectively, the net bias would be -50 points for the superior immigrants and +150 points for the inferior immigrants. With this in mind, it was demonstrated that the average performance of contending immigrants has seldom been better than that of contemporary natives, and frequently very much worse. There was however, some justification for the view that the selection method had been able to exercise at least some discrimination among breeds, so that in terms of success they ranked roughly as expected.

For a given selection objective, immigration would only be worthwhile in the sire-line if selection with immigration resulted in a faster rate of genetic improvement than would have been possible by selection alone in a closed line of the same size. At present the only clue to the success of the immigration policy has been the contemporary performance of the line at M.L.C. testing stations, described in Chapter 5.

The suggestion has already been made that an unselected control line should be maintained in order to monitor genetic progress. This would not, however, indicate whether supplementing selection with immigration was of any extra benefit to the rate of genetic improvement. An alternative would therefore be to maintain a selected, but "non-immigrated" control line against which the fruits of immigration could be judged directly.

Ignoring cost, the value of immigration as a means of genetic improvement in a sire-line must depend solely on the accuracy of selection. "Holding-back" of the rate of improvement by immigration would only be expected to occur in the event of incorrect selection decisions on the incorporation of immigrants. If the rate of progress in the line is so high that it advances beyond the reach of other populations, then immigrants would be expected to become less and less successful until finally the line became closed of its own accord and no outside stock was capable of making a further improvement. However, the findings of this chapter indicate that the selection bias is expected to be most serious in the situation where the immigrants lag behind the natives. The methods of alleviating the bias suggested earlier are of limited value since they depend on large numbers of immigrants on test, and on accurate and repeatable estimates of heterosis. Is there an alternative method of testing immigrants for admission to the line which would be free of one or both sources of bias?

Before considering alternative selection methods for immigrants it is necessary to review the circumstances under which immigration is carried out. In the A.B.R.O. sire-line immigration was adopted in three different cases, listed below:

(a) importations of small samples of foreign breeds,

(b) individuals of exceptionally high merit from populations believed inferior,

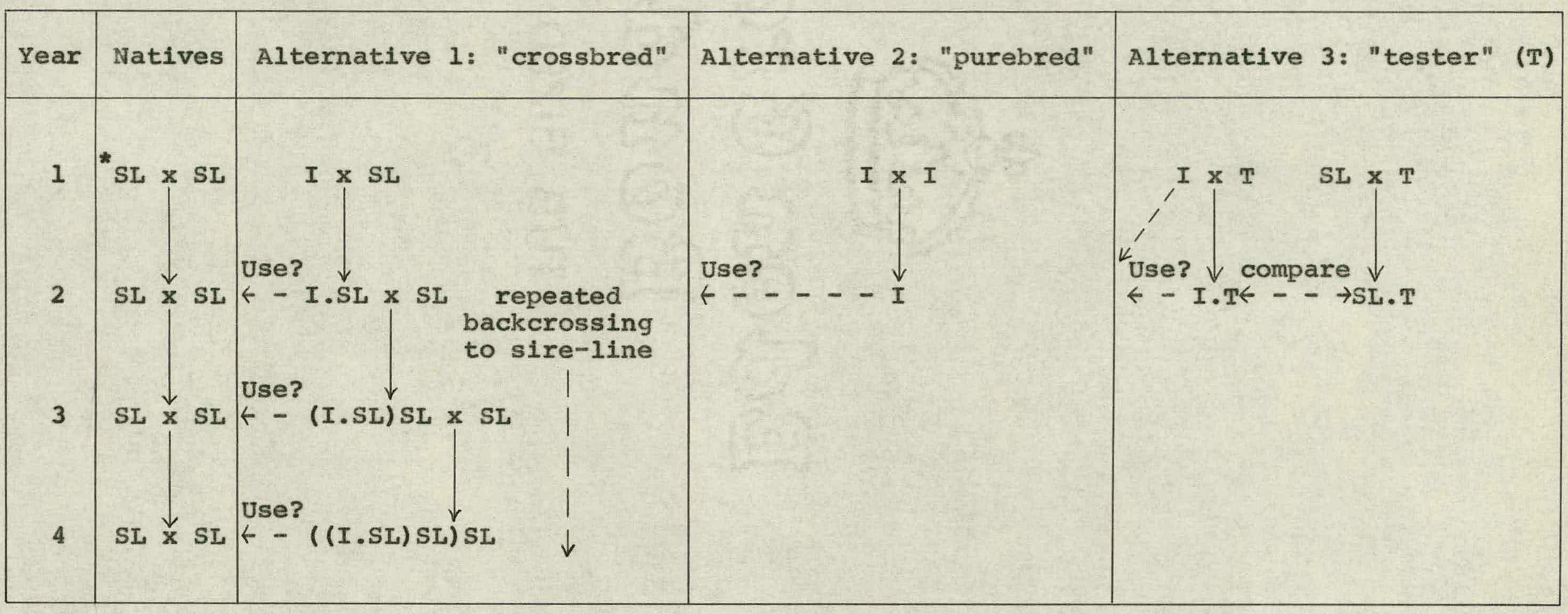
(c) easily available strains or sub-populations believed to be superior for one or more traits.

Examples of (a) would be the first importations of the Pietrain Hampshire, Lacombe and Yorkshire breeds, while examples of (b) would be high index-pointed Large Whites or Landrace standing at national A.I. centres. Clearly there might be difficulties in obtaining large numbers of immigrant progeny in these circumstances, and heterosis estimates in (a) would probably be ruled out. Examples of (c) would be larger samples of imported breeds such as the Norwegian Landrace, strains or herds of British breeds such as the Large White, or specialised commercial hybrids. In this case there might be an opportunity to test larger numbers of immigrants and possibly to measure heterosis.

The readily available alternative methods of testing immigrants have been set out diagrammatically in Figure 8.8. Alternative 1 represents the procedure hithertoo adopted in the sire-line, but with the added option of repeated back-crossing before finally allowing the immigrant to contribute to the line. Without backcrossing Alternative 1 has been used in the past for all eventualities (a) to (c) above, and is prone to both types of bias as already discussed at length. While heterosis would be halved and the complication of

Figure 8.8.

Schematic Representation of 3 Alternative Methods of Testing Immigrants (I) for Admission to the Sire-Line (SL).



*sire always precedes dam

unknown population means would be reduced in the backcross progeny, the immigrant genes would become further diluted and one or more generations of selection would be lost. In addition a strategy of backcrossing would increase the number of immigrant matings in any one generation. The backcross test might however have an application where the F_1 immigrant performance is unexpectedly good and confirmation is required before formal entry to the line. Where sufficient numbers of unrelated immigrant parents are available, as in case (c), there would be an opportunity to make an F_2 rather than a backcross after the F_1 and possibly to accompany this with selection. On the other hand, the bias due to differences between means would not be reduced in the F_2.

The heterosis bias could be avoided altogether by adopting Alternative 2 in Figure 8.8, which involves the mating of immigrant parents inter se for purebred comparison with the sire-line. This would not be possible where the available immigrants were all of the same sex or closely related to one another as might be the case for imported stock (a) or individuals of high merit (b). It would have the disadvantage of doubling the difference between immigrant and native test population means, and would therefore only be feasible where there were sufficient numbers to estimate the difference with some degree of accuracy. No time would be lost in the initial test, but after the decision had been made to use the immigrants in the line, selection of the F_1 crosses would be biased by heterosis as before.

Alternative 3 provides for the contemporary testing of natives and immigrants by crossing each to a third "tester"

(T) breed. This would take the form of a comparative progeny test of one or more individual immigrants, which would be relatively free of heterosis, but the bias resulting from differences in means would remain and require correction. In addition one generation would be lost before crossing the original immigrant to the sire-line, and the extra resource of a third breed could probably rarely be justified. Again, if the immigrant was successful, the problems of bias would recur in the F_1.

