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BREEDING OBJECTIVES AND GENETIC EVALUATION TO IMPROVE PIG FARM PROFITABILITY

A thesis presented in partial fulfilment
of the requirements for the degree of
Doctor of Philosophy in Animal Science
at Massey University,
Palmerston North, New Zealand

Mariusz Tadeusz Skorupski

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Errata Note

- It was recently found (D. Johnson private communication) that the AIREML programme was incorrectly calculating the standard errors (s.e.) of variance and covariance components. The standard errors in Table 4.5 (page 107) and in Table 4.7 (page 110) are underestimated by a square root of 2. For example, the s.e. of 0.015 should be $0.015*\sqrt{2} = 0.021$.
- The Duroc annual genetic trend in ADG (page 140, line 8) should read 4.33 g/day, as in the preceding Table 5.6.

ABSTRACT

The optimal design of a pig improvement programme requires the choice of an appropriate breeding objective and relevant economic values for objective traits, the choice of selection criteria and consequent genetic and phenotypic parameters, determination of selection indices and predicted genetic gains, and choice of an appropriate population structure.

A computer model simulating life cycle production of a breeding sow and growth performance of her offspring was developed to estimate economic values (EV's) of reproduction and growth performance traits. A biological growth model simulating the digestion and metabolism of dietary energy and nitrogen in growing pigs, based on the linear/plateau relationship between daily protein deposition and digestible energy intake, was part of the life cycle model. The upper limit to body protein deposition rate (Pdmax), mean daily ad libitum digestible energy intake (DEi) and minimum lipid to protein deposition ratio (R_{\min}) were assumed the major genetic determinants of pig growth. EV's were calculated per gilt life cycle by simulating effects of genetic changes in several biological components, in a farrow-to-finish production system, assuming ad libitum feeding. For unimproved genotypes ($Pd_{max} < 140 \text{ g/day}$, DEi > 30 MJ/day, $R_{\min} \ge 1$), the EV of 1 g/day improvement in Pd_{max} ranged from \$12 to \$22, DEi EV's ranged from \$-20 to \$-123 per 1 MJ/day increase, and EV's below \$-500 were found per one unit increase in R_{\min} . EV's for number born alive/litter (NBA) were below \$12 per extra pig. For improved genotypes, EV's for Pd_{max} had values below \$14 per unit increase and became zero at high Pd_{max} levels exceeding 180 g/day, when full expression of Pd_{max} was restricted by insufficient digestible energy intakes. The DEi EV's for improved genotypes with insufficient amounts of metabolisable energy became positive. Improved genotypes had high EV's for NBA, exceeding \$70 per 1 extra pig. Relatively low negative EV's were found for one unit increase in other reproduction traits: gilt age at first oestrus, interval weaning-oestrus, and pre-weaning mortality percentage. Results demonstrated EV's of traits depended on the average genetic merit in the pig herd and its interaction with the management circumstances (level of feeding, nature of the diet, life cycle length) of the production system.

Multivariate animal models and Restricted Maximum Likelihood (REML) methods were used to estimate (co)variance components, heritabilities, genetic correlations and common environmental effects of reproduction and growth performance traits for on-farm tested Large White, Landrace and Duroc pigs. Best Linear Unbiased Prediction (BLUP) methods were applied for breeding value estimation allowing determination of genetic, environmental and phenotypic trends in the studied populations. The annual realised genetic gains ranged from 2.1 to 4.3 g/day for average daily gain (ADG) and -0.2 to -0.3 mm for ultrasonically-measured backfat thickness (BF). The realised genetic trends in ADG and BF compared favourably with the rate of improvement found in similar overseas studies but were substantially lower than the respective predicted gains of 4.13 g/day/year and -0.88 mm/year, except for the Duroc ADG where predicted and actual gains were similar. The NBA genetic trends were negligible for Large White and Landrace, but favourable (+0.07 pigs/litter/year) for the Duroc breed. Mixed model techniques (BLUP and REML) offered efficient and accurate prediction of breeding values and estimation of parameters, utilising all available information from relatives, traits and environments.

Different selection strategies were investigated and predicted genetic gains were estimated, based on indices derived for a range of improved and unimproved pig genotypes. The effect of different sets of selection criteria on the efficiency of selection, use of restricted selection indices, and sensitivity to changes in the economic values and in the structure of future costs and returns were studied, and the effects of these changes on the predicted selection response were analysed. The increase in profit resulting from further selection was lower in pig populations representing improved genotypes, as a result of lower predicted genetic gains in growth and carcass traits. This reduced rate of increase in profit was partially offset by the increase in predicted genetic gains in reproductive performance. For improved genotypes, the predicted increase in profit per gilt life cycle after one generation of selection ranged from \$26 to \$98 for one standard deviation of index selection with a selection intensity of 1. For unimproved genotypes, higher genetic gains in growth and carcass traits resulted in profits exceeding \$120 per generation of selection. Greater economic emphasis on litter size resulted in lower predicted genetic gains in growth and carcass traits.

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INTRODUCTION

The purpose of every animal breeding programme is to improve performance in one or more traits. The first step in designing a selection programme is to define a breeding objective. In commercial pig breeding, the primary objective would be to maximise the net profit of the enterprise. This implies improvement in efficiency of a production system, taking into account all major inputs (production costs) and outputs (income) of the system. Traits of economic importance should be included in the breeding objective and their economic weights estimated. Changes in inputs and outputs caused by changes in genetic merit need to be quantified and valued to allow calculation of economic values of traits. Given a breeding objective, the design of an improvement programme requires knowledge of genetic parameters, in order to define selection criteria, and the choice of a suitable population structure and methods of animal measurement.

The main objective of this study was to optimise pig breeding programmes by accounting for genetic changes in performance, differences in systems of production and genetic associations between economically important production and reproduction traits. The aims were to:

- (a) develop a system for deriving economic values,
- (b) determine genetic parameters of component traits,
- (c) examine the application of best linear unbiased prediction for the genetic evaluation of on-farm tested pigs, and
- (d) investigate methods of optimising genetic response to selection using mixed model procedures.

Animal breeders must identify the traits that offer greatest opportunity for genetic improvement in a particular production system. The traits involved in pig

production can be divided into production (growth and carcass characteristics) and reproduction (fertility and longevity of sows) traits (Smith, 1964). Until recently, nucleus pig breeders concentrated on the improvement of the production traits by selection of general purpose lines. These traits were moderately-to-highly heritable, economically important, easy to measure, and required relatively small (100 to 200 sows) nucleus herds for selection. However, the breeding objectives for some pig improvement programmes are likely to change, as the deterioration in meat quality, decline in voluntary feed intake, and lack of improvement in reproductive performance shifts the emphasis in selection towards lean growth rate, meat quality and reproductive ability (Ollivier *et al.*, 1990).

Once the breeding objectives have been chosen, it is then necessary to decide the relative economic importance of each of them in the aggregate genotype. One of the problems in designing a breeding programme is to account for future changes in the economic weightings for the various traits relative to each other (Blair, 1989). These relative weightings may be influenced by the genetic changes in performance (Tess et al., 1983b), and by the changes in future management-marketing systems and feed prices (Tess et al., 1983c). Different approaches to obtaining the relative economic values of breeding objective traits are reviewed in Chapter 1.

Past experience shows that periodical re-evaluation of the breeding objective is necessary to adapt the breeding programme to constantly changing genetic levels of performance and production conditions. As pointed out by Ollivier et al. (1990), the breeding objective defined at any given time can never be optimal with regard to later situations, because of the genetic lag in the dissemination of genetic improvement. Breeding goals and relative economic values of traits are likely to differ between production systems within countries and between countries. Computer models simulating pig production of a

particular country have been developed (e.g. Tess et al., 1983a; de Vries, 1989), to calculate relative values of traits for specific economic environments and production-marketing systems of those countries.

One of the objectives of this thesis was to develop a computer model simulating the life cycle production of a breeding sow and growth performance of her offspring to estimate economic values of biological traits influencing income and expense. These economic values should be included in the breeding objective appropriate to New Zealand pig production systems. The aim was to obtain economic values of reproduction and growth performance traits, by simulating the effects of genetic changes in several biological components. The construction of this model is described in Chapter 2. The application of the model to the estimation of economic values of traits and the effects of different genetic levels of performance on the profitability are presented in Chapter 3.

Choice of the correct breeding objective and the optimum performance testing regime depend on knowledge of genetic parameters (heritabilities and genetic correlations). Reliable estimates of genetic parameters are needed for accurate prediction of breeding values. Genetic correlations should be accounted for to allow for antagonistic relationships among traits, to enhance the accuracy of selection through using the information on related traits, and to permit improvement in genetically related and economically important, but difficult or expensive to measure traits (Blair, 1989).

Traditional methods of estimation of genetic parameters used analysis of variance (ANOVA) or analogous procedures. Restricted Maximum Likelihood (REML) methods allow more precise estimation of genetic parameters in unbalanced data sets containing many environmental effects, by utilising all available records, accounting for the loss in degrees of freedom due to fixed effects in the model and maximising only that portion of the likelihood which is

invariant to the fixed effects (Patterson and Thompson, 1971). Early REML applications were limited to univariate models and described an animal's record in terms of sire and dam effects. Recently, multivariate animal models which include additive genetic effects for each animal and trait have become widely used in genetic evaluation schemes. These models utilise information from all known relationships among animals, take into account correlations among traits, and can incorporate additional random effects, such as maternal genetic or permanent environmental effects.

Restricted maximum likelihood methods were applied in this study to obtain estimates of (co)variance components and subsequently heritabilities, phenotypic and genetic correlations and common environmental effects for production and reproduction traits for on-farm tested Large White, Landrace and Duroc pigs in New Zealand nucleus herds. Methods for variance component estimation are briefly reviewed and results of REML analyses are given in Chapter 4.

Estimating covariance matrices on the basis of mixed model methodology (Henderson, 1949) has the added advantage of allowing the same models to be used in the estimation of variance components and prediction of genetic merit. Current methodology for estimating breeding values of continuously varying traits is based on the Best Linear Unbiased Prediction (BLUP) method of Henderson (1963; 1973). The BLUP method has superseded the earlier methods of comparing the performance of contemporary animals in a common environment (Garrick, 1991). One of the advantages of BLUP is in using information from all relatives of an individual, allowing more accurate prediction of the genetic merit of that animal. Another advantage is in partitioning genetic and non-genetic effects on performance, allowing comparisons between animals born and tested in different management regimes, time periods, and subjected to different amounts of prior selection.

Application of BLUP methodology for the estimation of breeding values of growth performance and reproduction traits of pigs tested on-farm was examined. Breeding values generated by this approach allowed genetic, environmental and phenotypic trends in purebred populations of pigs to be monitored. The realised annual genetic gains, generation intervals and selection differentials estimated for New Zealand nucleus herds are reported in Chapter 5.

Nucleus herds of 100 to 200 sows per line have been sufficient to improve lean growth rate at a satisfactory rate. However, selection on poorly inherited traits, such as litter size, requires larger populations in order to implement family index selection, to avoid inbreeding and to maximise selection intensity (Webb, 1991). The ability of BLUP to compare merit across herds offers a cost-effective means to achieve this by allowing selection with a large number of families in multi-herd populations. Accuracy of genetic evaluation can be influenced by the degree of genetic connectedness between herds or management units. Alternative measures of genetic connectedness proposed by Kennedy and Trus (1993) were applied in this study to estimate the degree of connectedness between two nucleus herds. The effects of increasing the number of reference sires on the degree of genetic connectedness were studied. The results are presented in Chapter 6.

Breeding values predicted by BLUP for measurable selection criteria can be combined into an economic index to predict an "aggregate breeding value" made up of economically important traits and their associated economic values. The index weights depend on genetic variances and covariances among the selection criteria and the traits in the aggregate genotype, and on economic values of these traits. The predicted genetic gains from selection on the economic index can be estimated for traits in the aggregate genotype and for selection criteria in the index. A study was conducted to investigate predicted genetic gains in growth performance and reproduction traits using indices based on economic values

derived for a range of improved and unimproved pig genotypes. The effect of different sets of selection criteria on the efficiency of selection, use of restricted selection indices, and sensitivity to changes in the economic values and in the structure of future costs and returns were studied, and the effects of these changes on the predicted selection response are reported in Chapter 7.

The model simulating life cycle pig production developed in this study and the programmes designed to measure genetic response to selection, together with the estimates of relative economic values, genetic parameters and index weights, can be used by pig breeding organisations to optimise their improvement programmes.

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CHAPTER 1

REVIEW OF METHODS FOR DERIVING RELATIVE ECONOMIC VALUES TO ENABLE CONSTRUCTION OF SELECTION INDICES

1.1 Introduction

Index selection is a common way of evaluating future genetic and economic worth of the pig. The index selection theory was developed by Smith (1936) and further extended by Hazel (1943) for use in livestock breeding programmes. One of the problems in construction of the selection index is accurate estimation of the relative economic value (REV) of each trait, that is a net economic gain to be returned for improving that trait by one unit. The difficulty lies in identifying all the costs which influence the change in an animal's performance, and in using current market prices to determine REV's, when selecting animals for future market requirements.

Different methods of obtaining REV's for index construction are reviewed, including economic, biological and bioeconomic approaches.

1.2 Comparison of Economic, Biological and Bioeconomic Approaches to Defining Economic Values of Traits

The primary objective of an economic model used in construction of the selection index is to describe genetic improvement in terms of the increase in profitability of the animal within a specified set of conditions of production and marketing (Fowler $et\ al.$, 1976). It is often assumed that net merit (T) of an individual as a future parent may be described as a linear function of its separate breeding values, weighted by their respective economic weights. This overall merit, often called aggregate genotype, can be written as:

$$T = v_1 g_1 + v_2 g_2 + ... + v_n g_n$$

where ν 's are the REV's which express the relative importance attached to each character and g's are the true breeding values for the n characters to be improved. REV's are the money values which can be placed on a unit change in the expression of each trait. After deciding which traits should be included in the aggregate genotype and finding their relative economic importance, it is then to decide which traits are to be measured (selection criteria), in order to predict each of the breeding values (Harris et al., 1984; Blair, 1989).

This classical, economic approach in constructing a selection index may be criticised on several grounds (Fowler *et al.*, 1976):

- (a) The economic relativities may not remain stable due to changes in technology of production and methods of meat processing.
- (b) The choice of the objectives and their weights may relate only to a restricted set of conditions.
- (c) Genetic and phenotypic parameters may vary with the conditions of testing, with breed and strain.
- (d) The economic model does not take into account a physiological background of the measured traits, expressing only a current monetary value of a given improvement.

Smith (1983) has shown that considerable losses in efficiency can occur if important traits are omitted from breeding objective or unimportant traits are given importance, and when the direction of selection is reversed for an important trait. However, it was found that the efficiency of the economic selection index was fairly insensitive, even to large changes in economic weights, particularly when traits were favourably correlated (Simm and Smith, 1986; Simm et al., 1987a). If economic weights differ considerably from one breed or

production system to the next, then it is preferable to derive a different index for each breed or system.

An alternative approach is based on the concept of biological efficiency. It attempts to define desirable physiological changes to improve the overall value of a meat-producing animal. The classic example relates to selection for lean tissue or the use of 'simple' biological indices such as lean tissue growth rate (LTGR) and lean tissue feed conversion efficiency (LTFC), (Fowler *et al.*, 1976). LTFC was defined as the feed consumed divided by the gain in lean tissue. LTGR and LTFC were estimated as the products of growth rate or feed conversion efficiency and killing-out and carcass lean percentage estimates.

The advantage of using the biological model is its utilisation of recent knowledge in animal physiology which enables prediction of performance in a specified production environment. The biological indices do not require estimates of genetic parameters or economic values for component traits. However, the components of product traits are still weighted in selection, and a biological index still contains implied economic values, dependent on the correlations between traits, heritabilities of product traits and variation in component traits of the index. The biological index is therefore an economic index with an implied set of economic weights (Smith, 1967; Simm et al., 1987a). If one component of the biological index is much more variable than the other, this component will tend to dominate the product. The lower the economic value and heritability of the most variable trait, the lower is the relative efficiency of selection on the biological index. In general, selection aimed at the components of product traits is only worthwhile in special situations, such as when there are significant differences in the heritability and in the variation of the traits concerned, and when the traits are highly correlated. There may be large differences in the weighting given to components of product traits in selection using biological index, under different conditions of testing. Hence, sometimes it

is better to use an economic selection index to give more appropriate weightings to component traits, even when economic values and genetic parameters are not estimated precisely.

The biological indices may be useful in pigs, but they have a limited value in ruminants because of the relatively low variation in carcass composition (killing-out and carcass lean proportion), compared to the high coefficients of variation of growth rate and feed conversion efficiency (Simrn and Smith, 1986; Simm and Dingwall, 1989). In ruminants, there would be little extra response from direct selection on product traits, such as LTGR or LTFC, compared with indirect selection solely for growth rate and feed conversion efficiency.

Summarising, the economic selection indices give theoretically optimal responses to selection, but they depend on estimates of genetic parameters and economic values which are expensive or difficult to obtain. On the other hand, biological indices require no prior information on genetic parameters or economic values, hence they may be more stable, and of longer-term use than classical economic selection indices, as well as being simpler to use. However, they could lead to a less controlled response to selection, which may be far from the economic optimum. In general, the move is away from the biological approach, as it is now recognised that the true objectives of selection are more complex than either LTGR or LTFC. The breeding objectives in pig production must take into account both efficiency in feed utilisation and the rate of lean tissue deposition, and the balance between them must be based on economy of production (Smith et al., 1988).

Efficiency measured at only one point in the life cycle may not accurately reflect the changes in performance traits and their influence on the total production system. A third approach, the so-called 'bioeconomic' model accounts for the whole life-time production efficiency, including feed inputs,

viability, reproductive rate, age at breeding, mature size, length of production life and role of the breed or stock in the production system. Rather than using a limited set of breeding objectives, for example growth-carcass traits, the bioeconomic model involves a series of deterministic equations that simulate growth, reproduction and viability, allowing a more rational derivation of economic values. A bioeconomic approach can be sought as a complex economic model which utilises our knowledge of biology of production. The effects of genetic changes in performance on the biological and economic production efficiency can be simulated and analysed.

Several models simulating pig production were reported in the literature. Some of the models described the whole life cycle production and included simulation of reproductive performance, estimating economic values of fertility, longevity and carcass traits (e.g. Tess *et al.*, 1983; de Vries, 1989). Several other models described only pig growth in terms of efficiency of meat production (Whittemore and Fawcett, 1976; Whittemore, 1983; Moughan and Smith, 1984; Moughan *et al.*, 1987; de Vries and Kanis, 1992). These models incorporated concepts of energy and amino acid partitioning, predicting whole-body protein and lipid deposition controlled by the upper limit to body protein deposition ratio (Pd_{max}), minimum lipid to protein deposition ratio (R_{min}), and the amount and quality of nutrients supplied and ingested.

1.3 Differences in Methods of Derivation of Relative Economic Values Depending on the Perspective Taken

It was indicated by Moav (1973), that the results of deriving economic weights varied depending on the perspective taken; whether it was based on a unit of product, the individual animal, the producer or production unit, a new

investor or the nation (consumer) as a whole. In case of the long term national interest, genetic improvement reduces the cost of production without increasing the volume of sales. For this type of a national improvement programme, economic values for selection indices are calculated in the interests of the national economy (Simm and Smith, 1986), assuming the total volume of produce remains fixed, so improvement reduces the cost of production (faster, more efficient growth), without increasing the total volume. An existing small farmer may use genetic improvement to increase the volume of sales without a reduction in profit per unit of produce (Simm et al., 1987b). A new investor would be interested in maximising profit per unit of investment.

Those apparent differences in interests between the investor, the farmer and the consumer were resolved by Brascamp et al. (1985) by setting profit to zero, by including the producer's margin or profit as a cost of production, before estimating economic weights. Smith et al. (1986) imposed two conditions to remove the differences in deriving economic weights using different methods with different bases and perspectives. The first condition implies, that any extra profit due to rescaling (increasing output) is discounted from the profit due to genetic improvement. Only savings in cost per unit of product value should be included. The second condition is, that profit due to correcting previous inefficiency in the production system is not counted. The assumption is made that resources are efficiently used, and changes in output will require proportional changes in input. This implies that fixed costs should be expressed per unit of output, rather than as a fixed total enterprise cost. Real genetic improvement can be obtained by improving the efficiency of the production system, that is reducing the cost of production per unit of product value. The above two conditions were supplemented by de Vries (1989) with a third, that the limitations of individual farms should not be considered for the overall improvement in a particular trait.

1.4 Derivation of Economic Values Using Different Combinations of Income and Expense

Overall efficiency can be measured in one of the following ways, combining income (I) and expense (E):

- (1) Profit (P) = I E
- (2) Return on investment (R) = I/E
- (3) Cost per unit production (Q) = I/E.

These alternative economic goals of genetic improvement in livestock were discussed by Harris (1970), Dickerson (1970), Brascamp et al. (1985), Smith et al. (1986) and Ponzoni (1988). Dickerson (1970) had chosen to measure overall efficiency by the ratio of total costs to total animal product from females and their progeny over a given period of time. The objective was to reduce costs by increasing total product value per female, with minimum increase in metabolic body size or in non-feed costs per female. Smith et al. (1986) proposed deriving economic values by using the cost of production per unit of product value, in agreement with Dickerson (1970). It was suggested that using ratios (2) and (3) is more appropriate than the difference (1), because the changes in profit may also be obtained by rescaling the production enterprise, without any genetic improvement.

In a simulation model developed by de Vries (1989) derivation of economic values was based on a ratio, cost per unit of product, calculated as total net costs per kg offspring output (kg carcass weight) less adjustment of price for carcass quality. Total net costs were calculated as sow costs minus returns for culled sows plus costs for offspring. The effect of a small change in level of performance on efficiency of production was calculated for each trait. The

economic value for each trait was calculated as a ratio of change in efficiency per slaughter pig, to a unit change of that trait. The performance levels of all other traits remained constant.

In a sheep production model developed by Ponzoni (1986 and 1988), the producer's margin was included in the fixed costs, thus total income was equal to total expense, so the economic profit was equal to zero. The economic value of each trait was obtained as the partial derivative of profit (P), return on investment (R) or cost per unit production (Q), expressed as functions of the traits in the breeding objective. It was shown that combining income and expense as R was the same as combining them as Q. If P was equal zero, the economic values obtained were the same for P, R and Q. Correlations between breeding objectives and selection indices derived from P and R or Q were close to one, which suggests that the way in which income and expense are combined will have a negligible effect on selection decisions. Also, it is much simpler to derive economic values from the difference, I - E = P, rather than from R or Q ratios, because in case of P equation fixed costs can be ignored. These findings were consistent with theoretical predictions made by Brascamp $et\ al.\ (1985)$ and Smith $et\ al.\ (1986)$.

Profit as the difference between income and expense was also used in derivation of economic weights in models developed by Dempfle (1986), Munoz-Luna et al. (1988) and Groen (1988 and 1989). Costs and returns in terms of energy were computed and converted into monetary values. The economic weight for each trait was determined by differentiating the profit function with respect to each trait.

Defining a breeding objective for New Zealand pigs, Morris *et al.* (1978) indicated, that the linear breeding objective (T_L) , which was measured in terms of \$ net income/animal, and incorporated four traits: average daily gain (ADG), feed

conversion ratio (FCR), carcass grading profile (FAT) and carcass weight (CW), did not account for the extra feed to produce heavier carcasses. The T_L was redefined and the multiplicative (non-linear) breeding objective T_M was chosen, expressed in terms of \$ net income/kg carcass, as it gave more accurate value of the feed cost of the genetic change per unit of measurement (kg carcass), and because of supply and demand being determined by the price paid per kg carcass. The economic values for traits in the breeding objective were derived using costs per pig place, price of food and carcass grade structure. To obtain the economic value of ADG, a cost saving from 1kg liveweight improvement per pig per day in relation to faster throughput was calculated. The cost saving in feed consumed per one unit improvement in FCR was used as the economic value of feed conversion ratio and total feed intake. The value of 1 mm change in the intrascope fat measurement was taken as the basis for estimating the economic value of a change in carcass quality. The economic value of carcass weight was calculated as the extra net income from 1 kg increase in carcass weight.

In the economic selection model developed by Simm et al. (1987b) economic values for carcass lean and fat weights were derived by estimating the marginal profit or loss (marginal return less marginal cost), resulting from a 1 kg increase in lean weight at a constant fat weight, compared with the average physical and financial data. These marginal profits were partial regressions of profit on lean weight, at a constant fat weight, and of profit on fat weight at a constant lean weight, and were expressed per phenotypic standard deviation unit. It was suggested, that a linear approximation to an overall merit would be adequate, since genetic change is likely to be slow.

1.5 Conclusion

Comparing economic and biological approaches to REV's derivation, it was concluded that biological efficiency would have limited use, because it does not account for differences in feed prices or for the influence of non-feed costs on efficiency. Biological indices require no prior information on genetic parameters or economic values, but ultimately they require some implied economic values, as the components of product traits are still weighted in selection. There would be little extra response from direct selection on product traits in species with low variation in carcass traits, and high variation in growth rate and feed conversion efficiency.

On the other hand, economic models may relate only to a restricted set of conditions selected for a particular breeding objective, and they do not take into account a physiological background of the measured traits, expressing only a current monetary value of a given improvement.

Bioeconomic simulation models account for the whole life cycle production efficiency, combining the advantages of biological and economic models and allowing more rational derivation of economic values. The bioeconomic model approach seems to be a preferred method to be used for derivation of relative economic values for New Zealand pig production systems. Breeding objectives for those systems may include improvement in several reproduction traits such as litter size, age at puberty, piglet survival and piglet litter weight, as well as production traits such as Pd_{max} , R_{min} and voluntary feed intake.

Derivation and use of accurate economic values for traits in the aggregate genotype is required for the optimum selection for carcass quality, growth rate, feed intake and reproductive performance.

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CHAPTER 2

ECONOMIC VALUES OF TRAITS FOR PIG IMPROVEMENT.

I. A SIMULATION MODEL

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2.1 Abstract

A computer model simulating life cycle production of a breeding sow and growth performance of her offspring was developed to estimate economic values of reproduction and growth performance traits. A biological growth model, simulating the digestion and metabolism of dietary energy and nitrogen in growing pigs (20 to 85 kg), was part of the life cycle model. The growth model was based on the linear/plateau relationship between daily protein deposition and digestible energy intake. A farrow-to-finish production system, with slaughter pigs marketed at fixed liveweights, was simulated. Input variables were: gilt age at first oestrus, weaning to oestrus interval, number of pigs born alive per litter, and pre-weaning mortality for each parity. Economic inputs included prices of feed ingredients, carcass returns and non-feed costs. The upper limit to body protein deposition rate, mean daily ad libitum digestible energy intake and minimum lipid to protein deposition ratio were assumed the major genetic determinants of pig growth. The model output included average daily gain, ad libitum daily feed intake, backfat thickness, and life cycle reproductive performance and profit. The combined life cycle profit was expressed in the form of an Annualised Present Value. Life cycle profit was calculated for a range of simulated pig genotypes.

Keywords: Pigs, growth, reproduction, breeding objective, simulation, life cycle efficiency.

2.2 Introduction

Maximisation of profit is the main objective of modern pig production. Definition of a breeding objective is the first step in optimisation of a breeding programme (Harris *et al.*, 1984). Traits of economic importance should be included in the breeding objective and their economic weights estimated (Gjedrem, 1972). The traits involved in selection for pig meat production can be divided into reproduction (breeding performance of sows) and production (growth and carcass characteristics of their progeny) traits (Smith, 1964).

The effects of genetic changes in performance on biological and economic production efficiency can be simulated and analysed. Moughan and Verstegen (1988) suggested pig growth models be used to calculate the relative economic values of traits and to provide information on the physiological consequences of genetic improvement. Some of the recently developed models with mainly nutritional applications simulated pig growth in terms of efficiency of meat production and incorporated concepts of energy and nutrient partitioning (Whittemore and Fawcett, 1976; Whittemore, 1983; Moughan and Smith, 1984a; Moughan et al., 1987; Black et al., 1986; Pomar et al., 1991). Models simulating the whole life cycle of pig production have also been developed (Tess et al., 1983; de Vries, 1989) and applied in estimating economic values of traits.

The objective of this paper is to describe a model capable of simulating life cycle production of a breeding sow and growth performance of her offspring. The model can be used to estimate economic values of reproduction and production traits influencing income and expenditure.

Base parameters included in the model represent current average performance of New Zealand commercial pig farms. Alternatively, input parameters representing other genotypes and different production systems could be used. In a companion paper (Skorupski *et al.*, 1995), relative economic values will be presented for several pig genotypes fed *ad libitum* and the effects of genotypes on profitability will be discussed.

2.3 Materials and Methods

2.3.1 Strategy and Model Design

Simulations were based on life cycle production of a replacement gilt from her purchase to removal (up to 10 parities), producing bacon pigs under a farrowto-finish management system. Whole life cycle production efficiency was accounted for, including feed inputs, viability, reproductive rate, age at breeding, mature size, and length of the production life, as well as efficiency in growthcarcass traits. Marginal sow culling rates, sow mortalities, daily growth rates of mature sows and their liveweights at weaning, as well as numbers of pigs born alive per litter, litter birth weights, average daily gains from birth to weaning and pre-weaning mortality percentages were provided as input variables, by sow parity. It was assumed the farm production system was operating at an optimum, and environmental and management factors such as temperature of the grower shed, herd disease status, and the number of sows (herd size) had no effect on the estimation of relative economic values of traits, calculated as a change in profit per gilt life cycle (Smith et al., 1986). The proportion of sows retained from the previous parity was determined by the marginal sow culling rates and sow mortality at each parity. Number of offspring produced per sow was dependent on the litter size and pig mortality percentage at each parity.

Figure 2.1 illustrates a flow diagram of the model subroutines. The net return from each parity was calculated as the difference between production returns (income from stock sales) and costs (expense). Production costs included aggregated costs of keeping gilts and sows plus offspring costs. The combined life cycle profit per replacement gilt was expressed as an Annualised Present Value (APV), taking into account the time preference for consumption (Smith, 1978).

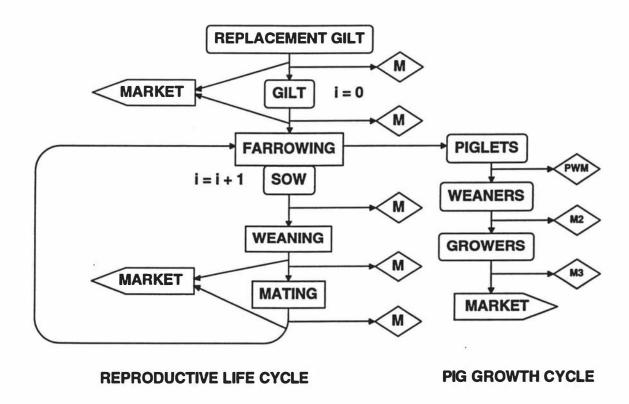


Figure 2.1 Generalised model flow diagram

Meaning of symbols: i = Parity number; M = gilt/sow mortality; PWM = Preweaning mortality; M2 and M3 = Mortality in growth stage 2 and 3.

A biological pig growth model, simulating the digestion and metabolism of dietary energy and nitrogen in growing pigs (20 - 85 kg liveweight), was built into the life cycle model. Physiological interactions and constants given by Moughan and Smith (1984a) and Moughan et al. (1987) were used in the growth model. The three controlling variables: upper limit to body protein deposition rate (Pd_{max} , g/day), mean daily ad libitum digestible energy intake (DEi, MJ/day), and minimum lipid to protein deposition ratio (R_{min}) were assumed to be the major genetic determinants of pig growth.

Ad libitum daily feed intake was calculated dividing daily DEi by the digestible energy density of the diet, with daily DEi specified as a function of pig liveweight. It was assumed that growing pigs have the ability to adjust food intake, when fed diets containing differing energy densities, in order to maintain a constant DEi, such that intake decreased linearly with increases in dietary energy concentration (Chadd and Cole, 1989). It was also assumed that intake was not influenced by the quality of diets, animal health and/or environmental circumstances.

This model used the linear/plateau relationship between daily protein deposition and energy intake, as proposed by Kielanowski (1969), Whittemore and Fawcett (1976) and Whittemore (1983). Under conditions of adequate nutrient supply, protein deposition or lean tissue growth rate (LTGR) increased linearly with increasing protein intake until it reached a genetically determined maximum value of Pd_{max}. Further increase in energy and protein intake caused deamination of excess protein and increased deposition of body lipid. This plateau to daily protein deposition rate for pigs of defined sex and genotype was assumed to be constant over the 20 to 85 kg liveweight range (Whittemore, 1983; Whittemore *et al.* 1988). It was assumed in the model that protein deposition was always accompanied by deposition of a physiologically essential proportion of lipid. When the ratio of whole-body lipid to protein content was lower than the

genetically determined R_{min} constraint, deamination of dietary protein was activated to provide energy required for lipid deposition.

The model was implemented using Microsoft Foxpro® programming language and included two main subroutines:

- Reproductive life cycle simulation (Appendix A)
- Pig growth simulation (Appendix B).

2.3.2 Gilt and Sow Costs and Returns

The reproductive cycle consisted of a replacement gilt period (from purchase to conception), a mated gilt period (from conception to farrowing), followed by consecutive sow parities.

Gilt and sow costs were calculated using the following input variables:

- (a) replacement gilt purchase cost;
- (b) non-feed costs (annual housing depreciation, opportunity cost of capital, labour, administration, health, repair and maintenance, cost of power and general expenses);
- (c) feed costs;
- (d) marketing costs of culled gilts and sows (Pork Industry Board levy, Federated Farmers levy, meat inspection and freight).

These inputs, based on average New Zealand commercial pig farm costs (1990-1991 data), provided the basis for calculation of daily costs, which were multiplied by the number of total gilt and sow days in each parity. Boar costs were built into the overall costs of gilts and sows. The values of input variables

used in the simulation of the breeding sow life cycle are in Table 2.1 and 2.2. They represent unpublished average commercial pig farm performance based on 10 years' results (1980 to 1989) from 18 New Zealand farms (24,754 farrowings).

Table 2.1 Values of reproductive input variables (base level) compared with the New Zealand field data

	N.Z. field	Model	
	Mean	±s.e.¹	Input
Replacement gilt age at purchase (days)	190.57	0.792	190
Replacement gilt purchase weight (kg)			95
Replacement gilt culling rate (%)			2.0
Gilt age at first oestrus (days)			200
Gilt age at first mating (days)	241.67	1.213	242
Oestrus number when first mated			3
Mated gilt culling rate (%)			5.0
Length of gestation (days)	114.95	0.016	115
Length of lactation (days)	27.82	0.139	28
Weaning to oestrus interval (days)	7.16	0.091	7
Gilt and sow mortality rate (% / year)	2.64	0.088	
Gilt mortality (%)			0.1
Sow mortality per parity (%)			1.0
Average stillborn percentage (%)	7.01	0.122	7.0

standard error of the mean.