There is therefore no easy alternative to the present method of performance testing F_1 immigrants alongside natives which would bypass the biasing effects of heterosis and differences between means. It is unfortunate that the effects of bias are most difficult to handle in the situation where immigration might be of most value, that of utilising small imports of foreign breeds or individuals of unusual merit. In this case the effects of bias could be reduced by backcrossing in Alternative 1, or heterosis alone could be eliminated by resorting to Alternative 3. For larger samples of immigrants an adjustment could be made for the estimated difference between immigrant and native sub-populations on Alternative 1. On the other hand if heterosis estimates are not available, and these would normally be expensive to obtain, the "purebred" Alternative 2 would provide a heterosis-free comparison. Alternative 2 might therefore be put into operation for groups of immigrants in which there are unrelated members of both sexes, and which a priori are not expected to contribute to the line but are nevertheless being screened.

In the past immigrant matings have constituted a proportion greater than one third of the total, so that if an inferior immigrant population was tested and failed to contribute, the net result was an effective reduction of the selection differential among natives. This leads to the recommendation that the native population size should be kept constant at an acceptable minimum allowing useful selection, after which the immigrant "test population" should be as large as the available stock and facilities will permit. The selection or rejection of crossbred immigrant progeny could be greatly influenced by the degree of assortative mating of immigrants with the sire-line. Unless there is good prior evidence that the immigrants are superior, it might therefore be better to mate immigrant boars to average sire-line gilts only, making the test slightly more conservative. The natives could then be mated assortatively and the immigrants assigned to as many remaining females as necessary. Putting the immigrants at a slight disadvantage in this way will have little effect, since if an immigrant is substantially better it will be incorporated anyway, whereas if it is only marginally better and is not admitted little will be lost.

In a single trait selection programme, the native population should theoretically be replaced by any immigrant population which turns out to be superior. For example, in the early years of the A.B.R.O. sire-line when selection was for backfat and body length (Chapter 3), the Tamworth-Wessex-Large White-Landrace synthetic line might well have been replaced by pure Landrace, but for the intention of increasing the genetic variability. Where the number of superior immigrants was limited, for example by a small importation, total replacement would be ruled out, and immigrant genes should then be spread as rapidly as possible avoiding inbreeding. The situation is less clear when selection is for more than one trait. In principle an immigrant population of superior aggregate genotype ($\bar{M}$) should replace the sire-line. In practice, however, there are many combinations of traits which could lead to the same value for $\bar{M}$, since deficiencies in one trait can be counterbalanced by superiority in others. Under these circumstances the aggregate genotype itself could be misleading due to non-linear economic changes, such as exist for example as a result of a threshold grading system. The crossing of populations having equal values of $\bar{M}$ made up of different attributes could also lead to an improvement in the overall aggregate genotype. For example, ignoring genetic correlations the values of $\bar{M}$ for the following two populations are equivalent at -2166 points, using the economic weightings given in Table 6.5.

Population	Daily Gain (lbs/day)	Food Conversion Ratio(lbs feed/ lb L.W.G.)	Av.Backfat (cms.)	$\bar{M}$
A	2.00	2.90	2.10	-2166
B	2.00	3.00	2.01	-2166
A x B	2.00	2.95	2.05	-2160

As a result of crossing the two populations, however, the mean aggregate genotype is 6 points better, and immigration of one population into the other would appear worthwhile. Calculations such as this could be performed for each F_1 immigrant x sire-line sub-population to gain some idea of the effect of introduction on the aggregate genotype. Current evidence and thinking (Chapter 3) would indicate that immigration for the sake of obtaining an increase in additive genetic variance or recombination among genes affecting different traits would be unjustified.

The aim of the A.B.R.O. sire-line project has been to produce a line of pigs with an outstanding capacity for the production of lean meat. A possible pitfall of an enterprise of this type is that attempts might be made to introduce by immigration stock with attributes which could not be fully "recognised" by the aggregate genotype. The aggregate genotype in the sire-line has been defined very narrowly, for practical reasons, as the economically weighted sum of daily gain, food conversion and backfat. Taking the Pietrain and Hampshire as examples, poor food conversion and growth rate coupled with moderate reductions in backfat (e.g. King, 1966) probably resulted in fairly low ratings on the present selection index. Inclusion of carcass traits such as eye muscle area, % lean in the rump-back or killing-out percentage would have enabled these traits to be taken into account through their genetic correlations with those measured phenotypically. The result would have been to change the index weighting (b_i) on the measured traits, and possibly to have made more use of the considerable advantages of the Pietrain and Hampshire in lean meat production. Gjedrem (1972) indicated that the aggregate genotype should include <u>all</u> economically important traits even when they are not recorded. The effect of this on the sire-line would be to place less emphasis on economy of production and more emphasis on carcass quality. In addition less reliance would be placed on average backfat as a predictor of lean content between breeds.

Chapter 9. Concluding Discussion.

In the foregoing chapters an analysis has been made of the first 12 generations of the development of the A.B.R.O. open synthetic sire-line. An initial period of strong phenotypic response to selection for average ultrasonic backfat after X-ray predicted body length was followed by a period of very little response to selection for growth rate, food conversion and backfat. It was unfortunate that the apparent tailing off of selection response coincided both with the introduction of formal performance testing and with the successful immigration of some freshly imported breeds, and the results might have been easier to interpret if single trait selection for backfat had been continued throughout. However an examination of the performance testing procedure and selection index (Chapter 7) showed that genetic progress could have been expected in a closed population of the same size, so that suspicion fell heavily on immigration as the reason for the lack of improvement after 1966. In Chapter 8 it was demonstrated that erroneous decisions on the selection of immigrants were more likely when the prospective immigrant population was poorer on average than the native population. Between 1965 and 1970 it was shown that the average performance of all immigrants lagged behind that of natives, and this was taken as an indication that a number of past selection decisions on immigrants may well have been in error. Lack of additive genetic variation was ruled out as a possible reason for the lack of selection response in backfat (Chapter 6).

The "success" of the A.B.R.O. sire-line was difficult to assess directly. In the absence of estimates of genetic progress or of data on the performance of the line in its intended role as a commercial sire-line, the contemporary performance of the line in comparison with Large Whites from nucleus herds at national testing stations was the best indicator of success. This showed the sire-line to be one half standard deviation better than Large Whites on the M.L.C. index of predicted breeding values assuming equivalence of means, with an estimated extra return of 65_p per pig and all the superiority.being attributable to improved carcass quality. In terms of the aggregate genotype on which the sire-line itself was selected, comprising daily gain, food conversion and average backfat, the sire-line boars and slaughtered sibs were respectively 0.24 and 0.78 standard deviations better than contemporary Large Whites. This level of performance was not outstanding considering the duration of the project and the resources devoted to it, and a similar level of economic merit might very well be achieved by sampling the best Large White herds at the present time, although the superiority would probably stem from a different set of characters less well suited to a " meaty" sire line.

The A.B.R.O. sire-line approach has combined two relatively new methods of pig improvement: the philosophy of having separate sire and dam lines, rationalised by Smith (1964), which defines the selection objective within a given population, and immigration which is a possible means of attaining that objective most rapidly. As well as providing a potential method of obtaining additive improvements in lean meat production, immigration has caused the sire-line to become sufficiently genetically distinct to exhibit heterosis in crosses with Large Whites. For this reason the sire-line ought to be especially well suited to act as the third breed C in the C x (A x B) commercial situation, improving the carcass quality of the slaughter progeny and enhancing their preweaning growth and viability. The "success" of the line should therefore strictly be judged under commercial conditions, and plans are under way for a large scale field trial comparing a sire-line boar with a producer's own boar on 22 farms in south-east Scotland.