Total replacement gilt days were dependent on the number of days from gilt purchase to conception, replacement gilt culling rate, average culling time after gilt purchase and the replacement gilt mortality percentage. Gilt age when first mated was influenced by the gilt age at first oestrus (puberty), and oestrus

number when first mated. Total sow days for each parity were calculated using proportions of sows retained from the previous parity, average sow culling times after weaning and after first insemination, sow mortality percentage and the number of days between farrowings (farrowing interval). Within each parity, 50% of sow marginal culling occurred shortly after weaning and the remaining 50% sows were culled after two unsuccessful matings. In the last period, all remaining sows were culled shortly after weaning.

Gilts and sows were fed a balanced diet (12.7 MJ DE, 15.3% crude protein, total lysine 0.52 g/MJ DE), based on barley, meat and bone meal, fish meal and mineral premix ingredients commonly used in New Zealand. This diet fully met their total feed requirements for growth, maintenance, pregnancy and milk production. It was assumed that feed wastage was accounted for in feed inputs. Daily feed inputs for replacement gilts and mated gilts were 2.70 and 2.43 kg/day respectively. Feed requirements for dry sows and boars were assumed at 2.6 kg/day. Total lactation feed inputs for the first and second parity were assumed at 5 and 6 kg/day respectively, and 7 kg/day for the following parities. Daily growth rates for replacement gilts were assumed at 0.60 kg/day and 0.30 kg/day for mated gilts. Sow liveweights after weaning and their average daily growth rates at each parity are in Table 2.2. The farrowing interval was increased by 10 non-productive days (extra days open due to oestrus problems and remating) for the first parity sows, 7 extra days were added for the second parity sows, and 6 days were assumed in the following parities.

Table 2.2 Reproductive parameters by sow parity, based on 10 years' information from the New Zealand pig industry

Sow parity:	1	2	3	4	5	6	7	8	9	10
Farrowing distribution (%)	20.0	17.6	15.2	12.7	10.4	8.2	6.2	4.5	3.2	2.1
Marginal culling (%) 1		12.0	13.9	16.0	18.5	21.4	24.0	27.0	30.0	33.0
Sow liveweight after weaning (kg)	154	180	198	211	219	224	227	230	232	233
Sow daily growth rate (g/day)		168	111	84	53	34	25	25	25	25
No. pigs born alive	9.8	10.6	11.2	11.4	11.4	11.3	11.1	10.7	10.7	9.9
Pre-wean mortality (%)	13.5	10.5	11.5	13.5	15.0	14.5	14.5	14.5	15.0	16.0

¹ Marginal culling includes 1% sow mortality per parity.

Returns from culled sows were determined by their average liveweights at weaning, daily growth rates from weaning until sale, marginal culling and mortality rates at each parity, age at first oestrus and weaning to oestrus interval. Carcass yield from cull sows was 80% of liveweight.

Simulated life cycle performance of a breeding sow (base level) is summarised in Table 2.3 and compared with the data representing average New Zealand commercial farm performance.

Table 2.3 Simulated performance of a breeding sow (base level) compared with the New Zealand field data

	Simulated	N.Z. 1	field data
	Averages	Mean	±s.e.¹
Number Born Alive/litter	10.8	10.83	0.021
Number Weaned/litter	9.4	9.43	0.016
Number Sold/litter	9.1		
Average Pre-weaning Mortality (%)	13.1	13.22	0.133
Litters / Sow / Year	2.3	2.30	0.004
Total born / Sow / Year	27.0		
Born alive / Sow / Year	25.1		
Weaned / Sow / Year	÷21.8	21.41	0.003
Sold / Sow / Year	21.2		
Farrowing Interval (days)	157.0	156.10	0.263
Farrowing Rate (%)	92.3	87.66	0.228
Sow Feed per Weaner (kg)	55.0		
Feed Input / Sow / Year (kg)	1197.8		
Feed to Pigmeat Ratio (kg/kg)	3.9		
Average Cull Sow Liveweight (kg)	199.6		
Cull Sow Carcass Weight (kg)	159.7		

standard error of the mean.

2.3.3 Offspring Costs and Returns

Offspring costs and returns were calculated in three separate growth stages:

- 1. from birth to weaning (piglet stage);
- 2. from weaning to transfer (weaner stage);
- 3. from transfer to slaughter (grower stage).

Litter sizes and pre-weaning mortality percentages were input variables for each parity. Birth weights for first, second, third and later parities were 1.38, 1.41, 1.42 and 1.46 kg per piglet. Average daily gains and daily feed intakes in the first two stages of growth were model inputs (Table 2.4).

Table 2.4 Simulated average performance of growing pigs (base level), assuming $Pd_{max} = 140 \text{ g/day}$, DEi = 30.6 MJ/day and $R_{min} = 1.0$

Trait	Growth Stage					
	1	2	3	Overall 1		
Average Daily Gain (g/day)	210	450	844	629		
Feed Intake (g/day)	70	1200	2186	1538		
Number Days	28	28.2	78	134.2		
Feed Conversion Ratio (kg/kg gain)	0.33	2.67	2.59	2.43		
Slaughter Weight (kg/pig)				65.06		
Carcass Yield (%)				75.80		
Average Carcass Backfat (mm)				16.75		
Average Carcass Price (\$/pig)				174.00		
Average Price/Kg Carcass (\$/pig)				2.67		
Gross Margin per Pig (\$/pig)				38.35		
Gross Margin per Pig Place per				177.19		
Year (\$/pig place/year)						

Birth to slaughter.

Numbers of pigs transferred and slaughtered were calculated by accounting for the weaning to transfer and transfer to sale mortality set at 1.5% each. The combined weaning to sale mortality was equal to 2.98%. Number of days in the first growth stage was equal to the length of lactation, and the average number of days in the weaner stage was calculated as a difference between transfer weight and weaning weight, divided by the average daily gain for that growth stage. The

length of the third growth stage was obtained as an output from the pig growth model simulation. Total offspring days were calculated by multiplying the proportion of sows retained from the previous parity by the number of pigs produced and the length of each growth stage. For the proportion of pigs that died during stages 2 and 3 of growth, only half of the feed and non-feed costs were counted. It was assumed that pre-weaning mortality occurred mainly in the first few days after birth and the dead piglets did not significantly contribute to overall feed and non-feed costs.

The following components were included in calculation of offspring costs:

- (a) non-feed costs (annual housing depreciation, opportunity cost of capital, labour per growing pig place, health, administration, repairs and maintenance, cost of power and general expenses). The non-feed costs per growing pig were excluded from the first stage of growth (being part of the sow non-feed costs in the farrow to wean stage), with the exception of the cost of health, which was calculated for the whole growth stage (birth to slaughter) on a per pig per day basis. Daily cost per pig place was multiplied by the number of grower days in each of the weaner and grower stages;
- (b) feed costs (calculated separately for each growth stage as a total feed intake (kg) multiplied by the cost per kg of creep, weaner or grower diet and adjusted by the feed wastage factor);
- (c) marketing costs per pig sold (Pork Industry Board levy, Federated Farmers levy, meat inspection and freight).

Pigmeat returns were calculated from a polynomial function (Figure 2.2) that predicted average carcass value (AVCP) from carcass weight and backfat (Equation in Appendix B). The polynomial function, with the adjusted coefficient of determination (r^2) maximised at 0.91, was obtained by weighted

regression of the dollar values of carcasses against carcass weight and backfat depths from 12,053 slaughter records obtained between 1989 and 1990. The data represented payment schedules from major New Zealand pig markets (37 abattoirs located in Auckland, lower North Island and Canterbury areas).

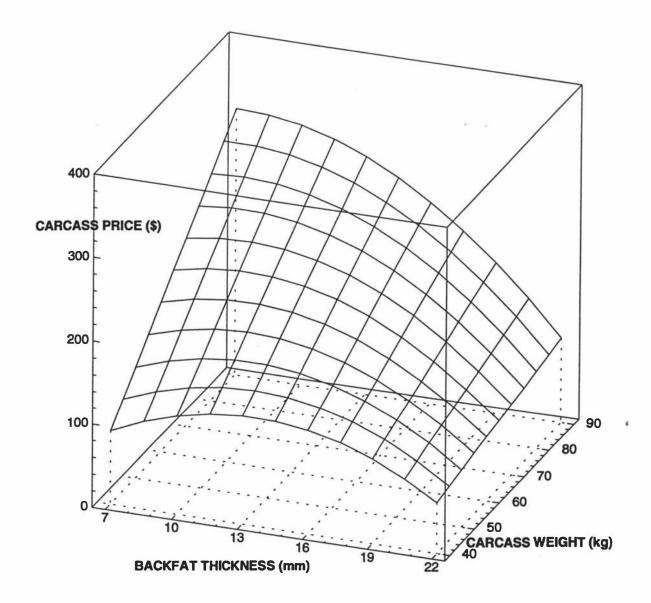


Figure 2.2 Effect of carcass weight and backfat thickness on carcass price (from polynomial regression).

The average price per kg of bacon carcass (AVPKG) was calculated, dividing AVCP by the estimated mean carcass weight. The minimum price per

kg of bacon carcass was set to the price paid per kg of cull sow carcass, based on the 1990 New Zealand carcass schedules. An aggregated offspring life cycle return was obtained from the total number of slaughter pigs produced multiplied by the average bacon carcass price.

The combined life cycle profit from gilts, sows and their offspring was converted to an Annualised Present Value (APV), to account for time preference for consumption (Chisholm and Dillon, 1971; Smith, 1978). Equations for calculation of the APV are given in Appendix A.

2.3.4 Simulation of Pig Growth

The growth model predicted daily deposition of whole-body protein and lipid for pigs between 20 and 85 kg liveweight. The output from pig growth simulation was used to calculate average daily liveweight gain, daily feed intake, feed conversion ratio, carcass weight, and backfat thickness at slaughter (Table 2.4), and to generate offspring costs and returns in the third stage of growth (from transfer to slaughter).

Growth model input variables included the genotype of a pig for Pd_{max} , DEi and R_{min} . Additional input included body lipid content at the start of growth simulation and type of grower diet in terms of digestible energy density, crude protein content, apparent ileal digestibility of nitrogen and chemical score. Initial (transfer) and slaughter weights were also supplied.

The daily ad libitum DEi was specified as a function of pig liveweight (W), calculated at the end of the previous day of growth. The base level of DEi was calculated, using equation [2.1] developed by Smith and Pearson (1986), which represented average intake levels for most common New Zealand breeds of pigs:

$$DEi = 4.21*W^{0.507}$$
 [2.1]

Ad libitum daily feed intake (DFI) was calculated dividing daily DEi by the digestible energy density of the diet (DEd). At lower liveweights (below 35 kg), where feed intake may be limited by gut capacity, the DFI was calculated, using equation [2.2] (Moughan, 1986):

$$DFI = (0.046*W + 0.40).$$
 [2.2]

Five distinct genetic levels of DEi were simulated by changing the base DEi (equation [2.1]) by +20%, +10%, 0%, -10% and -20%. The DFI in equation [2.2] was also changed by similar percentages.

A $5 \times 5 \times 5$ factorial design was used to simulate pig production over a wide range of pig genotypes. Five levels of Pd_{max} (in equal steps from 120 to 200 g/day) were used in combination with five levels of DEi and five levels of R_{min} (ranging from 0.8 to 2.2). That is, a total of 125 $Pd_{max} \times DEi \times R_{min}$ combinations were simulated.

It was assumed that pig growth was in a thermoneutral, disease-free environment, and a least-cost diet was supplied for each combination of Pd_{max} , ad libitum DEi and R_{min} . Only the one, optimal diet was used over the 20 to 85 kg liveweight range. In commercial practice however, two or more diets may be fed over this weight range. Level of meal wastage for growing pigs was set at 5%. Differences in average maintenance requirements and activity were not taken into account. In practice however, these factors may be variable and heritable (Foster et al., 1983).

Sex of the pig has not been explicitly considered, although its significant influence on the level of Pd_{max} is recognised. Most of the possible genotype-sex combinations were examined by simulating a wide range of pig genotypes.

2.3.5 Diets Used in the Growth Model Simulations

It was recognised that different optimum diets are needed for different levels of Pd_{max} , ad libitum DEi and R_{min} . A wide range of least-cost diets commonly used in intensive commercial pig farming was defined. The diets covered a range of digestible energy densities (DEd) from 12.5 to 14.5 MJ DE/kg, with various dietary lysine concentrations calculated for several combinations of crude protein (CP) concentrations and chemical scores (cs). Chemical score was defined as a minimum ratio of the absorbed amount of a limiting amino acid (g amino acid / kg protein) to the ideal level of that amino acid (Whittemore, 1983). Five levels of DEd (in equal steps from 12.5 to 14.5 MJ DE/kg) were combined with three levels of chemical scores (0.5, 0.6 and 0.7), and three levels of crude protein (16%, 20% and 24%), giving a total of 45 combinations of DEd, CP and cs. Lysine was assumed as a limiting amino acid, with an ideal level for lysine protein synthesis equal to 79.4 mg/g of absorbed protein (Moughan and Smith, 1984b, Moughan et al., 1987). All amino acids other than lysine were provided at "ideal" levels relative to lysine (Agricultural Research Council, 1981). Dietary lysine concentrations and lysine/DEd ratios were obtained for each DEd x CP x cs combination. The DEd, CP, cs and lysine/DEd ratio constraints were used to formulate 45 least-cost diets, using linear programming. Commonly available ingredients, such as barley, maize, wheat, peas, pollard, meat & bone meal, blood meal, fish meal, meat meal, skim milk powder, soya meal, soya oil, and synthetic lysine and methionine were used. Vitamin-mineral premix was added to each diet to meet requirements of the growing pig. Apparent digestible crude protein percentage (CPd%) was

calculated for each diet, based on the ingredient composition of each diet, the crude protein content and the amino acid composition of each ingredient, and the apparent ileal digestibility percentage of each amino acid in each dietary ingredient (Holmes *et al.*, 1980; Moughan and Smith, 1984*a*; Moughan *et al.*, 1987).

The ideal level of each amino acid in the diet was multiplied by the chemical score to obtain a balanced amount of protein (Bp). The balanced protein in the diet was multiplied by the digestible crude protein intake (CPd) to give an "ideal" dietary protein available (Pa) for growth and maintenance.

Following formulation of the least-cost diets, pig growth was simulated for each of the 125 combinations of Pd_{max} , DEi and R_{min} , using nutrient specifications (DEd, CP, cs, lysine/DEd ratio and CPd) of each of the diets. A diet that maximised life cycle profit was selected for each combination.

2.3.6 Growth Model Description

A model simulating the digestion and metabolism of dietary energy and nitrogen in the growing pig was constructed following the approach of Moughan and Smith (1984a) and Moughan et al. (1987).

The chemical composition of the whole-body of the pig at the beginning of the third stage of growth was calculated (Appendix B). Initial empty body weight was 95% of the pig liveweight at transfer (W_0), and the whole-body lipid content for an average young pig was assumed at 15% of the empty body weight.

Daily dietary intake determined the amount of amino acids and protein-free energy supplied, given a nutrient specification of the diet. Simulation of energy

flow and partitioning of nitrogen was used to predict daily rates of whole-body protein (Pd) and lipid (Ld) deposition. Physiological interactions between energy and protein flow were influenced by genetic levels of Pd_{max} , DEi and R_{min} . The daily amount of protein available for growth (Pgr) was calculated, subtracting the daily maintenance protein requirement (Pm) calculated as a function of pig liveweight (W), from the daily amount of "ideal" protein available for growth and maintenance (Pa). The amount of protein that can possibly be deposited (Ppd), given dietary and physiological constraints, was dependent on the genetic level of Pd_{max} and the daily level of Pgr. When the daily amount of Pgr was greater than Pd_{max}, the excess of dietary protein over Pd_{max} was deaminated. The daily level of whole-body protein deposition had to satisfy the constraint R_{\min} applied iteratively. This constraint was only activated, when the calculated ratio of whole-body lipid content to whole-body protein content was smaller than the genetically determined (model input) R_{\min} ratio. In order to meet the R_{\min} constraint, the energy required for lipid deposition was supplied from deamination of dietary protein, and the nitrogen from deamination was excreted in the urine.

The net yield of metabolisable energy from the deamination of imbalanced dietary amino acids (E_1) and the energy yield from the deamination of dietary protein supplied in excess of Pd_{max} constraint (E_2) were calculated and added to the dietary protein-free energy intake (E_{pf}) . This combined energy (E_a) , available for growth and maintenance, was corrected for the energy cost of maintenance (MEm), to give the energy available for growth (E_g) . The energy yield from deamination of protein required for maintenance (Pm) was negligible, compared to other metabolisable energy sources, and was not taken into account. MEm was given as a function of the whole-body protein content (Whittemore, 1983). Assuming the energy content of protein to be 23.6 MJ/kg (Whittemore and Fawcett, 1976), the energy content of the Ppd was calculated and added to the E_g

to give the total dietary energy available for tissue deposition (E_t) . E_t was apportioned between Ld and Pd, based on the R_{min} constraint.

At the end of each day of growth, chemical composition of the whole-body of the pig was calculated, including ash deposition and the whole-body ash content, protein content, lipid content and water content, using equations given by Kotarbinska (1969) and Whittemore (1983) (Appendix B). The empty body weight and liveweight at the end of each day were predicted and the simulation continued until target slaughter liveweight (W_s) was reached.

Average daily liveweight gain (ADG, g/day) was calculated as the sum of weight gained in each of the growth stages, divided by the total number of days from birth to slaughter.

Average backfat (BF, mm), representing a slaughter measurement taken at P₂ position (6.5 cm off the mid-line at the position of the last rib), was estimated using an equation derived by Moughan *et al.* (1987):

$$BF=0.9*L_{s}$$

where L_s is whole-body lipid content at the end of growth.

Average carcass weight (CW) in kg was calculated (Whittemore 1983):

$$CW=0.01*W_s*(65.9 + 0.092*W_s + 0.12*BF).$$

Average feed conversion ratio (FCR), defined as the quantity of feed consumed per kilogram of liveweight gain, was calculated as a total amount of feed consumed (FT) over the third growth stage divided by the total liveweight gain in that period:

$$FCR = FT / (W_s - W_0).$$

Overall performance results for the base level simulation are presented in Table 2.4.

2.4 Discussion

A number of models incorporating nutrient partitioning and simulation of pig growth have been developed (Whittemore and Fawcett, 1976; Whittemore, 1983; Moughan and Smith, 1984a; Moughan et al., 1987; Black et al., 1986; Pomar et al., 1991) to assist efficiency of nutrition and management of pig herds. However, there are few models designed specifically to study economic values of traits in pig breeding (Tess et al., 1983; de Vries, 1989; de Vries and Kanis, 1992).

The major differences between this model and other models used in estimation of economic values of pig traits, are:

1. Inclusion of a biological pig growth model, based on three controlling variables: upper limit to body protein deposition rate (Pd_{max} , g/day), mean daily ad libitum digestible energy intake (DEi, MJ/day), and minimum lipid to protein deposition ratio (R_{min}), as part of the life cycle model. Economic values of Pd_{max} , DEi and R_{min} objective traits were previously estimated for alternative situations by de Vries and Kanis (1992); however, in the context of a growth model rather than a

life cycle model and without separately optimising dietary requirements for each genotype and management situation;

- Use of a wide range of grower diets in pig growth simulation, in recognition that food is the major item of expenditure on the pig unit and different least-cost diets are needed to optimise growth in various pig genotypes;
- 3. Calculation of the overall life cycle profit (see also Tess *et al.*, 1983 and de Vries, 1989), but accounting for time preference of consumption, by discounting the value of future net returns.
- 4. The method of calculation of economic values of growth performance traits, as partial derivatives of a polynomial profit equation. This equation was estimated by multiple regression analysis relating life cycle profit to controlling variables.

The assumptions and variables used in this model were based on commercial pig production field data and experimental results from scientific literature. A similar version of the growth simulation model had been previously evaluated in experimental field trials (Moughan and Smith, 1984a; Moughan, 1985; Moughan et al., 1987, de Greef et al., 1992b). The growth model predictions, particularly in terms of protein deposition rate and liveweight gain, were found to closely resemble those found in the field (de Greef et al., 1992b).

The genetic variability in growth performance and feed consumption for pigs under 20 kg was assumed to have small effect on the estimation of economic values of traits and was not simulated in this study. Whittemore *et al.* (1978) found that the proportion of protein in the empty body of young weaned pigs was independent of the proportion of lipid, and was not significantly affected by the

age of the pig, type of the diet, level of nutrient intake, or the weaning process. However, the proportion of lipid in the empty body was strongly influenced by the above factors, which was confirmed by Campbell and Dunkin (1983), Tess et al. (1986) and Smits et al. (1988). The variability in the initial whole-body lipid content (L_0) was accommodated by applying three categories of weaner body condition. The same approach was recommended by Whittemore (1983) and applied by Moughan et al. (1987). Based on the findings of Zhang et al. (1986), the effect of L_0 on growth performance and carcass characteristics at slaughter liveweights was expected to be minor.

The present model was used to simulate a wide range of possible pig genotypes and estimate economic values of their reproduction and growth performance traits. Several performance parameters, not associated directly with the estimation of economic values, were calculated to help calibrate the model output.

The simulation model provided predictions of growth performance, such as average daily gain (ADG, g/day, birth to slaughter), backfat thickness taken at P_2 position (BF, mm, measured at slaughter) feed conversion ratio (FCR, kg of feed consumed per kg of liveweight gain), and average *ad libitum* daily feed intake (DFI, g/day, for pigs growing from 20 kg to slaughter). These performance factors are consequences of the animal genotype and the present production circumstances. They can be used as selection criteria and measured on performance-tested pigs, but their levels are determined by interactions between the underlying genetic traits of Pd_{max} , DEi and R_{min} and the environmental circumstances of the production system.

The linear/plateau relationship between protein deposition and energy intake, applied in the simulation of pig growth, was based on the research work of Kielanowski (1969), Whittemore and Fawcett (1976) and Whittemore (1983).

Moughan and Verstegen (1988) reviewed studies in which Pd_{max} was assumed to range between 90 and 190 g/day and was dependent on sex, genotype and strain of pigs. Observations of Campbell and Taverner (1988) and Rao and McCracken (1991, 1992) confirmed the linear response in protein/lean tissue deposition to increasing energy intake. They found that the intense selection for growth performance under *ad libitum* feeding in pigs of high genetic potential had raised the Pd_{max} above 200 g/day and beyond the upper limit of appetite. Siebrits *et al.* (1986) found a curvilinear relationship between protein deposition and liveweight under *ad libitum* conditions and dependent on the animal's sex and genotype. In the present model, a constant Pd_{max} was used for pigs of defined sex and genotype growing over the 20 to 85 kg liveweight range. This approach is supported by the results of recent experiments of Whittemore *et al.* (1988) and Rao and McCracken (1991).

Several research studies adopted the minimum lipid to protein deposition ratio of 1:1, assuming that the rate of lipid deposition can not be lower than the rate of protein deposition (Kielanowski, 1966; Whittemore and Fawcett, 1976; Fowler, 1978; Moughan et al., 1987). However, for some improved strains of pigs, entire males in particular, R_{\min} may be lower than 1:1 (Whittemore, 1983; de Vries and Kanis, 1992). The experiment of Kyriazakis and Emmans (1992) found no minimum lipid to protein ratio at low levels of energy intake accompanied by a high level of protein intake. In the present model, pig growth was simulated with R_{\min} ranging from 0.8 to 1.2. The genetically determined level of R_{\min} was assumed constant throughout the liveweight range of 20 to 85 kg. However, the results of an experiment conducted by de Greef et al. (1992b) suggest that R_{\min} increases with weight. Recently, it was also found that nutritional history may influence the relation between lipid and protein deposition (de Greef et al., 1992a), and a nutrition-induced increase in lean tissue deposition rate may cause a substantial increase in body fatness (de Greef and Verstegen, 1993).

It is commonly accepted that voluntary feed intake is primarily determined by the capacity of the animal to utilise nutrients, but it may be restricted by gut capacity when diets containing low concentrations of digestible energy are fed. The amount of daily feed consumed and its quality determines the availability of protein and energy necessary for pig growth and maintenance. An ad libitum feed intake curve was not predicted within the model of Moughan et al., (1987), because of the likely differences in ad libitum digestible energy intake between individual pig farms. The model of Black et al., (1986) predicted voluntary feed intake from the potential capacity of an animal of specified genotype and physiological state to utilise metabolisable energy. In the present model, daily ad libitum feed intake was specified as a function of liveweight. Voluntary feed intakes appear to show significant genetic differences both between and within breeds (Agricultural Research Council, 1981; Smith and Pearson, 1986, 1987; Chadd and Cole, 1988, 1989; Cole and Chadd, 1989). Several environmental factors may affect the voluntary feed intake of pigs, including type of diet, health of animals, environmental temperature, accommodation and degree of competition.

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Calculation of pigmeat returns should reflect the carcass classification system used by a specific pig industry. For example, the model of de Vries (1989) incorporated a Dutch grading system based on estimated lean meat percentage. The growth model of Moughan *et al.*, (1987) apportioned the simulated population of pig carcasses to three grades (prime, choice and standard) around the predicted average value of backfat. The model described here uses a polynomial function, based on a distribution of pig carcasses over a matrix of carcass weight and backfat thickness categories, as determined by the present New Zealand pig carcass classification scheme.

A life cycle production model allows derivation of economic values for both reproductive and growth performance traits. One of the objectives of this study was to better understand the biology and economics of animal production through the design and practical application of a simulation model. Biological and economic parameters assumed in the model represent current New Zealand production circumstances. However, future changes in understanding of pig growth, as well as changes to financial objectives, product values and management systems will require modifications to the basis of the model.

2.5 References

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2.6 Appendix A. Essential equations in the life cycle simulation model

2.6.1 Gilt and sow costs and returns

GAM = GAO + 21*(OE - 1) RGD = GAM - GAP + XD RGTD = NRG*RGD*[1 - 0.5*(RGCUL + RGM)] RGC = RGTD*[RGFI*SFP + RGNF*DSNF] + NRG*(RGPC + RGCUL*MC)

NG = NRG*[1 - RGCUL - RGM] $GTD = NG*[LG*(1 - 0.5*GM) - GCUL*(LG - SCT_2)]$ GC = GTD*[GFI*SFP + GNF*DSNF] + NG*GCUL*MC

$$\begin{split} & \text{SD}_{i} = \text{LL} + \text{IWO} + \text{LG} + \text{XD}_{i} \\ & P_{i=I} = \text{NG*}(1 - \text{GCUL} - \text{GM}) \\ & P_{i+I} = P_{i}*(1 - \text{SCUL}_{i} - \text{SM}) \\ & \text{SC}_{i} = P_{i}*\{[\text{SD}_{i}*(1 - 0.5*\text{SM}) - 0.5*\text{SCUL}_{i}*((\text{SD}_{i} - \text{LL} - \text{SCT}_{1}) \\ & + (\text{SD}_{i} - \text{LL} - \text{IWO} - \text{SCT}_{2}))]*(SF*SFP + \text{DSNF}) \\ & + \text{LL*}(\text{SFL}_{i} - \text{SF})*\text{SFP} + \text{SCUL}_{i}*\text{MC}\} \end{split}$$

GR = [NRG*RGCUL*(RGPW + 0.5*RGD*RGGR) + NG*GCUL*(RGPW + RGD*RGGR + SCT₂*GGR)]*DP*SCP

 $SR_i = [P_i * SCUL_i * \{SWW_i + 0.5 * SGR_i * (SCT_1 + IWO + SCT_2)\}] * DP * SCP$

2.6.2 Offspring costs and returns

$$\begin{split} \text{NW}_i &= \text{NBA}_i * (1 - \text{PWM}_i) \\ \text{NP}_i &= \text{NW}_i * (1 - \text{M2}) \\ \text{NSP}_i &= \text{NP}_i * (1 - \text{M3}) \\ \text{WD}_i &= (W_0 - \text{BW}_i - \text{LL*ADG}_1 * 10^{-3}) * 10^3 \text{ / ADG}_2 \\ \text{OC}_i &= P_i * \{ \text{NW}_i * \text{LL*}(\text{FI}_1 * (1 + \text{FW*}10^{-2}) * \text{CFC} + \text{DPH}) \\ &\quad + \text{NW}_i * \text{WD}_i * (1 - 0.5 * \text{M2}) * (\text{FI}_2 * (1 + \text{FW*}10^{-2}) * \text{WFC} + \text{DCP} + \text{DPH}) \\ &\quad + \text{NP}_i * T * (1 - 0.5 * \text{M3}) * (* \text{PFC*} * (1 + \text{FW*}10^{-2}) * \text{FT} \text{ / } T \\ &\quad + \text{DCP} + \text{DPH} + \text{NSP}_i * \text{MC} \} \end{split}$$

 $OR_i = P_i * NSP_i * AVCP$

2.6.3 Calculation of Annualised Present Value

To calculate the decrease in value of the future net returns, the net parity returns (NETR_i) were adjusted by an annual discount factor (DF), raised to the power of AJ_n (Chisholm and Dillon, 1971). The Annualised Present Value (APV) for the whole life cycle was derived by multiplying Aggregated Net Present Value (ANPV) by the life cycle amortisation factor (AMF), (Smith, 1978):

NETR₁ = GR + SR₁ + OR₁ - RGC - GC - SC₁ - OC₁
NETR_{i>I} = SR_i + OR_i - SC_i - OC_i
INT = (ARI - ARF) / (1 + ARF)
DF = 1 / (1 + INT)
AJ_i =
$$\sum_{i=1}^{i} \{ SD_i / 365 \}$$

AMF = INT / (1 - (1 + INT)^{-AJ_n})

$$ANPV = \sum_{i=1}^{n} \{DF^{AJ_i} * NETR_i\}$$

$$APV = ANPV * AMF$$

2.7 Appendix B. Growth model equations

2.7.1 Calculation of the chemical composition of the whole-body of the pig at the start of the third stage of growth

$$L_0 = BC*WE_0$$

 $PT_0 = 0.134*(WE_0 - L_0)^{1.120}$
 $A_0 = 0.03*WE_0$
 $G_0 = 0.05*W_0$
 $WA_0 = W_0 - (L_0 + PT_0 + A_0 + G_0)$

2.7.2 Simulation of energy flow and partitioning of nitrogen for each day of growth to predict daily protein and lipid deposition

$$CPd = DFI*CPd\%*10^{-2}$$
 $Pa = CPd*Bp*10^{-3}$
 $Ne = (CPd - Pa) / 6.25$
 $E_1 = 72*Ne*10^{-3}$
 $E_{pf} = DEi - (23.6*CPd*10^{-3})$
 $Pm = 0.17*W^{0.75}*6.25$
 $Pgr = Pa - Pm$
If $Pgr > Pd_{max}$, $Ppd = Pd_{max}$

If
$$Pgr < Pd_{max}$$
, $Ppd = Pgr$

If
$$Pgr > Pd_{max}$$
, $Nur = (Pgr - Ppd) / 6.25$

$$E_2 = 72*Nur*10^{-3}$$

$$E_{\rm a} = E_{\rm pf} + E_1 + E_2$$

$$MEm = 1.85*PT^{0.78}$$

$$E_{\rm g} = E_{\rm a} - {\rm MEm}$$

$$E_{\rm pr} = 23.6 * \rm Ppd * 10^{-3}$$

$$E_{\rm t} = E_{\rm g} + E_{\rm pr}$$

$$Pd = Ppd$$

Pd has to satisfy the constraint R_{\min} applied iteratively:

If
$$R_{\text{min}} > L / PT$$
 and $R_{\text{min}} > Ld / Pd$, $Pd = Pd - 1$

$$MEp = ep*Pd$$

$$MEl = E_t - MEp$$

$$Ld = MEl / el$$

2.7.3 Simulation of growth for each day until a specified slaughter liveweight is reached

$$Ad = 0.21*Pd$$

$$A_s = A_0 + \sum_{T=1}^{T} A_0 d^* 10^{-3}$$

$$PT_s = PT_0 + \sum_{T=1}^{T} Pd*10^{-3}$$

$$L_{\rm s} = L_0 + \sum_{T=1}^{T} L d*10^{-3}$$

$$WA_s = 4.9*PT_s^{0.855}$$

$$WE_s = A_s + PT_s + L_s + WA_s$$

$$W_{\rm s} = 1.05 * WE_{\rm s}$$

2.7.4 Calculation of average daily gain (ADG), backfat thickness (BF), carcass weight (CW), feed conversion ratio (FCR) and average price per carcass (AVCP), over the growth period

ADG₃ =
$$(W_s - W_0) / (T*10^{-3})$$

ADG = $(ADG_1*LL + ADG_2*WD + ADG_3*T) / (LL + WD + T)$
BF = $0.9*L_s$
CW = $0.01*W_s*(65.9 + 0.092*W_s + 0.12*BF)$
FCR = FT / $(W_s - W_0)$
AVCP = $-302.49 + 36.58*BF + 6.32*CW - 0.98*BF^2 - 0.25*BF*CW$.