Application to the Pig Industry.

Separate sire and dam lines are, in a sense, already widely in use in the pig industry, since different breeds or breed combinations often make up the sires and dams of pigs for slaughter. For example, the dam "line" is frequently a cross of two or more pure breeds, which in turn is finally crossed to a sire "line" consisting simply of one of the dam breeds or involving a third breed altogether, possibly as a crossbred. The question naturally arises of whether the open synthetic approach applied to the A.B.R.O. sire-line is strictly necessary for the development of a lean meat-type sire line, and of whether a similar approach would be justified if a specialised sire line was to be developed at the present time. The A.B.R.O. line was developed under a rather special set of "historical" circumstances.

Firstly, the sire-line was started from a crossbred foundation with the intention of showing whether a useful increase in the additive genetic variability available for selection would result. It is at least theoretically possible that the additive genetic variance would be increased in a synthetic (Chapter 2), but either there was no change in the variance, or, more likely, the change could not be detected (Chapter 6). Secondly, the sire-line project was in progress at a time when a variety of overseas breeds offering improvements in production characters were being imported into Britain for the first time. These imports often consisted of small samples of a breed which, if kept as a "pure" population, would have become rapidly inbred, and there was the very real problem of how best the genes from the new breeds could be used. In first crosses with Large Whites breeds such as the Pietrain and Hampshire were superior in lean meat production (e.g. King, 1966), and it was concluded that one way to make permanent use of these genes would be to incorporate them into a lean meat-type sire line. All imported breeds arriving at A.B.R.O. were therefore tried as immigrants to the sire-line. The situation where a number of small samples of new breeds are imported in rapid succession is, however, unlikely to be repeated in the future.

It has been shown that the selection of immigrants into an open synthetic line may be subject to biases which are very difficult to remove in the case of small sub-groups such as first imports or high-pointed individuals at national testing stations. It is therefore questionable whether immigration into an open line is the best way of utilising any superiority which they may offer. Clearly, high-ranking individuals from British breeds should be used extensively in their own nucleus populations as part of the normal cycle of selection. If an imported population is too small to be maintained "pure", there is little option to some form of immigration or cross-breeding such as the formation of a "half-bred" with a complementary British breed. If immigration is adopted, a sufficient number of immigrants should be tested to allow correction of the bias as suggested in Chapter 8. If it could be established that the immigrants were definitely superior, then of course their introduction could hardly fail to be beneficial. Experience with the A.B.R.O. sire-line, however, has indicated that immigrants are likely to be worse or only slightly better than the native population, with the result that all selection decisions are likely to be critical. If a situation arose in which immigrants were consistently better than natives, either the method of selection within the line or the choice of foundation stock would become suspect. The suggestion that all rare or exceptional genes be incorporated into a "gene pool" (e.g. Watson, 1968) is subject to the same reservations that apply to the A.B.R.O. sire-line, since the gene pool would have to be subjected to intense selection in order to remain competitive.

It is concluded that the open synthetic approach would be unlikely to offer a worthwhile increase in the rate of genetic progress in a sire line for lean meat production, provided the choice of foundation stock was correct. Choice of the foundation breeds for such a selection programme would probably be the most important determinant of profitability, since a high level of initial performance and selection response would ensure a rapid return on capital outlay, incurring less interest and allowing early reinvestment of returns (Hill, 1970; 1971a). There is no reason why a crossbred foundation should not be used, but breeds should be chosen strictly on the basis of their average additive performance in terms of the aggregate genotype. Breeds should not be included at the expense of the average performance simply to give a synthetic base (see for example Chapter 2). In a commercial situation immigration as practised in the A.B.R.O. line would be expensive, but the incorporation of one or two individuals of exceptional merit over three to five years or the frequent introduction of individuals of marginal superiority would not greatly increase the average performance of the whole population. Nevertheless in the event of a suitable condidate, the option of immigration is open to all selected populations whether they be deemed "open", "pure" or "synthetic".

Possible foundation breeds for a sire line aimed at lean meat production might be the Large White, Hampshire, Pietrain or the various strains of European Landrace. These might be complemented by dam lines containing Large White, Landrace, Welsh or British Saddleback genes, the "commercial" dam herself being an F_1 cross in order to give maximum heterosis. Choice of the correct combination of breeds could in principle be facilitated by manipulation of the parental types on a "profit diagram" as proposed by Moav (1966b, and see Chapter 2), but data on the contemporary performance of many of the breeds are scarce and economic values would differ among systems of production. There is a need for a "whole system of production" approach to the choice of breeds and crossing systems, taking into account the reproduction and maintenance costs of all purebred stock contributing to the final cross and the revenue of the overall production process as if it was a single integrated operation.

Future of the A.B.R.O. Sire-Line.

It has been emphasized that the correct way to judge the A.B.R.O. sire-line would be in terms of producers' bacon gradings and feed costs in its commercial context as the sire of slaughter pigs. The results of the proposed field trial comparing sire-line boars with producers' own boars under farm conditions will therefore undoubtedly play an important part in determining the future of the line. The second experiment to measure heterosis in crosses of the sire-line with Norwegian Landrace will play a less important part but will help to establish the degree of heterosis bias on immigration decisions and will indicate the extent to which the sire-line can be regarded as genetically distinct from other breeds. In view of the evidence indicating rather little genetic progress in the second half of the life of the sire-line, it will be worthwhile to consider briefly the various alternative courses which future development of the line could take.

The question arises of whether the practice of immigration in the A.B.R.O. sire-line should cease, and the line be operated in future on a closed basis. It was argued earlier that immigration would have little application in a competitive commercial meat sire line. However, in the

A.B.R.O. experimental line, continued immigration would allow the methods of correcting bias put forward in this thesis to be tried out in practice. In addition the immigration of genes for carcass quality might be desirable if the aggregate genotype for selection was altered in the direction of lean meat content as suggested in the previous chapter. Following earlier recommendations, a reduction in the number of candidate immigrant populations, usually breeds, on test in any one generation and a reduction in the proportion of immigrant matings would allow more accurate selection of immigrants and more intense selection on natives.

Under what circumstances would there be a case for discontinuing the sire-line altogether? This course of action would probably only be justified if the line performed very badly in on-farm trials, and if no research-use could be found for the multi-breed hybrid population. For example, no steps have yet been taken to find out whether hormone levels or other parameters such as fat composition or the incidence of leg weakness have been changed by the pooling together of breeds. If, on the other hand, the field trials show the line to offer a significant improvement in the performance of the "final" cross, there would be an opportunity to expand and market the sire-line on a commercial basis.

In the preceding chapters two types of control lines were proposed for the A.B.R.O. sire-line. The first would be a sub-line from the existing population in which selection had been relaxed, and would provide a measure of the genetic progress resulting from selection and immigration together.

The second type of control would be a sub-line undergoing selection at the maximum intensity, which would show whether selection with immigration could produce a greater rate of genetic progress than selection alone in a closed line of the same size. The outcome of this second type of control, however, would depend on the relative superiority of the potential immigrant population, so that any conclusions drawn would apply to rather specific circumstances. The simpler unselected control line might prove to be of more general value in indicating the overall rate of progress in the line. It could be maintained with as few as 16 boars and 32 randomly mated gilts, turning over generations annually and ensuring that each sire contributes one son and each dam contributes one daughter so that the variance of family size is close to zero and the effects of random drift are minimised (Hill, 1972a). Hill pointed out that a control population formed by relaxation of a selected population may undergo some initial regression in the presence of epistatic loci which are not in linkage equilibrium, and may also be especially prone to the effects of natural selection. On the other hand, the difference between control and selected populations should probably include any regression in performance of the control, since it represents part of the measurable return to the selection programme.