2.8 Appendix C. List of symbols used in the model

 A_0 = initial whole body ash content (kg)

 A_s = whole body ash content at slaughter (kg)

Ad = ash deposition (g/day)

 ADG_1 = average daily gain in growth stage 1 (g/day)

 ADG_2 = average daily gain in growth stage 2 (g/day)

 ADG_3 = average daily gain in growth stage 3 (g/day)

ADG = overall average daily gain from birth to slaughter (g/day)

 AJ_n = length of a life cycle expressed in years

AMF = amortisation factor for life cycle with n parities

ANPV = Aggregated Net Present Value for life cycle with n parities (\$/gilt life cycle)

APV = life cycle Annualised Present Value (\$/gilt life cycle)

ARF = annual rate of inflation expressed as a decimal

ARI = annual rate of interest expressed as a decimal

AVCP = average bacon pig carcass value (\$/pig)

BC = weaner body condition coefficient (0.15)

BF = average backfat thickness (mm), representing a slaughter measurement taken at P_2 position

Bp = balanced protein in the diet (g/kg protein)

 $BW_i = birth$ weight per piglet in parity i (kg)

CFC = creep feed cost (\$/kg)

CP = dietary crude protein percentage (%)

CPd = digestible crude protein intake (g/day)

CPd% = apparent digestible crude protein in the diet (%)

cs = chemical score (minimum ratio of an absorbed amount of an amino acid to the ideal level of that amino acid)

CW = pig carcass weight at slaughter (kg)

DCP = daily total cost per growing pig place (weaning to slaughter) (excludes cost of pig health), (\$/day)

DEd = digestible energy density of the diet (MJ/kg)

DEi = mean daily ad libitum digestible energy intake (MJ/day)

DF = annual discount factor

DFI = daily feed intake in growth stage 3 (g/day)

DP = carcass yield (dressing percentage) of sows (gilts) expressed as a decimal

DPH = average daily cost of health per growing pig (birth to slaughter) (\$/pig)

DSNF = daily sow non-feed costs (\$/sow/day)

 E_1 = energy yield from deamination of imbalanced dietary amino acids (MJ ME/day)

 E_2 = energy yield from deamination of amino acids supplied in excess of the Pd_{max} potential (MJ ME/day)

 E_a = energy available for growth and maintenance (MJ ME/day)

 E_g = energy available for growth (MJ ME/day)

el = energy cost of depositing one gram of lipid (0.053 MJ ME/g 1)

ep = energy cost of depositing one gram of protein (0.053 MJ ME/g 1)

 $E_{\rm pf}$ = protein-free energy intake (MJ ME/day)

 E_{pr} = energy content of the protein which can be possibly deposited (MJ ME/day)

 $E_{\rm t}$ = total energy to be apportioned to the deposition of lipid and protein (MJ ME/day)

FCR = feed conversion ratio in growth stage 3 (kg feed / kg liveweight gain)

 FI_1 = average daily feed intake per piglet in growth stage 1 (g/day)

 FI_2 = average daily feed intake per weaner in growth stage 2 (g/day)

FT = total feed intake in growth stage 3 (kg/pig)

FW = feed wastage (%)

 $G_0 = \text{gut-fill at transfer (kg/pig)}$

GAM = gilt age when first mated (days)

GAO = gilt age at first oestrus (puberty, days)

GAP = gilt age when purchased (days)

GC = total mated gilt cost (\$/gilt life cycle)

GCUL = mated gilt culling rate expressed as a decimal

GD = number of days from gilt conception to farrowing (days)

GFI = mated gilt daily feed input (kg/day)

GGR = mated gilt growth rate (g/day)

GM = mated gilt mortality rate expressed as a decimal

GNF = proportion of daily sow non-feed costs, assumed at 0.25 for mated gilts

GR = total returns from selling culled replacement and mated gilts (\$/gilt life cycle)

GTD = total mated gilt days (days)

i = parity number

INT = inflation adjusted interest rate expressed as a decimal

IWO = weaning to oestrus interval (days)

¹ Taken from Pullar and Webster (1977)

 L_0 = initial whole body lipid content (kg/pig)

 L_s = whole body lipid content at the end of growth (kg/pig)

Ld = daily whole-body lipid deposition (g/day)

LG = length of gestation (days)

LL = length of lactation (days)

M2 = mortality in growth stage 2 expressed as a decimal

M3 = mortality in growth stage 3 expressed as a decimal

MC = marketing costs per pig sold (levy, freight, inspection) (\$/pig)

MEl = metabolisable energy required for lipid deposition (MJ ME/day)

MEm = metabolisable energy required for maintenance (MJ ME/day)

MEp = metabolisable energy required for protein deposition (MJ ME/day)

n =maximum number of parities

 $NBA_i = number born alive per litter in parity i$

Ne = urinary nitrogen loss (due to imbalanced protein) (g/day)

 $NETR_i = net returns in parity i$ (\$/gilt life cycle)

NG = number of replacement gilts retained for mating

 NP_i = number of grower pigs / litter (after transfer) in parity i

NRG = number of replacement gilts purchased or selected

 NSP_i = number slaughter pigs produced / litter from parity i farrowings

Nur = nitrogen excreted in urine from deamination of dietary protein (g/day)

 NW_i = number pigs weaned per litter in parity i

 $OC_i = offspring costs in parity i (\$/gilt life cycle)$

OE = oestrus number when gilt first mated

 $OR_i = off spring returns in parity i (\$/gilt life cycle)$

Pa = ideal protein available for growth and maintenance (g/day)

Pd = daily whole-body protein deposition (g/day)

 P_i = proportion of sows and litters farrowed in parity i in relation to the number of replacement gilts purchased

PFC = grower feed cost (\$/kg)

Pgr = protein available for growth (g/day)

Pm = protein required for maintenance (g/day)

Ppd = protein that can possibly be deposited, given dietary and physiological constraints (g/day)

 Pd_{max} = upper genetic limit to body protein deposition (g/day)

 PT_0 = initial whole body protein content (kg/pig)

 PT_s = whole body protein content at slaughter (kg/pig)

 PWM_i = pre-weaning mortality in parity *i* expressed as a decimal

RGC = total replacement gilt cost (\$/gilt life cycle)

RGCUL = replacement gilt culling rate expressed as a decimal

RGD = number of days from gilt purchase to conception (days)

RGFI = replacement gilt daily feed input (kg/day)

RGGR = replacement gilt growth rate (g/day)

RGM = replacement gilt mortality expressed as a decimal

RGNF = proportion of daily sow non-feed costs, assumed at 0.30 for replacement gilts

RGPC = replacement gilt purchase cost (\$/gilt)

RGPW = replacement gilt purchase weight (kg/gilt)

RGTD = total replacement gilt days (days)

 R_{\min} = minimum lipid to protein deposition ratio

 $SC_i = sow costs in parity i (\$/gilt life cycle)$

SCP = average cull sow carcass price (\$/kg)

 SCT_1 = average sow culling time after weaning (days)

 SCT_2 = average gilt/sow culling time after first insemination (days)

 $SCUL_i = sow marginal culling rate in parity i expressed as a decimal$

 SD_i = number of days between farrowings in parity i (farrowing interval)

SF = sow daily feed input (basic maintenance and growth) (kg/day)

 $SFL_i = sow feed requirement per day of lactation in parity i (kg/day) including feed wastage$

SFP = average sow feed price (\$/kg)

 $SGR_i = sow growth rate after weaning in parity i (g/day)$

SM = average sow mortality rate per parity expressed as a decimal

 $SR_i = \text{sow returns in parity } i \text{ (\$/gilt life cycle)}$

 $SWW_i = sow$ weight at weaning in parity i (kg/sow)

T = number of days in growth stage 3 (transfer to slaughter, days)

W = body weight at the end of one day of growth (kg)

 $W_0 = \text{pig liveweight at transfer (kg/pig)}$

 $W_s = pig liveweight at slaughter (kg/pig)$

 WA_0 = initial whole body water content (kg/pig)

 WA_s = whole body water content at slaughter (kg/pig)

 $WD_i = \text{number of days in growth stage 2 in parity } i \text{ (days)}$

 WE_0 = initial empty body weight (kg/pig)

 $WE_s = \text{empty body weight at slaughter (kg/pig)}$

WFC = weaner feed cost (\$/kg)

XD = extra days open due to oestrus problems and remating (days).

CHAPTER 3

ECONOMIC VALUES OF TRAITS FOR PIG IMPROVEMENT.

II. ESTIMATES FOR NEW ZEALAND CONDITIONS

Accepted for publication in Australian Journal of Agricultural Research

3.1 Abstract

A computer model simulating life cycle production of a breeding sow and growth performance of her offspring was used to estimate economic values of reproduction and growth performance traits. The model simulated digestion and metabolism of dietary energy and nitrogen in growing pigs (20 to 85 kg), based on the linear/plateau relationship between daily protein deposition and digestible energy intake.

Economic values (EV's) of reproduction and growth performance traits were calculated by simulating effects of genetic changes in several biological components, in a farrow-to-finish production system, assuming *ad libitum* feeding. EV's were calculated per gilt life cycle, for a wide range of pig genotypes, assuming the upper limit to body protein deposition rate (Pd_{max}), mean daily *ad libitum* digestible energy intake (DEi) and minimum lipid to protein deposition ratio (R_{min}) as the major genetic determinants of pig growth.

Results demonstrated economic values of traits depended on the average genetic merit in the pig herd and its interaction with the management circumstances (level of feeding, nature of the diet, life cycle length) of the production system.

Unimproved genotypes, with Pd_{max} below 140 g/day and DEi levels exceeding 30 MJ/day, had positive EV's for Pd_{max} , with 1 g/day improvement worth between \$12 and \$22 per gilt life cycle, negative EV's for DEi ranging from \$-20 to \$-123 per 1 MJ/day increase, and negative EV's exceeding \$-500 per unit increase in R_{min} . EV's for Pd_{max} had lower values for improved genotypes (below \$14 per unit increase) and became zero at high Pd_{max} levels exceeding 180 g/day, when full expression of Pd_{max} was restricted by

insufficient digestible energy intakes. These improved genotypes had positive economic values for DEi and negative EV's for R_{\min} . For genotypes with sufficient amounts of metabolisable energy available for lipid deposition to exceed that required by R_{\min} , rates of protein deposition were not affected and the EV for R_{\min} became zero. Pigs with high Pd_{\max} and low DEi capacity were lean, but slower growing. On the other hand, genotypes with lower Pd_{\max} potentials and high voluntary feed intakes had excess energy diverted to fat and in practice would be fed restricted diets.

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In practice, it is not currently possible to obtain reliable estimates of breeding values (BV's) for Pd_{max}, DEi and R_{min}. Accordingly, economic values were calculated for those traits for which BV's are routinely available, such as average daily gain (ADG), backfat thickness (BF) and ad libitum daily feed intake (DFI), and for several reproduction traits. EV's for ADG were positive in all studied genotypes (\$1.1 to \$5.0 per 1 g/day increase), negative for BF (\$-51 to \$-118 per 1 mm increase) and negative for DFI (\$-0.2 to \$-0.9 per 1 g/day increase). Number born alive/litter (NBA) had high EV's for improved genotypes, exceeding \$70 per 1 extra pig. Unimproved genotypes had EV's for NBA below \$12 per extra pig. Relatively low, negative EV's were found for one unit increase in other reproduction traits: gilt age at first oestrus (GAO), interval weaning-oestrus (IWO), and pre-weaning mortality percentage (PWM).

Assuming ADG, BF, DFI and NBA as objective traits, the aggregate breeding objective (T) expressed in terms of \$ net profit per gilt life cycle for improved New Zealand pig genotypes can be defined as:

$$T = (2.5*BV_{ADG}) - (74.3*BV_{BF}) - (0.4*BV_{DFI}) + (86.7*BV_{NBA})$$

If BV's for Pd_{max} , DEi and R_{min} can be estimated the breeding objective becomes:

$$T = (4.2*BV_{Pd_{max}}) - (18.6*BV_{DEi}) - (305*BV_{R_{min}}) + (86.7*BV_{NBA})$$

Keywords: Pigs, growth, reproduction, breeding objective, selection criteria, economic values.

3.2 Introduction

The primary objective of a pig improvement programme is to increase profit. Growth performance and carcass quality traits, known to respond well to selection, have traditionally been included in the breeding objective, being moderately to highly heritable and of economic significance (e.g. Morris et al., 1978). Other lower heritability traits such as litter size, age at puberty, number of pigs weaned and litter weight at weaning, may be included in the breeding objective for dam lines. Given a defined breeding objective, a decision is required as to which characters will be measured to predict the genetic merit (breeding values) for the traits in the objective. These measured characters are called selection criteria and the present New Zealand on-farm performance testing programme includes average daily gain (ADG, g/day) from birth to test day at 70 to 90 kg liveweight, and ultrasonically measured backfat depths (BF, mm) obtained immediately prior to selection. Pigs are typically group fed and individual daily feed intakes (DFI) are not available.

Relative economic values for traits in the breeding objective are required for the construction of an economic index used to predict aggregate merit for the objective. Traits assumed to be the major genetic determinants of pig growth:

upper limit to body protein deposition rate (Pd_{max} , g/day), mean daily *ad libitum* digestible energy intake (DEi, MJ/day), and minimum lipid (Ld) to protein (Pd) deposition ratio (R_{min}), as well as several reproductive traits, including number born alive per litter (NBA), are part of an ideal breeding objective for a pig improvement programme.

Currently, it is not known how to predict genetic merit for R_{\min} , DEi and Pd_{\max} using, for example, ADG, DFI and BF. Nevertheless, it is possible to ascertain the relative economic values (REV's) for these traits. Experiments have been carried out between breeds and between lines of pigs within a breed to demonstrate that DEi and Pd_{\max} have been modified by selection (McPhee, 1985; Siebrits *et al.*, 1986; Smith *et al.*, 1991).

Pig improvement programmes routinely include prediction of genetic merit for ADG and BF. Unfortunately, the consequences of selection (and the genetic parameters) vary according to whether *ad libitum* or restricted feeding are practised. This can lead to undesirable changes as a result of selection, such as reduced appetite (Webb, 1989; Smith *et al.*, 1991). Nevertheless, REV's are required for these traits until such a time as procedures are developed for routine evaluation of individual pig merit for Pd_{max} , DEi and R_{min} .

The objective of this study was to estimate economic values of reproduction and growth performance traits influencing income and expenditure in the commercial pig production system. Effects of a wide range of Pd_{max} , DEi and R_{min} levels on profitability are discussed, and economic values of traits are presented for several pig genotypes.

3.3 Methods and Results

3.3.1 Strategy

Economic values of reproduction and growth performance traits were derived for a wide range of pig genotypes, using a computer model (Skorupski *et al.*, 1995) simulating life cycle pig production. This study investigated 125 pig genotypes represented by different combinations of the three major genetic control variables of pig growth: Pd_{max} , DEi and R_{min} . A $5 \times 5 \times 5$ factorial design was used to combine five levels of Pd_{max} (in equal steps from 120 to 200 g/day) with five levels of DEi (ranging from 24 to 36 MJ/day) and five levels of R_{min} (ranging from 0.8 to 1.2). The least-cost diet that maximised life cycle profit was selected from 45 available diets for each of the 125 combinations.

The life cycle profit calculated for each of the simulated genotypes was expressed in the form of an Annualised Present Value (APV). That is, net parity returns were adjusted by an annual discount factor (DF), to allow for a decrease in value of the future net returns (Chisholm and Dillon, 1971). DF was calculated using an equation:

$$DF = 1 / (1 + INT)$$

where INT is an inflation adjusted interest rate (Smith, 1978) assumed to be 4.67%.

3.3.2 Economic values for genetic growth control variables: Pd_{max} $DEi \ and \ R_{min}$

Multiple regression analysis of data obtained from these 125 simulations was used to derive the least-squares response surface for the APV₁ as a function of the three genetic control variables (equation [3.1]). The best fit equation incorporated linear, quadratic and interaction terms. The coefficient of determination (r^2) adjusted for degrees of freedom was maximised at 0.85.

$$APV_1 = -540.37 + 23.99*Pd_{max} + 93.30*DEi - 2564.35*R_{min} - 0.09*Pd_{max}^2$$
$$-3.61*DEi^2 + 0.46*Pd_{max}*DEi*R_{min}$$
[3.1]

Economic value for each growth performance trait in each of the 125 simulated genotypes was calculated as the partial derivative of APV₁ with respect to that trait, evaluated at the average values of growth traits for that particular genotype. Mean levels of Pd_{max} , DEi and R_{min} and economic values (EV's) for a small selection of unimproved and improved pig genotypes are in Table 3.1.

Genotypes 1 and 2 represent unimproved pig genotypes with low Pd_{max} levels, below 140 g/day, and DEi levels exceeding 30 MJ/day. High EV's for Pd_{max} were found for these genotypes, with 1 gram per day improvement in Pd_{max} worth between \$16 to \$19 per gilt life cycle. These genotypes had negative economic values for DEi, with an increase of 1 MJ/day changing the gilt life cycle profit by \$-60 to \$-67. EV's for R_{min} were negative. However, at high DEi levels exceeding 33 MJ/day, there was no change in profit due to change in R_{min} (within the simulated range of 0.8 to 1.2). These genotypes had sufficient amounts of energy available at all stages of growth, to meet the R_{min} constraint without affecting rates of protein deposition.

Table 3.1 Economic values (\$ / gilt life cycle) for growth performance and reproduction traits, calculated for a range of unimproved (1 to 2) and improved (3 to 9) pig genotypes

Phenotypic standard deviations ($\hat{\sigma}_p$) assumed for growth performance traits

Genotype	M	lean gen	etic leve	els of per	forman	ce	Economic values (\$ / gilt life cycle)									
	in selected population						Growth performance traits						Reproduction traits ¹			
	Pd_{max}	DEi	R_{\min}	ADG	BF	DFI	Pd_{max}	DEi	R_{min}	ADG	BF	DFI	NBA	PWM	IWO	GAO
	(g/day)	(MJ/d)	(ratio)	(g/day)	(mm)	(g/day)	(g/day)	(MJ/d)	(ratio)	(g/day)	(mm)	(g/day)	(pigs)	(%)	(days)	(days)
$(\hat{\sigma}_{p})$:	15	2.5	0.1	43	2.3	170										
1	120	30.0	1.0	590	18.6	2397	16.3	-67.1	-898.5	2.8	-94.4	-0.6	11.8	-1.5	-0.5	-0.1
2	120	30.5	1.2	599	19.3	2179	19.4	-59.9	-868.0	2.8	-103.5	-0.4	7.1	-0.9	-0.2	0.0
3	140	30.6	1.0	629	16.8	2186	13.1	-62.5	-578.9	3.0	-86.2	-0.5	48.7	-6.0	-2.6	-0.3
4	160	33.3	0.8	676	16.3	2564	7.6	-87.7	-93.4	4.0	-67.6	-0.8	55.4	-6.9	-3.0	-0.4
5	180	24.2	0.9	567	12.2	1729	1.8	-6.1	-546.0	1.4	-78.8	-0.3	85.1	-10.6	-4.7	-0.6
6	180	27.1	1.0	625	13.2	1935	4.2	-18.6	-305.0	2.5	-74.3	-0.4	86.7	-10.8	-4.8	-0.6
7	180	30.0	1.0	669	14.0	2224	5.6	-39.8	-60.5	3.4	-66.2	-0.6	84.1	-10.4	-4.6	-0.6
8	200	24.2	1.1	549	14.1	1730	0.5	20.6	-319.6	1.2	-90.5	-0.2	72.7	-9.0	-4.0	-0.5
9	200	27.1	1.0	627	13.3	1936	0.7	-9.4	-53.3	2.5	-74.2	-0.4	87.2	-10.8	-4.8	-0.6

¹ Mean genetic levels for reproduction traits (all genotypes): NBA = 10.8 pigs/litter, PWM = 13.1%, IWO = 7 days, GAO = 200 days.

Genotypes 3 and 4, with Pd_{max} levels ranging from 140 to 160 g/day, represent intermediate levels of growth performance, achievable by improved, contemporary New Zealand Large White, Landrace and Duroc breeds at the commercial level of production. A 1 g/day increase in Pd_{max} had positive economic values ranging from \$8 to \$13 per gilt life cycle. Negative economic weights were found for DEi, with values ranging from \$-63 to \$-88 per 1 MJ/day increase. EV's for R_{min} were negative and dependent on the amount of available energy (DEi).

Genotypes 5 to 9 represent current 'nucleus level' growth performance, with Pd_{max} levels exceeding 170 g/day and DEi's below 30 MJ/day. These genotypes had low EV's for Pd_{max} trait, which became zero when full expression of Pd_{max} was restricted by insufficient digestible energy intakes, combined with R_{min} 's exceeding 0.9. EV's for moderate-to-low DEi's (27 to 29 MJ/day), calculated for genotypes with high $Pd_{max} > 180$ g/day and $R_{min} \ge 1$, were close to zero. Further decrease in DEi had a negative effect on profitability, with EV's for that trait becoming positive (genotype 8). R_{min} EV's for high Pd_{max} and low DEi genotypes were high and negative. These genotypes were not able to reach their Pd_{max} genetic potentials, when high Ld to Pd ratio restricted the amount of metabolisable energy available for protein deposition, and the required energy for lipid deposition was gained from deamination of dietary protein. The optimum was reached around $R_{min} = 0.8$, and further decrease in R_{min} had no effect on pig growth and profitability, with EV for R_{min} becoming zero.

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3.3.3 Effect of Pd_{max} DEi and R_{min} on profitability

The effect of different levels of Pd_{max} and DEi on life cycle profitability, for pig genotypes with R_{min} equal to 1.0, is presented in Figure 3.1, based on the least-squares polynomial ($r^2 = 0.96$).

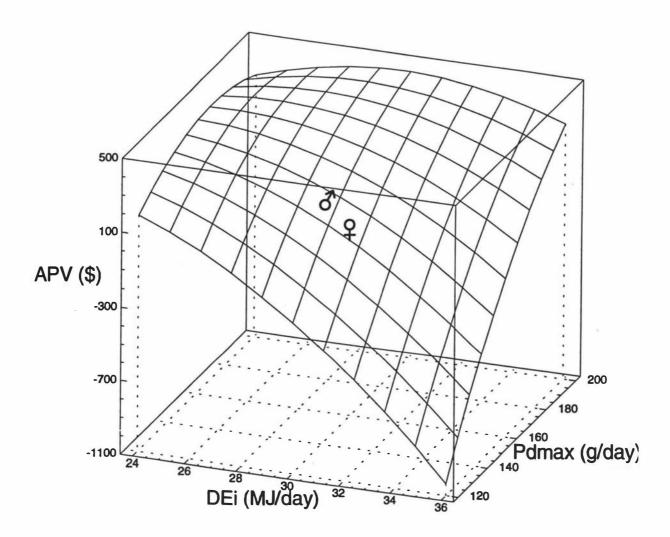


Figure 3.1 Effect of Pd_{max} and DEi on APV (\$ profit / gilt life cycle) for genotypes with $R_{min} = 1.0$. Expected differences in profit between sexes of the same breed of pigs in relation to Pd_{max} and DEi are marked with δ (males) and Φ (females).

Profit was maximised for mean digestible energy intakes ranging from 27 to 29 MJ/day, and high Pd_{max} levels above 160 g/day. At very low DEi's and high Pd_{max} levels exceeding 160 g/day, there were insufficient nutrients available to attain genetic growth potential of pigs. Increasing DEi within this range of Pd_{max} genotypes had a positive effect on profitability. However, when DEi exceeded the optimum feed intake required to meet the maximum protein retention, the oversupply of protein and energy was deposited as body lipid, causing a decrease in profit. The optimum DEi was different for each level of Pd_{max}, and was higher for pigs with high Pd_{max} levels. At low Pd_{max} levels, an increase in DEi capacity produced greater accumulation of body lipid, as a result of extra energy supplied converted into fat, together with energy from deaminated protein. The lowest profit was expected from unimproved pig genotypes with high DEi capacity fed *ad libitum*, and with low Pd_{max} potential.

The improvement in Pd_{max} had the largest effect on profit at low Pd_{max} (below 160 g/day) and high DEi levels. Selection for improved Pd_{max} in genotypes with low DEi's (below 27 MJ/day) and high Pd_{max} levels (over 180 g/day) had no effect on profit, due to a limited energy supply and dearnination of protein to meet the minimum Ld to Pd ratio. The Pd_{max} genetic potential for those pigs could not be fully expressed.

Significant differences are present for Pd_{max} and DEi between different breeds and genetic strains of pigs (Whittemore, 1983; Black *et al.*, 1986; Kalm, 1986; Moughan *et al.*, 1987; Smith and Pearson, 1986 and 1987; Webb, 1989). There is evidence that entire males of the same breed have higher Pd_{max} levels than females (Agricultural Research Council, 1981; Whittemore, 1983; Campbell *et al.*, 1985; Black *et al.*, 1986; Siebrits *et al.*, 1986; Moughan *et al.*, 1987; Whittemore *et al.*, 1988). Entire males were found to have lower intakes than females by about 3% (Cole and Chadd, 1989). The expected differences in Profit between sexes of the same breed of pigs in relation to Pd_{max} and DEi are

marked for the base level simulation with δ (males) and Φ (females) in Figure 3.1.

The effect of Pd_{max} and R_{min} on life cycle profit, for genotypes with intermediate levels of DEi (30 to 30.5 MJ/day), is presented in Figure 3.2 ($r^2 = 0.997$). Decreasing R_{min} had a small, positive effect on profitability, while improvement in Pd_{max} was economically more important in genotypes with low to intermediate levels of Pd_{max} . A plateau in profitability from improvement in Pd_{max} was reached for genotypes with high R_{min} levels ($R_{min} > 1.0$) and Pd_{max} exceeding 180 g/day.

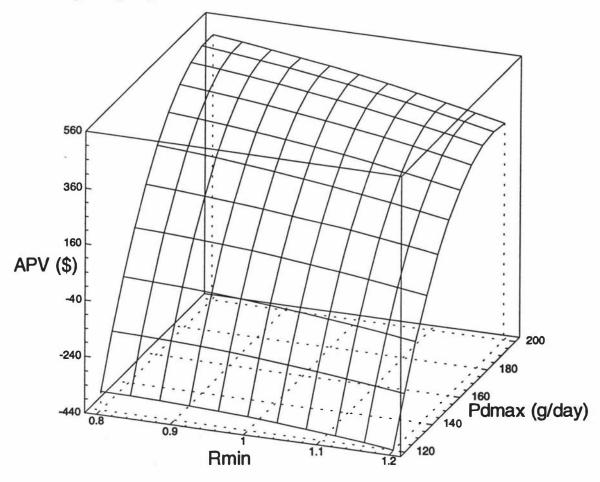


Figure 3.2 Effect of Pd_{max} and R_{min} on APV (\$ profit / gilt life cycle) for genotypes with intermediate levels of DEi (30 - 30.5 MJ/day).

The effect of DEi and $R_{\rm min}$ on profitability for improved genotypes with $Pd_{\rm max} = 160$ g/day is shown in Figure 3.3 ($r^2 = 0.995$). Decreasing DEi had a significant effect on profit in genotypes with moderate to high DEi levels. A plateau was reached at DEi levels between 25 and 27 MJ/day and further decreases in DEi had negative effects on life cycle profitability.

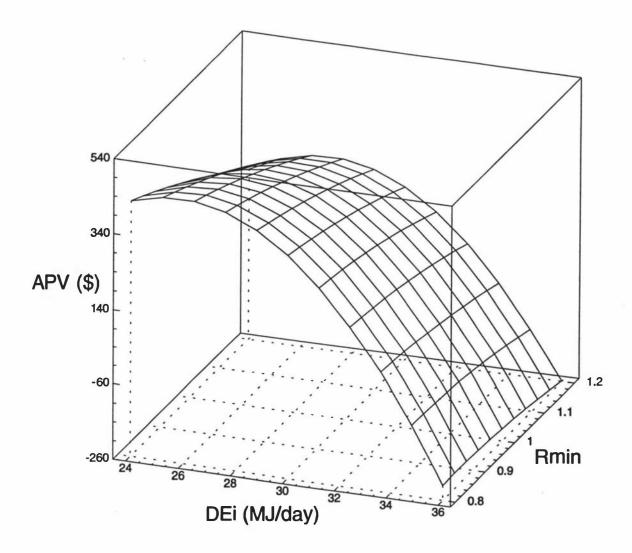


Figure 3.3 Effect of R_{min} and DEi on APV (\$ profit / gilt life cycle) for genotypes with $Pd_{max} = 160 \text{ g/day}$.

3.3.4 Effect of Pdmax, DEi and Rmin on ADG, BF and DFI

Effects of a wide range of pig genotypes on the average daily gain from birth to slaughter (ADG), carcass backfat thickness at slaughter (BF), and ad libitum daily feed intake in the third stage of pig growth (transfer to slaughter, DFI) were studied, using results from the 125 simulated combinations of Pd_{max} , DEi and R_{min} .

Polynomial functions for dependent variables, viz. ADG, BF and DFI, with independent variables Pd_{max} , DEi and R_{min} , were derived using multiple regression analysis. The best fit equations for ADG, BF and DFI had respective adjusted r^2 coefficients equal to 0.97, 0.93 and 0.95. The polynomial functions for ADG, BF and DFI, assuming base level for $R_{min} = 1.0$, are shown in Figures 3.4, 3.5 and 3.6. Base level simulation results for ADG, BF and DFI were 629 g/day, 16.8 mm and 2186 g/day respectively (marked with \star in the figures), corresponding to base level $Pd_{max} = 140$ g/day, DEi = 30.6 MJ/day and $R_{min} = 1.0$.

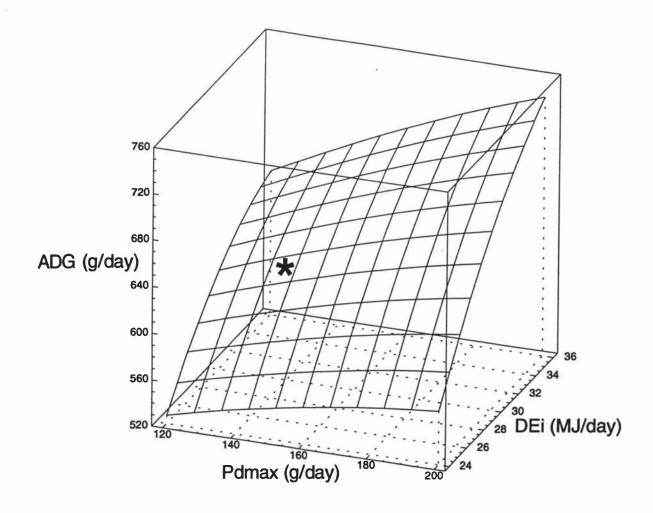


Figure 3.4 Effect of Pd_{max} and DEi on average daily gain (ADG) for genotypes with $R_{min} = 1.0$.

★ Base level: see text for explanation.

The highest ADG's were associated with high Pd_{max} and high DEi levels (Figure 3.4). One phenotypic standard deviation (σ_p) increase in Pd_{max} at the base level (+14 g/day) caused a 16 g/day increase in ADG, and one σ_p increase in base DEi (+3.1 MJ/day) increased ADG by 26 g/day. Increasing R_{min} by one σ_p (+0.1) from the base level had only a small effect on ADG, decreasing it by 1.8 g/day.

Effect of Pd_{max} and DEi on carcass backfat thickness is presented in Figure 3.5. The fattest pigs were those with the highest DEi's and with unimproved, low Pd_{max} genotypes. Those pigs were also the least profitable. One σ_p increase from the base level of Pd_{max} decreased BF by 1.5 mm, one σ_p increase in DEi raised BF by 2.5 mm, and one σ_p increase in R_{min} increased backfat by 0.06 mm.

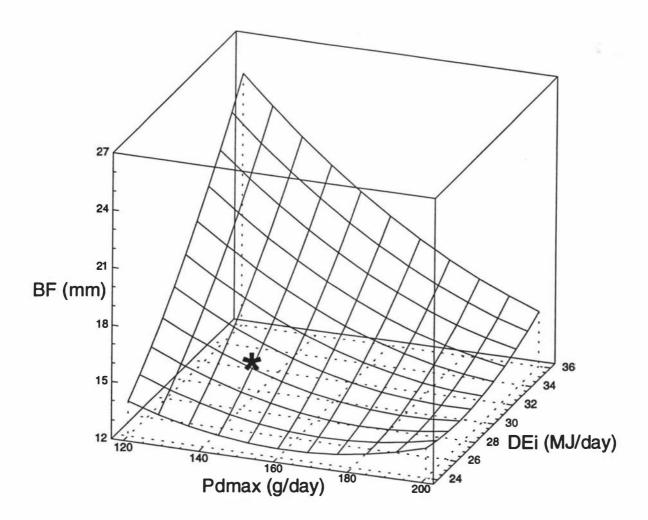


Figure 3.5 Effect of Pd_{max} and DEi on backfat thickness (BF) for genotypes with $R_{min} = 1.0$.

★ Base level: see text for explanation.

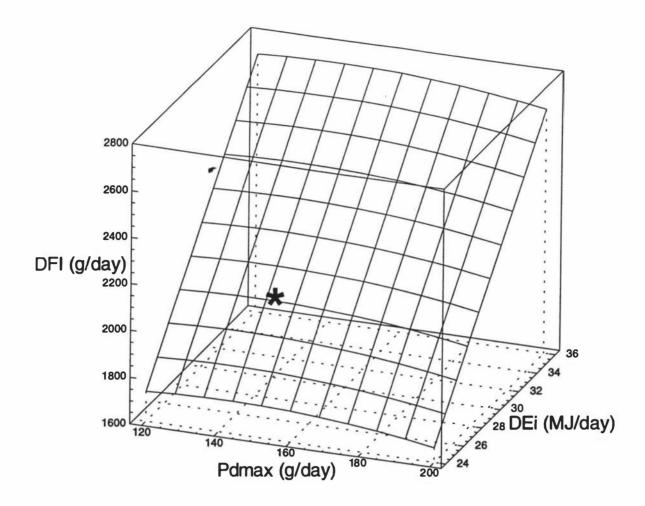


Figure 3.6 Effect of Pd_{max} and DEi on daily feed intake (DFI) for genotypes with $R_{min} = 1.0$.

★ Base level: see text for explanation.

Figure 3.6 represents effect of Pd_{max} and DEi on ad libitum daily feed intake. The effect of Pd_{max} was relatively small, compared to the effect of DEi, in all studied genotypes. One σ_p increase from the base level of Pd_{max} decreased DFI by 8 g/day, one σ_p increase in DEi had a large effect on DFI, increasing it by 220 g/day, and one σ_p increase in R_{min} decreased DFI by 5 g/day.

3.3.5 Economic values for growth performance output variables: ADG, BF and DFI

The polynomial profit equation [3.2] best fitting the Annualised Present Value model was obtained for three growth performance output variables: ADG, BF and DFI, calculated using output data from 125 simulations. The adjusted r^2 for APV₂ was equal to 0.98.

$$APV_2 = 2961.69 - 8.33*ADG + 0.86*DFI - 55.98*BF + 0.008*ADG^2$$
$$- 0.0004*DFI^2 - 2.75*BF^2 + 0.000045*ADG*DFI*BF.$$
[3.2]

Economic values for each output growth performance trait were calculated as partial derivatives of APV₂ [3.2] with respect to that trait. EV's for ADG, BF and DFI, calculated for a selection of improved and unimproved pig genotypes are in Table 3.1.

All genotypes studied had positive EV's for ADG and negative EV's for BF and ad libitum DFI. EV's for BF were relatively high for all genotypes, with the highest values for unimproved genotypes exceeding \$-100 per 1 mm of backfat increase. Improved genotypes with digestible energy intakes (DEi) below 30 MJ/day had smaller (less negative) EV's for DFI (\$-0.20 to \$-0.60 per 1 g/day increase in DFI), compared with genotypes with high DEi levels, with EV's for ad libitum DFI exceeding \$-0.60.

3.3.6 Economic values for reproduction performance traits: NBA, PWM, IWO and GAO

Economic values for reproduction performance traits: average number born alive/litter (NBA), pre-weaning mortality percentage (PWM), interval weaning-oestrus (IWO) and gilt age at first oestrus (GAO), were calculated for each of the 125 simulated pig genotypes, by independently changing a base value of each trait by one unit, with all other performance levels remaining constant, and running the life cycle simulation to determine resultant change in profit. EV's for NBA, PWM, IWO and GAO, calculated for a selection of improved and unimproved pig genotypes are in Table 3.1.

Economic values for NBA were dependent on the overall life cycle profit, as influenced by the genotype. The highest EV's for NBA, exceeding \$70 per 1 extra pig born alive per litter, were found for sows of improved genotypes, producing lean, fast growing progeny, with low-to-moderate DEi levels (Table 3.1). Unimproved genotypes had low EV's for NBA, below \$12 per extra pig. These genotypes represented slow-growing pigs, with high voluntary feed intakes and high levels of backfat. In practice, these pigs and any other pigs for which the EV of DEi was negative should be fed a restricted diet.

Relatively low, negative EV's were found for one unit increase in other reproduction traits: PWM, IWO and GAO. They were also influenced by the average genetic level of performance in the selected population. EV's for PWM, IWO and GAO were economically important for improved genotypes only, i.e. those already capable of achieving high levels of life cycle profit.

Larger litters born alive increased the total number of progeny weaned and sold per sow per year, spreading gilt and sow costs over more offspring and generating more profit from sales of bacon pigs (provided that offspring costs

were lower than offspring returns). An increase in the number of pigs born alive per litter caused a small increase in the breeding sow costs, as larger weight of conceptus and higher milk production required higher feed intakes. Maintaining the same amount of feed for more productive sows had a negative effect on their post-weaning condition, decreasing sow slaughter weights, and generating less income from sales of cull sows.