An alternative and less expensive method of monitoring genetic progress would be the regular submission of samples of the sire-line to the M.L.C. for central testing in comparison with Large Whites. However, fluctuations in the station contemporary mean might cause the estimated difference between sire-line and Large White to be an unreliable indicator of the rate of response. A further alternative would be to test sire-line pigs alongside those from existing British control herds at Newcastle, Bangor or Wye, again using central testing stations. This might prove unacceptable because of the distances involved and the need for reorganisation so that sire-line progeny would be produced at the same time as control herd progeny. In addition, either alternative would necessitate a repeat mating of sire-line parents in each generation to produce sufficient progeny for testing, and this would require almost as much farrowing accommodation as a control line. A control herd started from the sire-line in its own environment would have the advantage of giving a disease-free comparison, and of demonstrating the magnitude of environmental fluctuations under the conditions in which selection takes place.

In the past the size of the sire-line breeding population has tended to be rather low as a consequence of the lack of inbreeding following continued immigration. However, the phenotypic correlation between native mates for backfat thickness was only 0.09 ± 0.07 (Chapter 6) indicating that the intention to carry out positive assortative mating was not fully realised in practice. This is attributed to small population size and the need to avoid full- and half-sib matings. In addition, the highest ranking boars in any generation have tended to be the sons of two or three sires only, and their genetic superiority could not be fully utilised in order to ensure genetic diversity in future generations. Both these factors may have resulted in a "hidden" reduction in selection differential, which an increase in population size might help to remove. Fredeen and Martin (1967) found that increasing the size of a breeding unit beyond 4 boars and 20 sows resulted in little improvement in selection intensity ($\bar{i}$) compared with increasing the number of sows per boar. A widening of the boar: sow ratio in the A.B.R.O. sire-line would be inadvisable since inbreeding would certainly result, which immigration could not be relied on to relieve. It should be remembered that, in a "synthetic", replacement stock could not be brought in from outside in the event of a build up of inbreeding as would be possible for a "pure" breed. In an open "synthetic" the need to avoid inbreeding may have the advantage of causing a rapid spread of immigrant genes through the line.

The possibility of changing the object of selection or the aggregate genotype has already been discussed (Chapter 8). The way in which the selection objective is achieved could also be changed by an alteration in the number or identities of the traits which are measured phenotypically. For example, the option exists of returning to a simplified improvement scheme in which growth rate and food conversion ratio are not recorded. Reasons for this could be inaccuracies in the recording of feed consumption, rendering it worthless, or a desire to concentrate on carcass characteristics and rely on positive genetic correlations (e.g. Smith and Ross, 1965) to ensure at least that no genetic decline occurs in food conversion. When sufficient data have accumulated from the sire-line, the heritability of food conversion will provide a convenient guide to its usefulness in the selection programme. If more emphasis was to be placed on carcass traits such as killing out percentage , sib testing for carcass assessment could be introduced, but would reduce the number of pigs available for selection.

As well as altering the traits which are actually measured, the method of feeding on which pigs are selected could easily be changed. Alternatives to the present ad libitum method would be twice daily feeding to appetite, often referred to as "semi-ad libitum", or feeding to a time or live-weight scale (e.g. M.L.C. Scientific Study Group, 1970). Ad libitum feeding was chosen originally in order to give adequate variability in ultrasonic backfat measurements. However, "semi-ad libitum" feeding has proved satisfactory for performance testing at M.L.C. central testing stations. At present it is an open question as to which of the two diets would provide the greatest rate of genetic progress, and the effect of the appetite component on ad libitum feeding is poorly understood. Intuitively, it would seem that any measure of efficiency should be at a fixed level of input, which in this case is food. For experimental purposes, a change of diet may be disadvantageous in rendering subsequent analyses of data based on the whole life of the line more difficult to interpret.

Concluding Remarks.

In conclusion, the A.B.R.O. sire-line venture has provided valuable experience of the practical problems of immigration in an open synthetic line of pigs. It has shown that while the multi-breed synthetic approach itself has no disadvantages in terms of reproductive performance, there are equally no recognisable advantages in terms of increased genetic variation. In pig production a policy of continual immigration as a means of genetic improvement would not generally be recommended, unless the superiority of the immigrant population was well established and there was a good reason why it should not totally replace the native population. In the future it is recommended that immigration be reduced in the A.B.R.O. sire-line, and it is suggested that genetic progress could be monitored through an unselected control line.

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APPENDIX A

MEANS, VARIABILITY and SEX DIFFERENCES FOR ROUTINELY RECORDED CHARACTERS BY YEARS (GENERATIONS)

Table A1.

Average Ultrasonic Backfat Thickness Corrected to 180 lbs. Live Weight (cms.)

YEAR	BOARS				GILTS				BOARS-GILTS	
	No.	Mean	S.E.[$]	S.D.[†]	No.	Mean	S.E.	S.D.	Difference	S.E.[††]
1960	33	2.61	0.07	0.40	62	2.92	0.05	0.36	-0.31^{***}	0.08
1961	39	2.27	0.04	0.26	73	2.61	0.04	0.31	-0.34^{***}	0.06
1962	33	1.95	0.04	0.24	87	2.27	0.03	0.23	-0.32^{***}	0.05
1963	38	1.85	0.05	0.32	63	2.05	0.03	0.27	-0.20^{**}	0.06
1964	41	1.72	0.06	0.35	75	1.97	0.04	0.31	-0.25^{***}	0.06
1965	35	1.52	0.04	0.26	65	1.84	0.04	0.29	-0.32^{***}	0.06
1966	31	1.78	0.04	0.24	47	1.85	0.05	0.31	-0.07	0.07
1967	58	1.59	0.03	0.23	88	1.90	0.03	0.26	-0.31^{***}	0.04
1968	77	1.74	0.03	0.24	173	1.93	0.02	0.26	-0.19^{***}	0.04
1969	76	1.76	0.03	0.24	109	1.96	0.03	0.28	-0.20^{***}	0.04
1970	73	1.67	0.03	0.28	134	1.89	0.03	0.32	-0.22^{***}	0.04
1971	120	1.99	0.03	0.30	141	2.24	0.02	0.29	-0.25^{***}	0.04

$^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$

[$] standard error of mean

[†] standard deviation

[††] standard error of difference

Table A2.

Daily Gain on Test. (lbs/day).

	BOARS				GILTS				BOARS-GILTS	
YEAR	No.	Mean	S.E.	S.D.	No.	Mean	S.E.	S.D.	Difference	S.E.
1966	31	1.61	0.02	0.12	-	-	-	-	-	-
1967	58	1.69	0.03	0.24	88	1.46	0.02	0.22	0.23***	0.04
1968	75	1.66	0.02	0.20	172	1.59	0.02	0.20	0.07**	0.03
1969	76	1.68	0.02	0.18	109	1.44	0.02	0.17	0.24***	0.03
1970	73	1.68	0.02	0.19	134	1.68	0.02	0.23	0.00	0.03
1971	120	1.86	0.03	0.29	141	1.89	0.03	0.32	-0.03	0.04

Table A3.

Food Conversion Ratio (lbs Food/lb Liveweight Gain).

	BOARS				GILTS				BOARS-GILTS	
Year	No.	Mean	S.E.	S.D.	No.	Mean	S.E.	S.D.	Difference	S.E.
1966	31	3.36	0.05	0.23	-	-	-	-	-	-
1967	58	3.46	0.05	0.34	88	3.53	0.06	0.56	-0.07	0.08
1968	75	3.15	0.04	0.37	172	3.40	0.03	0.38	-0.25***	0.05
1969	76	3.24	0.04	0.34	109	3.78	0.04	0.39	-0.54***	0.06
1970	73	3.50	0.04	0.33	134	3.51	0.03	0.34	-0.01	0.05
1971	120	3.05	0.03	0.34	141	3.11	0.02	0.24	-0.06	0.04

*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

Table A4.