Lower pre-weaning mortality rate had a similar effect of spreading breeding stock costs over more offspring sold, by increasing the average number weaned per litter by 0.1 for each 1% decrease in mortality.

An increase in the interval weaning to oestrus caused a decrease in the number of litters per sow per year, smaller numbers weaned and sold per sow per year, and higher sow costs. However, returns from culled sows were slightly higher, as those sows were older and had higher liveweights when culled.

Increased average age at first oestrus caused higher gilt costs, and returns from culled gilts and sows were also slightly higher, because culled animals were older and heavier at slaughter. The overall economic value of a one unit increase in GAO was small and negative.

3.4 Discussion

To date, there is only one documented attempt to define breeding objectives and economic, values of traits for New Zealand pig improvement (Morris et al., 1978). That study included only growth, carcass and feed efficiency traits in the breeding objective. The reasons for ignoring reproductive traits were lower heritability and economic importance of these traits, and an assumption that improvement in litter size could be achieved mainly by crossbreeding.

A major determinant of profit in pig production is the efficiency of converting food into the growth of lean tissue. Relatively high economic values for carcass leanness and feed conversion, compared with economic value for average daily gain, results in selection programmes that lead to a reduction in the rate of fat deposition via a decline in intake (Fowler et al., 1976; Webb, 1989; Smith et al., 1991). As pig populations get leaner, further genetic improvement in feed efficiency and carcass leanness may be more difficult, due to reductions in heritabilities and variances (Smith et al., 1983). Continued reduction in digestible energy intake will ultimately limit future improvement in lean growth rate and sow productivity. This limiting effect was simulated in genotypes with low DEi and high Pd_{max} levels. It is expected that future improvement will come from increases in Pd_{max} and rate of lean tissue deposition, accompanied by an increase in appetite. Therefore, DEi should not be allowed to decrease, especially as it can be easily modified downwards by management practices. The optimum change in DEi requires defining correct economic weights for DEi, R_{\min} and Pd_{max}, considered as genetic determinants of pig growth. Assuming a certain proportion of lipid deposition as physiologically essential and associated with lean deposition, the limiting role of R_{\min} in the full expression of Pd_{max} genetic potential will vary, depending on genotype, age,

liveweight and sex of growing pigs. This study demonstrates that the relative economic importance of carcass leanness compared to sow productivity traits is likely to decrease in the future. These results are in agreement with Ollivier *et al.* (1990) and Webb (1991).

A model simulating life cycle production of a breeding sow and growth performance of her offspring used in the present study allows estimation of economic values of both reproduction and growth performance traits for a wide range of genetic and management circumstances of the production system. Inclusion of number born alive/litter (NBA) in the breeding objective was important for populations of improved genotypes, with high economic values estimated for that trait. EV's for average pre-weaning mortality percentage (PWM), interval weaning-oestrus (IWO) and gilt age at first oestrus (GAO) were economically less important.

Effects of sow culling rate and life cycle length on profitability were investigated and optimal returns were found to depend on the average genetic level of performance in the pig herd. In New Zealand conditions the optimal life cycle length was found to vary from 4 to 10 parities, with improved pigs having less parities at optimal returns. In order to accommodate different production circumstances, REV's for reproduction and growth performance traits were expressed in terms of a gilt life cycle. For improved genotypes, shorter life cycle optimised overall APV profit, as the initial gilt costs were compensated more quickly by the lower offspring costs and higher offspring returns.

The results shown here demonstrate the change in relative economic values of traits, depending on production circumstances and average genetic level of performance. The highest, positive economic values for Pd_{max} and negative EV's for DEi and R_{min} were found for unimproved pig genotypes, with low Pd_{max} levels and moderate to high voluntary feed intakes. For some improved

lines of pigs with low DEi levels, ad libitum feed intake was too low to realise Pd_{max} , and further decreases in DEi had negative effects on profitability. Insufficient DEi levels restricted full expression of Pd_{max} potential, with EV's for Pd_{max} becoming zero. The economic value of R_{min} was negative when DEi was insufficient to provide adequate levels of metabolisable energy required for lipid deposition and prevented pigs from reaching their Pd_{max} potential, confirming findings of de Vries and Kanis (1992). In the long term, the biological constraint of protein deposition being accompanied by some minimum fat deposition, as well as meat quality requirements are likely to place a limit on R_{min} decrease. Therefore, its importance as a trait in the breeding objective is expected to decrease (Kanis and de Vries, 1992).

The simulation model permitted estimations of relative economic values for predictions of growth performance, such as ADG, DFI and BF, currently used as selection criteria in pig improvement programmes. EV's for these traits were dependent on the average genetic level of performance in the selected population. High, negative economic values for BF were estimated for all studied genotypes, representing price signals imposed by meat processors to decrease fat levels in slaughter pigs. However, REV's for BF ranged from -20 to -35 (assuming REV for ADG = 1), considerably less than the REV for BF to ADG of -83 to 1 used by Morris et al. (1978). Ad libitum DFI had relatively small and negative economic values in all studied genotypes. The polynomial profit function for three growth performance output variables: ADG, BF and DFI did not explain some of the biological dependencies between genetic lean growth potential and nutrient availability. As pointed out by de Vries and Kanis (1992), economic value for DFI will always be negative, based on models not accounting for an undesirable decrease in appetite, as extra food increases costs of production. The present model confirmed the findings of Kanis and de Vries (1992), demonstrating the advantage of using REV's of Pd_{max} , DEi and R_{min} as

traits in the breeding objective, rather than predictions of growth performance, such as ADG, DFI and BF.

A routine method may have to be developed for estimating ad libitum digestible energy intakes and feed wastage to assist prediction of genetic levels of Pd_{max} for individual pigs, thereby allowing for direct selection on an objective incorporating Pd_{max} and DEi. Knowledge of genetic associations between DEi, Pd_{max} and R_{min} and strategies for predicting genetic merit for each of these traits are required to determine improved selection programmes.

The reproduction and growth performance REV's estimated for improved genotypes may be applied in selection programmes of nucleus pig breeding herds in New Zealand. Continued selection for production traits will bring their levels closer to optimum, leading to increasing emphasis on other traits, such as reproduction and meat quality.

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CHAPTER 4

ESTIMATION OF GENETIC PARAMETERS FOR PRODUCTION AND REPRODUCTION TRAITS USING RESTRICTED MAXIMUM LIKELIHOOD

4.1 Abstract

Restricted Maximum Likelihood (REML) procedures for multiple trait animal models were used to estimate (co)variance components, heritabilities, genetic correlations and common environmental effects for average daily gain (ADG), backfat thickness (BF) and number of pigs born alive per litter (NBA) for on-farm tested Large White, Landrace and Duroc pigs from 3 New Zealand nucleus herds recorded over the period 1980 to 1993. A bivariate animal model for ADG and BF contained fixed effects for herd-year-test day, sex and age as a linear covariable, as well as random litter and animal effects. The NBA model included fixed season of farrowing and parity effects, and random animal (sow) and permanent environmental effects. Repeated records for NBA were accommodated by fitting a permanent environmental effect for each sow, uncorrelated to additive genetic effects. The estimates of heritability (h^2) for ADG were 0.20, 0.18 and 0.16, and the estimates of the litter variance in proportion to the phenotypic variance (c^2) were 0.11, 0.12 and 0.09 for Large White, Landrace and Duroc breeds, respectively. The h^2 estimates for BF were 0.44, 0.45 and 0.46 for Large White, Landrace and Duroc breed, respectively, and c^2 estimates were 0.06 for all breeds. The phenotypic, genetic and litter correlations between ADG and BF ranged from 0.32 to 0.54. The h^2 estimates for NBA were 0.13, 0.09 and 0.16, permanent environmental variance ratios (m^2) were 0.06, 0.05 and 0.05, and repeatability estimates (t) were 0.19, 0.14 and 0.21 for Large White, Landrace and Duroc breed, respectively.

4.2 Introduction

Reliable estimates of genetic parameters are needed for accurate prediction of breeding values. Estimation of genetic parameters involves partitioning of phenotypic covariances between relatives into components due to additive genetic effects, dominance, epistasis, permanent and temporary environmental effects (Falconer, 1981). Estimates of heritabilities and common environmental effects are functions of variance components, and these parameters will be specific for a particular population and time period. Reliable parameter estimates are essential in developing an efficient improvement programme.

Estimates of variance components for unbalanced data in animal breeding were obtained until recently using one of the three methods of Henderson (1953). In all three methods, sums of squares of the observed values are equated to their expectations and the resulting equations are solved for the unknown variance components. Method 1 can be used only for completely random models. Method 2 can be applied to mixed models, where estimates of the fixed effects are used to pre-adjust the data prior to analysis similar to Method 1 along with modification of the expectations (Searle, 1968, 1971). Method 2 is not appropriate for models containing interactions between fixed and random effects. The "fitting of constants" Method 3 uses reductions in sums of squares due to fitting different subgroups of factors in the model and estimating variance components by equating each reduction to its expected value. Random effects are fitted after fixed effects. Method 3 eliminates bias due to non-random influence of the fixed effects, but it lacks uniqueness in unbalanced data (different estimators of variance components can be obtained from the same set of data depending on the reductions in sums of squares used) and is more difficult computationally than Methods 1 and 2.

The above three methods assume that data are randomly sampled. In animal breeding, data frequently originate from selection experiments or livestock improvement schemes, which involve continuous culling of animals on the basis of their performance. Variance components estimated by one of these methods are likely to be subject to selection bias. This concern prompted development of a maximum likelihood (ML) method of estimation of variance components by Hartley and Rao (1967), and its application to the mixed model equations of Henderson (1973). The algorithm for ML estimation requires the inverse of the random effects portion of the mixed model equations which can be computationally demanding to obtain. Use of ML estimators account for some forms of selection bias as discussed by Thompson (1979). However, the major disadvantage of ML is that this method does not account for the loss of degrees of freedom from estimation of the fixed effects under a mixed model (Harville, 1977). In animal breeding applications this method may not be appropriate when a large number of fixed effects are included in the model.

A modification of ML for the estimation of variance and covariance components, known as restricted maximum likelihood (REML) was proposed by Patterson and Thompson (1971) and has become the method of choice for genetic parameter estimation in animal breeding due to its desirable statistical properties. Only that portion of the likelihood which is invariant to the fixed effects is maximised under REML. The REML approach takes into account the loss in degrees of freedom resulting from the inclusion of unknown fixed effects in the model, but its application presents major computational requirements (Kennedy, 1981). The properties of REML estimators have been discussed by Harville (1977). There are several iterative algorithms for obtaining REML estimates of (co)variance components, the expectation maximisation (EM) algorithm of Dempster *et al.*, (1977) being one of the most frequently used. Henderson (1984) advocated the EM algorithm for its comparative computational simplicity and for its property of constraining estimates to be within the permissible parameter

space. However, EM algorithms are typically slower to converge than algorithms based on second derivatives such as Fisher's Method of Scoring (Thompson, 1982). Early REML applications were generally limited to univariate models with one random effect only, and genetic variances were commonly estimated from covariances among paternal half-sibs fitting a so-called sire model. Recently, multivariate animal models have become widely used in the genetic evaluation of animals. These models include an additive genetic effect for each animal, utilise information on all known relationships among animals, take into account correlations among traits, and can incorporate additional random effects, such as maternal genetic or permanent environmental effects. Kennedy and Sorensen (1988) discussed genetic properties of animal models and how they account for changes in genetic means and variances.

REML algorithms can use information from first or second derivatives (or their expected values) of the likelihood function to locate the maximum. The examples are EM algorithm, Newton-Raphson and Fisher's Method of Scoring. These algorithms are computationally demanding, involving inversion (or approximation of elements of the inverse) of a matrix of size equal to the total number of levels of all random effects fitted in each round of iteration. A derivative-free restricted maximum likelihood (DFREML) algorithm has been suggested by Graser et al. (1987) for univariate analyses under animal or reduced animal models, involving explicit evaluation of the likelihood and maximisation by direct search. The reduced animal model involves setting up equations only for animals with progeny and absorbing equations for animals without progeny directly into equations for their parents (Quaas and Pollak, 1980). derivative-free approach can be extended (Meyer, 1989b; 1991a) to include additional random effects and multivariate analyses. Several different optimisation strategies have been proposed, including the Simplex method of Nelder and Mead (1965) recommended for analyses requiring the likelihood to be maximised with respect to several parameters. This direct search method relies

on a comparison of function values without attempting to utilise any statistics related to derivatives of the function.

The derivative-free approach for estimating variance components by restricted maximum likelihood for a multivariate mixed animal model was chosen in this study. The objective was to estimate (co)variance components, heritabilities, phenotypic and genetic correlations and common environmental effects for the average daily gain (ADG), backfat thickness (BF) and number of pigs born alive per litter (NBA) for on-farm tested Large White, Landrace and Duroc pigs in New Zealand nucleus herds.

4.3 Materials and Methods

4.3.1 Data

Performance test records from on-farm tested boars and gilts and reproductive sow records from purebred Large White (LW), Landrace (LR) and Duroc breeds were obtained from 3 New Zealand nucleus farms recorded over the period from 1981 to 1993. The on-farm test data contained, after editing, 38,622 individual performance records for average daily gain (ADG, g/day) from birth to test day and ultrasonically measured backfat thickness (BF, mm) obtained on test day immediately prior to selection. Backfat thickness was the average of two fat depth measurements taken 4 cm (C4) and 8 cm (K8) off the mid-line at the position of the last rib. The distribution of individual performance records by breed is in Table 4.1. All Duroc records were collected on one farm, while LW and LR records came from two nucleus herds. A small number of records (approximately 0.3% of all records) with only one recorded measurement, either ADG or BF, were eliminated from the analysis. Pigs were tested weekly or

fortnightly with age at test ranging from 125 to 165 days (test liveweight ranging from 60 to 100 kg). The approximate average age and liveweight at test were respectively, 143 days and 79 kg for LW and LR, and 148 days and 76 kg for Duroc pigs. Each performance record contained identifications of the tested pig, its sire and dam id's, herd-year-test number, sex, litter number, age at test, and raw ADG and BF data. The numbers of tested pigs, sires, dams, test days and litters for ADG and BF by breed are in Table 4.1.

Table 4.1 Numbers of tested pigs, sires, dams, test days¹ and litters for average daily gain (ADG) and backfat thickness (BF) by breed

Breed	Large White	Landrace	Duroc
Animals	19,283	14,308	5,031
Sires	282	254	90
Dams	719	605	252
Test Days	641	637	103
Litters	2,348	1,876	817

One test day each week or fortnight.

The reproductive data contained 5,561 purebred litter records. The distribution of farrowing records by breed is in Table 4.2. Each sow record included identification numbers for dam and her parents, information on herd-year-season (HYS) of farrowing, parity of dam and number of piglets born alive (NBA). The data were edited to eliminate crossbred litter records, records with missing information, and HYS's with single farrowing records. The number of records, sires, dams, farrowing seasons and parities by breed are presented in Table 4.2.

Table 4.2 Numbers of purebred farrowing records, sires, dams with records, animals in the model, farrowing seasons and parities for number of pigs born alive per litter (NBA) by breed

Breed	Large White	Landrace	Duroc
Sow Records	2,599	2,171	791
Sires of Sows	256	230	77
Dams with records	778	670	288
Animals 1	1,082	950	375
Farrowing seasons ²	54	54	25
Max. No. of Parities	10	8	8

Total number of animals in the model, including sires and dams without records

Means and phenotypic standard deviations for ADG, BF and NBA by breed are given in Table 4.3.

Table 4.3 Means (\bar{x}) and phenotypic standard deviations $(\hat{\sigma}_p)$ for average daily gain (ADG), backfat thickness (BF) and number born alive per litter (NBA) by breed

Breed		Large White	Landrace	Duroc
ADG (g/day)	\bar{x}	550.0	551.0	515.7
	$\hat{\sigma}_p$	43.89	40.92	49.45
BF (mm)	\bar{x}	13.61	14.42	13.03
	$\hat{\sigma}_p$	2.35	2.14	2.28
NBA (pigs)	\overline{x}	10.69	9.91	9.29
	$\hat{\sigma}_p$	2.76	2.52	2.79

³⁻monthly farrowing seasons defined as January to March, April to June, July to September and October to December.

4.3.2 Mixed Model Definition

Separate analyses were undertaken to estimate parameters for performance test records and reproductive sow performance. The analyses were carried out within breeds. Variance components were estimated by restricted maximum-likelihood (REML) methods (Patterson and Thompson, 1971; Harville, 1977; Meyer, 1989b, 1991a). Initially, an univariate sire model was used to obtain starting values for the univariate and multivariate animal model analyses. The detailed descriptions of each model are in the following sections. In matrix notation, the basic mixed linear model (Henderson, 1949) describing the records for each animal is:

$$y = Xb + Zu + e$$

where y is a vector of N observations for ADG, BF or NBA;

b is a vector of NF fixed effects (herd-year-test, sex and age at test covariable or herd-year-season of farrowing and parity of the dam, depending on the model); u is a vector of all NR random effects fitted (ADG and BF models included animal additive direct genetic $\sim (0, A \sigma_g^2)$ and common environmental (litter) effects $\sim (0, I \sigma_c^2)$, with the covariance between additive direct and litter effects equal zero; repeatability models for NBA included additive direct genetic $\sim (0, A \sigma_g^2)$ and permanent environmental effect of the sow $\sim (0, I \sigma_m^2)$, with the covariance between additive genetic and permanent environmental effects equal zero);

X is a $N \times NF$ incidence matrix, relating fixed effects to observations;

Z is a $N \times NR$ incidence matrix for random effects:

e is a vector of N random residual effects $\sim (0, I\sigma_e^2)$;

A is the numerator relationship matrix;

and σ_g^2 , σ_c^2 , σ_m^2 and σ_e^2 are the additive direct, litter, permanent environmental and residual variances, respectively.