Live Weights at Start and Finish of Performance Test (lbs).

START

YEAR	BOARS				GILTS			
	No.	Mean	S.E.	S.D.	No.	Mean	S.E.	S.D.
1966	31	70	1	7	-	-	-	-
1967	58	69	1	8	88	64	1	8
1968	75	70	1	11	172	65	1	8
1969	76	63	1	5	109	64	1	8
1970	73	66	1	5	134	69	1	10
1971	120	72	1	15	141	67	1	12

FINISH

YEAR	BOARS				GILTS			
	No.	Mean	S.E.	S.D.	No.	Mean	S.E.	S.D.
1966	31	201	2	11	-	-	-	-
1967	58	201	2	13	88	187	1	7
1968	75	207	2	19	172	196	1	11
1969	76	205	2	16	109	190	1	12
1970	73	195	2	15	134	195	1	13
1971	120	198	1	16	141	194	1	15

Table A5.

Teat No. at 50 Days.

YEAR	BOARS				GILTS				BOARS-GILTS	
	No.	Mean	S.E.	S.D.	No.	Mean	S.E.	S.D.	Difference	S.E.
1960	133	14.3	0.1	1.1	133	14.1	0.1	0.9	0.2	0.12
1961	142	14.1	0.1	1.0	130	14.1	0.1	1.0	0.0	0.12
1962	133	14.2	0.1	1.0	118	14.3	0.1	1.1	-0.1	0.13
1963	76	14.0	0.1	1.0	86	14.0	0.1	1.1	0.0	0.17
1964	139	13.7	0.1	1.2	146	13.7	0.1	1.1	0.0	0.14
1965	94	13.3	0.1	1.4	98	13.6	0.1	1.4	-0.3	0.20
1966	119	12.8	0.1	1.1	112	12.8	0.1	1.1	0.0	0.14
1967	109	13.4	0.1	1.0	113	13.5	0.1	1.2	-0.1	0.15
1968	211	13.0	0.1	1.3	222	13.3	0.1	1.3	-0.3*	0.12
1969	176	13.1	0.1	1.3	184	13.5	0.1	1.2	-0.4**	0.13
1970	234	12.6	0.1	1.3	203	12.8	0.1	1.3	-0.2	0.13
1971	255	13.2	0.1	1.4	224	13.3	0.1	1.2	-0.1	0.12

*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

Table A6.

Birth Weight (lbs).

YEAR	BOARS				GILTS				BOARS-GILTS	
	No.	Mean	S.E.	S.D.	No.	Mean	S.E.	S.D.	Difference	S.E.
1960	133	3.16	0.06	0.71	133	3.02	0.06	0.64	0.14	0.08
1961	142	3.42	0.05	0.57	130	3.36	0.05	0.58	0.06	0.07
1962	133	3.15	0.04	0.50	118	3.06	0.05	0.51	0.09	0.06
1963	76	3.26	0.07	0.63	86	3.07	0.06	0.55	0.19*	0.09
1964	141	3.08	0.05	0.60	146	3.11	0.05	0.65	-0.03	0.07
1965	95	3.17	0.06	0.62	98	3.12	0.05	0.51	0.05	0.08
1966	119	3.15	0.04	0.48	112	2.97	0.05	0.51	0.18**	0.07
1967	109	3.40	0.05	0.54	114	3.31	0.05	0.56	0.09	0.07
1968	211	3.21	0.05	0.69	222	3.15	0.04	0.63	0.06	0.06
1969	177	2.98	0.05	0.61	184	2.85	0.04	0.58	0.13*	0.06
1970	234	3.07	0.05	0.72	203	3.09	0.05	0.67	-0.02	0.07
1971	255	3.29	0.05	0.74	227	3.21	0.05	0.70	0.08	0.07

$^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$.

Table A7.

Weaning Weight (lbs).

	BOARS				GILTS				BOARS-GILTS	
YEAR	No.	Mean	S.E.	S.D.	No.	Mean	S.E.	S.D.	Difference	S.E.
1960	106	28.79	0.82	8.46	104	27.13	0.67	6.79	1.67	1.07
1961	115	29.60	0.59	6.33	114	29.39	0.62	6.60	0.21	0.85
1962	120	30.38	0.60	6.58	111	29.08	0.56	5.88	1.30	0.82
1963	68	30.19	0.61	4.99	81	28.18	0.60	5.38	2.01*	0.86
1964	112	31.14	0.58	6.11	121	30.38	0.64	7.00	0.76	0.86
1965	83	27.51	0.71	6.50	86	27.24	0.57	5.26	0.27	0.91
1966	97	29.16	0.56	5.48	88	28.45	0.59	5.56	0.71	0.81
1967	93	31.11	0.75	7.24	98	31.04	0.69	6.80	0.07	1.02
1968	170	31.46	0.46	5.98	196	30.94	0.47	6.57	0.52	0.66
1969	152	30.29	0.53	6.56	153	29.93	0.49	6.01	0.36	0.72
1970	170	29.44	0.56	7.28	171	29.30	0.56	7.30	0.14	0.79
1971	189	30.41	0.43	5.96	165	29.87	0.49	6.33	0.54	0.65

$^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$.

Table A8.

150-Day Weight of Pigs Reared for Breeding.(lbs).

YEAR	BOARS				GILTS				BOARS-GILTS	
	No.	Mean	S.E.	S.D.	No.	Mean	S.E.	S.D.	Difference	S.E.
1960	33	153.1	3.7	21.3	62	150.7	2.4	18.7	2.4	4.2
1961	39	154.2	2.8	17.6	73	142.5	2.0	16.7	11.7^{***}	3.4
1962	33	162.4	3.6	20.7	87	154.3	1.7	15.6	8.1^{*}	3.5
1963	38	134.1	2.4	14.7	63	132.7	2.4	19.0	1.4	3.6
1964	41	150.0	3.4	21.7	75	142.2	1.8	15.7	7.8^{*}	3.5
1965	35	147.7	2.7	16.1	65	138.6	1.9	15.3	9.1^{**}	3.3
1966	31	162.5	3.4	18.7	46	141.6	2.8	19.0	20.9^{***}	4.4
1967	58	171.8	2.9	21.9	88	165.2	2.1	19.8	6.6	3.5
1968	77	172.0	2.1	18.4	168	169.7	1.4	18.1	2.3	2.5
1969	74	174.4	2.6	22.3	107	161.8	1.9	19.8	12.6^{***}	3.2
1970	67	173.4	2.8	23.1	130	167.6	1.8	20.4	5.8	3.2
1971	117	174.7	2.4	26.5	136	173.7	2.4	28.4	1.0	3.5

$^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$.

Table A9.

Growth Rate from 50 to 150 Days - Pigs Reared for Breeding (lbs/day).

	BOARS				GILTS				BOARS-GILTS	
YEAR	No.	Mean	S.E.	S.D.	No.	Mean	S.E.	S.D.	Difference	S.E.
1960	33	1.25	0.03	0.17	62	1.23	0.02	0.16	0.02	0.04
1961	39	1.24	0.02	0.15	73	1.11	0.02	0.13	0.13***	0.03
1962	33	1.31	0.03	0.16	87	1.24	0.01	0.13	0.07**	0.03
1963	38	1.04	0.02	0.12	63	1.04	0.02	0.17	0.00	0.03
1964	41	1.18	0.03	0.20	75	1.12	0.02	0.14	0.06*	0.03
1965	35	1.17	0.03	0.15	65	1.10	0.02	0.14	0.07*	0.03
1966	31	1.31	0.03	0.16	46	1.13	0.03	0.17	0.18***	0.04
1967	58	1.40	0.03	0.19	88	1.33	0.02	0.16	0.07*	0.03
1968	77	1.39	0.02	0.16	168	1.38	0.01	0.16	0.01	0.02
1969	74	1.43	0.02	0.19	107	1.32	0.02	0.17	0.11***	0.03
1970	67	1.42	0.03	0.21	130	1.37	0.01	0.17	0.05	0.03
1971	116	1.45	0.02	0.23	136	1.44	0.02	0.25	0.01	0.03

*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

Table A10.

Farrowing Performance of Sire-Line Gilts.

	No. Born Alive[1]				Av. Piglet Wt. at Birth (lbs)				Total Live Wt. of Litter (lbs)[1]			
YEAR	No.	Mean	S.E.	S.D.	No.	Mean	S.E.	S.D.	No.	Mean	S.E.	S.D.
1960	21	8.1	0.8	3.5	20	3.46	0.09	0.40	21	27.2	2.5	11.2
1961	23	10.2	0.6	2.7	23	3.09	0.06	0.28	23	31.5	1.7	7.9
1962	17	9.5	0.6	2.4	17	3.24	0.10	0.41	17	30.4	1.8	7.4
1963	24	8.2	0.5	2.5	24	3.11	0.09	0.45	24	24.9	1.5	7.4
1964	18	8.6	0.5	2.3	18	3.22	0.09	0.39	18	27.7	1.8	7.6
1965	19	8.3	0.7	3.0	19	3.14	0.07	0.30	19	25.7	2.1	9.0
1966	28	7.4	0.7	3.6	28	3.47	0.09	0.45	28	24.9	2.2	11.5
1967	40	9.4	0.4	2.3	40	3.30	0.08	0.50	40	30.3	1.2	7.8
1968	41	9.3	0.4	2.9	41	2.87	0.09	0.56	41	27.2	1.4	9.2
1969	38	9.4	0.4	2.4	38	3.11	0.08	0.52	38	28.9	1.2	7.5
1970	49	10.6	0.4	2.8	49	3.35	0.08	0.54	49	34.5	1.1	7.9
1971	23	6.9	0.7	3.2	23	3.58	0.13	0.62	23	24.4	2.3	11.3

Table A11.

Litter Performance of Sire-Line Gilts at 50 Days.

	No. Alive at 50 Days (1),(2)				Av. Piglet Wt.[2] at 50 Days (lbs)				Total Live Wt. of Litter (lbs) (1),(2			
YEAR	No.	Mean	S.E.	S.D.	No.	Mean	S.E.	S.D.	No.	Mean	S.E.	S.D.
1960	21	7.3	0.7	3.3	19	28.4	1.1	4.8	21	202.6	19.4	88.9
1961	23	9.5	0.5	2.3	23	29.3	0.8	3.9	23	272.8	12.5	59.8
1962	17	8.9	0.6	2.5	17	30.0	1.0	4.1	17	259.4	14.5	59.9
1963	24	7.0	0.6	3.0	22	31.1	1.1	5.2	24	213.3	17.6	86.0
1964	18	8.1	0.5	2.1	18	27.5	1.1	4.6	18	218.0	14.3	60.7
1965	19	7.1	0.8	3.5	18	29.2	0.9	3.9	19	201.0	20.8	90.7
1966	28	6.7	0.6	3.0	28	32.7	1.1	5.7	28	207.3	14.3	75.7
1967	40	8.3	0.4	2.3	40	31.9	0.8	4.8	40	257.4	10.8	68.1
1968	41	8.1	0.5	2.9	38	30.3	0.7	4.5	41	241.3	13.1	84.0
1969	38	7.8	0.5	2.9	36	29.1	1.0	6.2	38	225.1	14.1	87.1
1970	49	8.2	0.4	2.5	48	30.6	0.7	4.8	49	246.0	10.0	69.7
1971	23	6.1	0.8	3.8	19	31.1	1.7	7.3	23	178.6	21.2	101.7

(1) Includes all records on gilts reaching farrowing house.
(2) Includes fostered pigs.

Table A12.

The Incidence of Congenital Abnormalities Affecting Viability in the A.B.R.O. Sire-Line.

(a) MALES

CONDITION	1960	1961	1962	1963	1964	1965	1966	1967	1968	1969	1970	1971	TOTAL	% INCIDENCE
Umbilical hernia	0	0	0	0	0	0	0	0	0	0	0	10	10	0.53
Scrotal hernia	3	3	0	3	1	2	4	1	0	4	4	0	25	1.33
Atresia ani	0	0	1	0	2	0	1	0	3	0	0	0	7	0.37
Other (including splaylegs)	0	1	3	0	2	2	0	0	1	3	0	0	12	0.64
Two or more defects	0	0	0	0	0	0	0	0	0	0	0	1	1	0.05
Intersexes	0	0	4	0	0	0	0	0	0	0	0	0	4	0.21
Rigs (monorchid, cryptorchid)	2	2	0	0	0	0	0	3	3	3	0	1	14	0.75
No defects	125	136	136	71	129	90	106	110	211	191	258	255	1803	--
Total Pigs Observed	130	142	144	74	134	94	110	114	218	201	262	267	1876	3.88

(b) FEMALES

CONDITION	1960	1961	1962	1963	1964	1965	1966	1967	1968	1969	1970	1971	TOTAL	% INCIDENCE
Umbilical hernia	1	0	0	0	0	0	0	1	2	0	0	11	15	0.83
Atresia ani	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Other (including splaylegs)	1	0	0	0	5	2	0	2	0	1	1	0	12	0.67
Two or more defects	0	0	0	0	0	0	0	0	0	0	0	0	0	0
No defects	123	126	117	80	134	92	109	110	220	203	237	227	1771	--
Total Pigs Observed	125	126	117	80	139	94	109	113	222	204	238	238	1798	1.50

APPENDIX B

CARCASS MEASUREMENTS TAKEN AT LOCAL SLAUGHTERHOUSES

(unadjusted for carcass or live weights)

Table B1.

Maximum Backfat Thickness at the Shoulder (mm.).

	HOGS				GILTS			
YEAR	No.	Mean	S.E.	S.D.	No.	Mean	S.E.	S.D.
1962*	66	36.3	0.6	4.7	--	--	--	--
1964*	6	34.3	1.2	2.9	20	28.9	1.2	5.3
1967*	--	--	--	--	38	33.0	0.9	5.8
1968	--	--	--	--	94	38.9	0.6	5.7
1969	--	--	--	--	46	42.7	0.8	5.4
1971	--	--	--	--	40	45.7	0.8	4.9

Table B2.

Mid-Back Fat (mm.).

	HOGS				GILTS			
YEAR	No.	Mean	S.E.	S.D.	No.	Mean	S.E.	S.D.
1962*	66	20.6	0.4	2.9	--	--	--	--
1964*	6	19.5	1.0	2.4	20	15.6	1.0	4.2
1967*	--	--	--	--	38	16.3	0.6	3.9
1968	--	--	--	--	94	21.5	0.5	5.0
1969	--	--	--	--	46	19.9	0.6	4.0
1971	--	--	11	--	40	22.7	0.6	3.8

Table B3.

Minimum Backfat Thickness at the Loin (mm.).

	HOGS				GILTS			
YEAR	No.	Mean	S.E.	S.D.	No.	Mean	S.E.	S.D.
1962*	66	17.8	0.5	4.2	--	--	--	--
1964*	6	20.3	1.9	4.6	20	15.0	1.1	5.0
1967*	--	--	--	--	38	14.5	0.7	4.3
1968	--	--	--	--	94	19.0	0.4	3.6
1969	--	--	--	--	46	19.6	0.5	3.5
1971	--	--	--	--	40	19.3	0.6	3.7

*Measured after skinning.

Table B4.

Eye Muscle Area (sq. cms.).

YEAR	HOGS				GILTS			
	No.	Mean	S.E.	S.D.	No.	Mean	S.E.	S.D.
1964*	6	20.0	0.90	2.21	20	27.27	0.90	4.02
1967*	--	--	--	--	37	26.60	0.79	4.80
1968	--	--	--	--	94	33.94	0.36	3.51
1969	--	--	--	--	46	34.85	0.84	5.72
1971	--	--	--	--	40	35.04	0.69	4.38

Table B5.

Fat Depth 'C' (mm.).

YEAR	HOGS				GILTS			
	No.	Mean	S.E.	S.D.	No.	Mean	S.E.	S.D.
1964*	6	9.9	0.8	3.5	20	17.7	1.9	4.8
1967*	--	--	--	--	37	13.4	0.5	3.1
1968	--	--	--	--	94	16.4	0.4	4.0
1969	--	--	--	--	46	15.3	0.6	4.3
1971	--	--	--	--	41	18.4	0.7	4.2

Table B6.

Fat Depth 'K' (mm.).

YEAR	HOGS				GILTS			
	No.	Mean	S.E.	S.D.	No.	Mean	S.E.	S.D.
1964*	6	22.0	2.3	5.7	20	15.8	1.1	5.0
1967*	--	--	--	--	37	18.7	0.6	3.4
1968	--	--	--	--	94	22.4	0.5	4.8
1969	--	--	--	--	46	17.7	0.7	4.7
1971	--	--	--	--	41	23.9	0.7	4.4

*Measured after skinning and curing.

Table B7.

Last Live Weight (lbs).

	HOGS				GILTS			
YEAR	No.	Mean	S.E.	S.D.	No.	Mean	S.E.	S.D.
1962	66	194.5	0.6	4.7	--	--	--	--
1964	6	192.5	1.4	3.3	20	196.3	1.3	5.8
1967	--	--	--	--	38	185.5	1.1	6.6
1968	--	--	--	--	67	205.6	1.1	9.1
1969	--	--	--	--	46	206.1	3.3	22.5
1971	--	--	--	--	41	202.0	1.9	12.5

Table B8.

Streak Thickness (mm.).

	HOGS				GILTS			
YEAR	No.	Mean	S.E.	S.D.	No.	Mean	S.E.	S.D.
1962*	66	16.6	0.4	3.5	--	--	--	--
1964*	6	15.2	1.8	4.4	20	12.4	1.0	4.5
1967*	--	--	--	--	38	16.6	0.7	4.4
1968	--	--	--	--	93	21.3	0.4	3.9
1969	--	--	--	--	46	27.7	0.6	4.1
1971	--	--	--	--	33	20.5	0.5	2.7

Table B9.

Fat Score (points 1 - 3).

	HOGS				GILTS			
YEAR	No.	Mean	S.E.	S.D.	No.	Mean	S.E.	S.D.
1962*	66	2.6	0.1	0.6	--	--	--	--
1964*	6	2.5	0.2	0.5	20	2.0	0.2	0.8
1967*	--	--	--	--	38	1.4	0.1	0.5
1968	--	--	--	--	93	2.1	0.1	0.7
1969	--	--	--	--	46	1.9	0.1	0.7
1971	--	--	--	--	40	2.4	0.1	0.6

*Measured after skinning.

APPENDIX C

CONSTRUCTION of THE A.B.R.O. SIRE-LINE SELECTION INDEX

Appendix C.

Construction of The A.B.R.O. Sire-Line Selection Index.

Between 1966 and 1971 boars and gilts in the A.B.R.O. sire-line were selected on an index using individual and full-sib family information from both sexes. In 1972 the index was modified to include half-sib family records. The following is a description of the method used in construction of the index, together with values adopted for the required parameters.

General Form of Index

A separate index was calculated for each individual according to the amount of family information available (e.g. Henderson, 1963). The index took the usual form:

$$I = \sum_i b_i y_i$$

where y_i is the i^{th} measurement on an individual or its relatives, and b_i the appropriate weighting factor; the object of the index being to predict the individual's aggregate genotype or "net merit" (M):

$$M = \sum_j a_j x_j$$

where x_j is the j^{th} trait to be improved and a_j is its economic partial regression coefficient.

More explicitly, until 1972 the index for a male, for example, was:

$$I = \sum_{T=1}^{3} \left[b_{T_1}(X_{M_{ijk}} - \hat{\mu}_M)_T + b_{T_2}(\bar{X}_{M_{ij}} - \hat{\mu}_M)_T + b_{T_3}(\bar{X}_{F_{ij}} - \hat{\mu}_F)_T \right],$$

for T = 1,.....,3 traits; daily gain, food conversion ratio and average ultrasonic backfat, where:

b_{T_n} .... weighting factor for the nth piece of information on trait T,

$X_{M_{ijk}}$ .... individual measurement taken on the kth male from the mating of the j dam with the ith sire,

$X_{F_{ijk}}$ .... individual measurement taken on the kth female from the mating of the j dam with the i sire,

$\bar{X}_{M_{ij.}}$ .... mean of k male full sibs from the mating of dam j with sire i ,

$\hat{\mu}_M$ .... observed population mean for all males tested in this generation,

and subscript T defines the relevant trait. In 1972 the index was extended to :

$$I=\sum_{T=1}^{3}\left[b_{T_1}(X_{M_{ijk}}-\hat{\mu}_M)_T+b_{T_2}(\bar{X}_{M_{ij.}}-\hat{\mu}_M)_T+b_{T_3}(\bar{X}_{F_{ij.}}-\hat{\mu}_F)_T+b_{T_4}(\bar{X}_{M_{i..}}-\hat{\mu}_M)+b_{T_5}(\bar{X}_{F_{i..}}-\hat{\mu}_F)_T\right],$$

where $\bar{X}_{M_{i..}}$, for example, is the mean of all male half-sibs from the ith sire family.

The aggregate genotype (M) was defined throughout as

$$M=\sum_{T=1}^{3}a_T x_T ,$$

in order to provide simultaneous improvement in the 3 measured traits: daily gain, food conversion ratio and backfat.

Computation.

Indices and their variances were computed using the standard matrix procedure (e.g. Cunningham, 1972) in which:

$b = P^{-1}Ga$, and $\hat{\sigma}_I^2 = b'Pb$, where

b	is the vector of index weights to be estimated
P	is the square symmetric phentoypic variance-covariance matrix,
G	is the genetic variance-covariance matrix,
a	is the vector of economic partial regression coefficients,
$\hat{\sigma}^2_I$	is the estimated variance of I.

Elements of the Phenotypic and Genetic Variance-Covariance Matrices.

It will be necessary to extend the existing notation so that two different traits are defined by X and Y and:

A_X	is the true breeding value of an individual for trait X,
A_Y	is the true breeding value of an individual for trait Y,
$Y_{M_{ijk}}$	for example, is an individual measurement for trait Y taken on the k^{th} male from the mating of the j^{th} dam with the i^{th} sire,
$K_{M_{ij}}$	is the number of male progeny derived from the mating of the j^{th} dam with the i^{th} sire,
$K_{M_{i.}}$	is the number of male progeny derived from all matings involving the i^{th} sire,
$\sigma^2_{A_X}$	is the additive genetic variance for trait X,
$\sigma^2_{M_X}$	is the "maternal" variance for trait X,
$\sigma^2_{E_X}$	is the "environmental" variance for trait X,
$\sigma^2_{P_X}$	is the total or phenotypic variance for trait X,
h^2_X	is the heritability of trait X,
c^2_X	is the proportion of maternal variance (σ^2_M/σ^2_P) for trait X.

Corresponding covariances and correlations are denoted by cov and γ respectively and it is understood that all parameter values are estimates. Elements of the two matrices were calculated from the quantities shown below. There were no missing observations.

(1) Phenotypic Matrix (P).

$$V(X_{Mijk}) = \sigma^2_{P_x}$$

$$Cov(X_{Mijk}, \bar{X}_{Mij.}) = V(\bar{X}_{Mij.}) = \sigma^2_{A_x}\left(\frac{1}{2} + \frac{1}{2K_{Mij}}\right) + \sigma^2_{M_x} + \frac{\sigma^2_{E_x}}{K_{Mij}}$$

$$\equiv \sigma^2_{P_x}\left[1 + \left(\frac{h_x^2}{2} + c_x^2\right)(K_{Mij} - 1)\right] / K_{Mij}$$

(computing form)

$$Cov(X_{Mijk}, \bar{X}_{Fij.}) = Cov(\bar{X}_{Mij.}, \bar{X}_{Fij.}) = \tfrac{1}{2}\sigma^2_{A_x}$$

$$Cov(X_{Mijk}, Y_{Mijk}) = cov_{P_{xy}}$$

$$Cov(X_{Mijk}, \bar{Y}_{Mij.}) = Cov(\bar{X}_{Mij.}, \bar{Y}_{Mij.})$$

$$= cov_{A_{XY}}\left(\frac{1}{2} + \frac{1}{2K_{Mij}}\right) + cov_{M_{xy}} + \frac{cov_{E_{XY}}}{K_{Mij}}$$

$$\equiv \sigma_{P_x}\sigma_{P_y}\left[\gamma_{P_{XY}} + \left(\tfrac{1}{2}\gamma_{A_{XY}} \cdot h_x h_y + \gamma_{M_{XY}} \cdot c_x c_y\right)(K_{Mij} - 1)\right] / K_{Mij}$$

$$\mathrm{Cov}(X_{M_{ijk}}, \bar{Y}_{FM_{ij.}}) = \mathrm{Cov}(\bar{X}_{M_{ij.}}, \bar{Y}_{F_{ij.}}) = \tfrac{1}{2}\,\mathrm{cov}_{A_{XY}}.$$

$$\mathrm{Cov}(X_{M_{ijk}}, \bar{X}_{M_{i..}}) = \mathrm{Cov}(\bar{X}_{M_{ij.}}, \bar{X}_{M_{i..}}) = V(\bar{X}_{M_{i..}})$$

$$= \sigma^2_{A_x}\left(\frac{1}{4} + \frac{\sum\limits_j K^2_{M_{ij}}}{4K^2_{M_{i.}}} + \frac{1}{2K_{M_{i.}}}\right) + \frac{\sum\limits_j K^2_{M_{ij}}\sigma^2_{M_x}}{K^2_{M_{i.}}} + \frac{\sigma^2_{E_x}}{K_{M_{i.}}}$$

$$\equiv \sigma^2_{P_x}\left[1 + \frac{h^2_x}{2}\left(\frac{K_{M_{i.}}}{2} + \frac{\sum\limits_j K^2_{M_{ij}}}{2K_{M_{i.}}} - 1\right) + c^2_x\left(\frac{\sum\limits_j K^2_{M_{ij}}}{K_{M_{i.}}} - 1\right)\right] \Big/ K_{M_i}$$

$$\mathrm{Cov}(X_{M_{ijk}}, \bar{X}_{F_{i..}}) = \mathrm{Cov}(\bar{X}_{M_{ij.}}, \bar{X}_{F_{i..}}) = \mathrm{Cov}(\bar{X}_{M_{i..}}, \bar{X}_{F_{i..}}) = \tfrac{1}{4}\sigma^2_{A_x}$$

$$\mathrm{Cov}(X_{M_{ijk}}, \bar{Y}_{M_{i..}}) = \mathrm{Cov}(\bar{X}_{M_{ij.}}, \bar{Y}_{M_{i..}}) = \mathrm{Cov}(\bar{X}_{M_{i..}}, \bar{Y}_{M_{i..}})$$

$$= \mathrm{cov}_{A_{XY}}\left(\frac{1}{4} + \frac{\sum\limits_j K^2_{M_{ij}}}{4K^2_{M_{i.}}} + \frac{1}{2K_{M_{i.}}}\right) + \frac{\sum\limits_j K^2_{M_{ij}}\,\mathrm{cov}_{M_{XY}}}{K^2_{M_{i.}}} + \frac{\mathrm{cov}_{E_{XY}}}{K_{M_i}}$$

$$\equiv \sigma_{P_x}\sigma_{P_Y}\left[\gamma_{P_{XY}} + \frac{\gamma_{A_{XY}}}{2}\cdot h_x h_y\left(\frac{K_{M_{i.}}}{2} + \frac{\sum\limits_j K^2_{M_{ij}}}{2K_{M_{i.}}} - 1\right) + \gamma_{M_{XY}}\cdot c_x c_y\left(\frac{\sum\limits_j K^2_{M_{ij}}}{K_{M_{i.}}} - 1\right)\right] \Big/ K_{M_{i.}}$$

$$\mathrm{Cov}(X_{M_{ijk}}, \bar{Y}_{F_{i..}}) = \mathrm{Cov}(\bar{X}_{M_{ij.}}, \bar{Y}_{F_{i..}}) = \mathrm{Cov}(\bar{X}_{M_{i..}}, \bar{Y}_{F_{i..}}) = \tfrac{1}{4}\,\mathrm{cov}_{A_{XY}}.$$

(2) Genetic Matrix (G)

$$Cov(X_{Mijk}, A_x) = \sigma_{A_x}^2$$

$$Cov(\bar{X}_{Mij.}, A_x) = \sigma_{A_x}^2\left(\frac{1}{2} + \frac{1}{2K_{Mij}}\right) \equiv \sigma_{A_x}^2\left[1 + \frac{(K_{Mij} - 1)}{2}\right] \Big/ K_{Mij}$$

$$Cov(\bar{X}_{Fij.}, A_x) = \frac{1}{2}\sigma_{A_x}^2$$

$$Cov(\bar{X}_{Mi..}, A_x) = \sigma_{A_x}^2\left(\frac{1}{4} + \frac{\sum_j K_{Mij}^2}{4K_{Mi.}^2} + \frac{1}{2K_{Mi.}}\right) \equiv \frac{\sigma_{A_x}^2}{2}\left[1 + \frac{\sum_j K_{Mij}^2}{2K_{Mi.}} + \frac{K_{Mi.}}{2}\right] \Big/ K_{M}$$

$$Cov(\bar{X}_{Fi..}, A_x) = \frac{1}{4}\sigma_{A_x}^2$$

$\sigma_{A_x}^2 = \sigma_{P_x}^2 h_x^2$ for computing. Corresponding covariances of measured variates with breeding values of different traits were obtained by substituting $cov_{A_{xy}}$ for $\sigma_{A_x}^2$ in the above. For example:

$$Cov(\bar{X}_{Mij.}, A_y) = cov_{A_{xy}}\left(\frac{1}{2} + \frac{1}{2K_{Mij}}\right) \equiv cov_{A_{xy}}\left[1 + \frac{(K_{Mij} - 1)}{2}\right] \Big/ K_{Mij},$$

where $cov_{A_{xy}} = \sigma_{P_x}\sigma_{P_y} h_x h_y \gamma_{A_{xy}}$ for computing.

Both common environmental and genetic "maternal" covariances between the two sexes were assumed to be relatively small, and were therefore ignored. Genetic covariances of half-sib family means with other variates of the same sex were correct for equal numbers of progeny per dam, but were only approximately correct in the unbalanced case.

Parameter Values.

The values of the genetic and phenotypic parameters used in calculating all indices are shown in Table 6.5 "Maternal" variances and covariances were fixed at 10% of the total variation for each character:

e.g.

$$\sigma_{M_x}^2 = 0{\cdot}1\,\sigma_{p_x}^2 \;;$$

$$cov_{M_{xy}} = 0{\cdot}1\,cov_{p_{xy}}.$$

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