It was further assumed that

E
$$(y) = Xb$$
;
 $V(u) = G$;
 $V(e) = R = I \otimes R_0$; and
 $Cov(u, e') = 0$

where R_0 is a $q \times q$ error covariance matrix for q traits, and \otimes denotes direct product.

This gives the phenotypic covariance matrix of the vector of observations

$$V(y) = \mathbf{V} = \mathbf{Z}\mathbf{G}\mathbf{Z}' + \mathbf{R}.$$

4.3.3 Univariate Sire Model Analysis

Starting values for a multivariate animal model were based on estimates obtained from the analysis of data using univariate sire model, written using the Microsoft Foxpro® programming language. REML estimates were obtained by first absorbing fixed effects (Searle, 1982), using the computing strategy described in Schaeffer (1979). Absorption of fixed effects reduces the mixed model equations (MME) of Henderson (1973) to:

$$(\mathbf{Z}'\mathbf{M}\mathbf{Z} + \alpha \mathbf{A}^{-1}) \hat{\mathbf{s}} = \mathbf{Z}'\mathbf{M}\mathbf{y}$$
 [4.1]

where $M = \mathbf{I} - X(X'X)^{\mathsf{T}} X'$;

 $\alpha = \sigma_e^2 / \sigma_s^2$ is a ratio of residual to sire variances;

A is an additive numerator relationship matrix (Henderson, 1975; 1976a, 1976b);

and \hat{s} is a vector of fredicted breeding values.

Estimation of variance components by REML (Patterson and Thompson, 1971) requires iterative solutions to the equation [4.1] where the assumed value of α varies with each iteration. The σ_s^2 and σ_e^2 can be estimated iteratively using an expectation-maximisation (EM) algorithm (Dempster *et al.*, 1977; Harville, 1977):

$$\hat{\sigma}_e^{2^{k+1}} = [y'My - \hat{s}_k(Z'My)]/[N - r(X)]$$

$$\hat{\sigma}_s^2^{k+l} = [(\hat{s}_k' A^{-1} \hat{s}_k) + \hat{\sigma}_e^2 \operatorname{tr}(A^{-1} (Z'MZ + \hat{\alpha}^k A^{-1})^{-1})]/s$$

where k = iteration number;

N = total number of observations;

s = number of random levels (sires);

tr = trace, sum of diagonals of a matrix;

$$\hat{\alpha}^k = \hat{\sigma}_e^2 / \hat{\sigma}_s^2;$$

 \hat{s}_k = sire breeding values predicted using $\hat{\alpha}^k$, and

$$r(X) = rank of X$$
.

Inversion of the coefficient matrix $(Z'MZ + \alpha A^{-1})$ in every round of iteration is computationally demanding. Alternative algorithms for estimation of variance components from MME including the relationship matrix were proposed

by Henderson (1980), Hudson and Van Vleck (1982), Lin (1987), Jensen and Mao (1988) and Mrode and Thompson (1989). Smith and Graser (1986) proposed to premultiply the MME after absorption of fixed effects by L', to factor A^{-1} from these equations, where L is a lower triangular matrix (Henderson, 1976b), obtained from the Cholesky decomposition of the numerator relationship matrix (i.e. A = LL' and $L'A^{-1}L = I$). Lin (1988) suggested an algorithm for the simultaneous diagonalisation of Z'MZ and A^{-1} in the coefficient matrix. After factorisation of A^{-1} and computing L'(Z'MZ)L, an orthogonal matrix Q is found, such that Q'L'(Z'MZ)LQ = D, where D is a diagonal matrix containing the eigenvalues of L'(Z'MZ)L as its diagonal elements. The columns of Q contain the corresponding eigenvectors. Following Lin (1988), equivalent REML equations for estimation of variance components simplify to:

$$\hat{\sigma}_e^2 = (y'My - \hat{s}_k^* 'q^*)/[N - r(X)]$$
 [4.2]

$$\hat{\sigma}_{s}^{2} = [\hat{s}_{k}^{*} \hat{s}_{k}^{*} + \hat{\sigma}_{e}^{2} \operatorname{tr}((D + \hat{\alpha}^{k} \mathbf{I})^{-1})]/s$$
 [4.3]

where
$$\hat{s}_k^* = (LQ)^{-1} \hat{s}$$
 and $q^* = Q'L'Z'My$.

The simultaneous diagonalisation approach requires calculating L'(Z'MZ)L and L'(Z'My) matrices. A recursive algorithm for overwriting Z'MZ (or Z'My) with L'(Z'MZ)L (or L'(Z'My)) without computing L (Garrick, 1988; Quaas, 1989) was implemented to reduce the computational effort. Final solutions to univariate REML iterations, obtained using the modified expectation-maximisation algorithm equations [4.2] and [4.3], were used as starting values for animal model estimation of (co)variance components. Covariances were estimated by the method suggested by Searle and Rounsaville (1974), based on

analysing the sum of two traits and using the resulting parameter estimates along with the variances of the individual traits to compute the covariances between the traits by difference.

4.3.4 Multivariate Animal Model Analysis

The performance test data for ADG and BF were analysed using the derivative-free approach for estimating (co)variance components by restricted maximum likelihood (DFREML) for a multivariate mixed animal model (Meyer, 1989a; 1991a). The programme used was written by Meyer (1991b). The advantage of this method was simultaneous likelihood evaluations for multiple right-hand sides and the ability to include an additional random (litter) effect. One disadvantage was that computations were time-consuming, due to the number of equations, and estimates were slow to converge. Meyer (1989b) examined different strategies to locate the maximum of the log likelihood function. One of them, the so-called Simplex procedure of Nelder and Mead (1965) was chosen as a robust and easy to use method for multivariate analysis. It relies on a comparison of function values without utilising any statistics related to derivatives of the function. Such optimisation techniques are referred to as direct search procedures. The convergence criterion was the variance of the function values in the Simplex, that is $var(-2log \mathcal{L})$ where \mathcal{L} is the likelihood. A value of 10⁻⁸ was used, suggested by Meyer (1989b) as giving good accuracy of estimation.

The natural log likelihood function (L) to be maximised was

$$\log \mathcal{L} = -\frac{1}{2} \left[const + \log |\mathbf{V}| + \log |\mathbf{X}^* \cdot \mathbf{V}^{-1} \mathbf{X}^*| + (y - \mathbf{X}\hat{b})' \mathbf{V}^{-1} (y - \mathbf{X}\hat{b}) \right]$$

assuming y has a multivariate normal distribution with mean Xb and variance V, where X^* (of order $N \times NF^*$) denotes a full column rank submatrix of X (Meyer, 1989b).

Fixed effects were the same for ADG and BF and included herd-year-test day and sex effects, and age at test covariable. The weight and age at test varied between pigs completing the performance test. Therefore, ADG and BF have been adjusted for age by fitting age at test as a linear covariable. The random effects were the additive genetic merit of each animal and trait, and litters as an additional, uncorrelated (common environmental) effect. The design matrices were equal, i.e. all traits were recorded for all animals. This was exploited to reduce computational requirements through transformation to canonical scale (Meyer, 1991a). For q correlated traits, the outcome of this transformation is a set of q genetically and phenotypically uncorrelated new traits, so-called canonical variables. A series of q univariate analyses can be carried out reducing substantially the computational effort. The data were required to be ordered according to traits within animals within time of recording (test day).

4.3.5 Univariate Animal Model Analysis for NBA

The repeatability model for NBA included all litters of a sow and required estimation of the animal's additive direct genetic effect, as well as a permanent environmental effect due to the animal (m). It was assumed that permanent effects had the same variances for all sows and were mutually uncorrelated, therefore the variance-covariance matrix of this effect (V_m) was proportional to the identity matrix (I), and assumed uncorrelated to additive genetic effects:

$$V_m = \mathbf{I}\sigma_m^2$$

where σ_m^2 is the permanent environmental variance.

A maternal genetic effect for NBA was not estimated. Fixed effects were herd-year-season of farrowing and parity of the dam. Variance components were estimated by the DFREML procedure under an animal model (Meyer, 1991b).

4.3.6 Approximation of Standard Errors

The standard errors of the estimates of variance and covariance components and hence the genetic parameters are derived from the inverse of the information matrix, i.e. the matrix of expected values of second derivatives of the $\log \mathcal{L}$. However, derivative-free REML algorithms do not provide the elements of the inverse of the information matrix and hence do not yield estimates of sampling errors (Meyer, 1991b). Smith and Graser (1986) proposed approximating standard errors as the square root of the diagonal elements of $(-2S)^{-1}$, where S is a symmetric matrix in the quadratic equation:

$$\mathcal{L}(\sigma) = s_0 + \sigma' s_1 + \sigma' S \sigma$$

where σ' is a vector of parameters (σ_g^2 , σ_c^2 , σ_m^2 or h^2 , c^2 , m^2), $\mathcal{L}(\sigma)$ is the log likelihood evaluated at σ , and s_0 , s_1 (a column vector) and S are unknown.

Frequently, however, the above procedure has been found to yield non-positive definite estimates of the information matrix, i.e. failed to provide valid sampling covariances, in particular for multivariate analyses or models including a maternal genetic effect (Meyer, 1991b). In this study, the approximation of sampling variances failed in several of the analyses performed using the

DFREML approach. This may have been caused, as suggested by Meyer (1991b), by high sampling correlations between parameters producing long, narrow ridges on the likelihood surface, so that its shape could not provide an adequate fit. Therefore, standard errors of heritabilities (h^2) , common litter effects (c^2) , permanent, environmental variance ratios (m^2) , and genetic and phenotypic correlations between ADG and BF were obtained using the REML algorithm based on first and second derivatives of the likelihood function (Johnson and Thompson, 1994; 1995). This algorithm, named Average Information REML (AIREML), uses the average of observed and expected values as the information matrix. The standard errors were derived from the inverse of the matrix of second derivatives called the observed information matrix (Madsen et al., 1994).

4.4 Results

Estimates of variances and covariances for average daily gain (ADG) and backfat thickness (BF) for each of the analysed breeds are given in Table 4.4. For the Landrace breed, the estimates of the additive genetic variance ($\hat{\sigma}_g^2$) and the litter variance ($\hat{\sigma}_c^2$) were lower than for the other two breeds. The estimate of the residual variance ($\hat{\sigma}_e^2$) of ADG for Duroc breed was much higher than for LW and LR breeds. Positive additive genetic ($\hat{\sigma}_{gg}$), common litter ($\hat{\sigma}_{cc}$) and residual ($\hat{\sigma}_{ee}$) covariances between ADG and BF were found for all breeds.

Table 4.4 Estimates of variances and covariances for average daily gain (ADG) and backfat thickness (BF) by breed

Breed		Large White	Landrace	Duroc
ADG (g/day)	$\hat{\sigma}_{g}^{2}$	385.5	309.5	391.3
	$\hat{\sigma}_c^2$	221.2	204.2	224.6
	$\hat{\sigma}_e^2$	1,319.5	1,160.4	1,829.3
BF (mm)	$\hat{\sigma}_g^2$	2.43	2.04	2.41
	$\hat{\sigma}_c^2$	0.33	0.29	0.30
	$\hat{\sigma}_e^2$	2.77	2.26	2.48
Covariances	$\hat{\sigma}_{gg}$	11.96	8.17	12.20
(ADG, BF)	$\hat{\sigma}_{cc}$	4.04	3.33	4.07
	$\hat{\sigma}_{ee}$	28.58	23.01	36.59

Table 4.5 presents estimates of heritability (h^2) , litter variance relative to the phenotypic variance (c^2) , the phenotypic (r_p) and genetic (r_g) correlations, and the correlations between litter (r_c) and residual (r_e) effects for all breeds. The heritability was estimated as $h^2 = \hat{\sigma}_g^2 / (\hat{\sigma}_g^2 + \hat{\sigma}_c^2 + \hat{\sigma}_e^2)$, and the litter variance, relative to the phenotypic variance, was estimated as $c^2 = \hat{\sigma}_c^2 / (\hat{\sigma}_g^2 + \hat{\sigma}_c^2 + \hat{\sigma}_e^2)$. The phenotypic, genetic and residual correlations, as well as the correlation between litter effects, were estimated from corresponding components of variance and covariance.

Table 4.5 Estimates of variance ratios and correlations of average daily gain

(ADG) and backfat thickness (BF) computed from estimates of

(co)variance components for Large White, Landrace and Duroc breeds

Breed		ADG	(g/day)	BF	(mm)	Co	orrelation	s (ADG,	BF)
		h^2	c^2	h^2	c^2	$\overline{\mathbf{r}_{g}}$	rp	r _c	r _e
Large Whi	ite	0.20	0.11	0.44	0.06	0.39	0.43	0.48	0.47
	s.e.	$(0.015)^1$	(0.006)	(0.018)	(0.004)	(0.026)	(0.006)		
Landrace		0.18	0.12	0.45	0.06	0.32	0.39	0.44	0.45
	s.e.	(0.016)	(0.007)	(0.020)	(0.005)	(0.032)	(0.007)		
Duroc		0.16	0.09	0.46	0.06	0.40	0.47	0.49	0.54
	s.e.	(0.021)	(0.011)	(0.029)	(0.008)	(0.046)	(0.010)		

Standard errors of estimates are given in parentheses where available.

Estimates of h^2 and c^2 for ADG were slightly larger for LW and LR than for the Duroc. The h^2 and c^2 estimates for BF were similar for all breeds. Positive (unfavourable) phenotypic, genetic, residual and litter correlations between ADG and BF were found, ranging from 0.32 to 0.54.

Table 4.6 shows estimates of variance ratios h^2 and c^2 , and the correlations found in the literature for average daily gain (ADG), backfat thickness (BF) and age adjusted to a constant weight (AGE).

The AGE trait was used for measuring growth rate, for example, by Johansson and Kennedy (1983), Kennedy et al. (1985), Keele et al. (1988) and Kaplon et al. (1991). The genetic correlation between ADG and age at a constant weight (AGE) close to -1 was found in preliminary analyses and was also reported by Kaplon et al. (1991) and Hofer et al., (1992), Therefore, estimates of AGE were included in Table 4.6.

The estimates of h^2 and c^2 obtained in the present study are in good agreement with most of the estimates in Table 4.6. Statistical models considered by Klassen *et al.* (1988), Cameron *et al.* (1990), Mrode and Kennedy (1993) and Rydhmer *et al.* (1995) did not include a litter effect, resulting in overestimation of heritabilities. On the other hand, litter variances found by Johansson and Kennedy (1983) were large for the performance traits, indicating large common environmental effects, and producing low h^2 estimates. The genetic and phenotypic correlations given in Tables 4.5 and 4.6 indicate an unfavourable relationship between ADG (or AGE) and BF.

Table 4.6 Published estimates of variance ratios and correlations of average daily gain (ADG), age adjusted for weight (AGE), and backfat thickness (BF)

Author	Breed 1	h^2	c^2	h^2	c^2	r _p	r _g
		AI	OG	B	F		
Cameron <i>et al.</i> (1990) ²	LW,LR	0.46	_	0.54		0.06	-0.05
Kaplon et al. (1991)	PLW	0.27	0.09	0.29	0.10	0.23	0.25
Klassen et al. (1988) ²	LW, LR	0.32		0.56			
Klassen and Long (1991)	LW, LR	0.24	0.10	0.45	0.10	0.22	0.12
Knap et al. (1985) ²	DY, DL	0.25	_	0.30	_	0.10	0.10
Kreiter and Kalm (1986)	GL,BL,P	0.44	0.22	0.30	0.15	0.00	0.00
Merks (1988) ³	DY	0.18	0.21	0.27	0.21	0.24	0.24
	DL	0.12	0.22	0.39	0.17	0.06	0.03
Mrode and Kennedy (1993) ²	CY,CL,D	0.43	-	0.59	_	0.28	0.32
Rydhmer et al. (1995) ²	SY	0.32	_	0.32	_	0.52	0.44
Savoie and Minvielle (1988) 4	CY	0.25	_	0.49		0.11	0.27
	CL	0.21		0.57	_	0.07	0.10
	D	0.24	_	0.51	_	0.11	0.48
	Н	0.38		0.77	_	0.07	0.56
Smith and Ross, (1965)	LW, LR	0.42	0.11	0.54	0.06	-0.07	-0.15
		AC	ЗE	В	F		
Johansson and Kennedy (1983)	SY	0.09	0.39	0.18	0.23	-0.35	-0.17
	SL	0.07	0.43	0.12	0.26	-0.25	-0.54
Kennedy et al. (1985)	CY	0.36	0.31	0.44	0.12	-0.09	-0.11
	CL	0.40	0.31	0.61	0.10	-0.07	-0.05
	D	0.27	0.37	0.44	0.13	-0.08	-0.17
	Н	0.46	0.31	0.40	0.17	-0.08	-0.43

LW - Large White, LR - Landrace, PLW - Polish Large White, DY - Dutch Yorkshire, DL - Dutch Landrace, GL - German Landrace, BL - Belgian Landrace, P - Pietrain, CY - Canadian Yorkshire, CL - Canadian Landrace, D - Duroc, H - Hampshire, SY - Swedish Yorkshire, SL - Swedish Landrace

 c^2 not available, assumed no environmental covariance among full-sibs

BF adjusted for weight, ADG not adjusted c^2 not available, but dam effect in the model.

Estimates of variances, variance ratios and repeatability (t) for number born alive per litter (NBA) by breed are in Table 4.7. Permanent environmental variance ratio was estimated as $m^2 = \hat{\sigma}_m^2 / (\hat{\sigma}_g^2 + \hat{\sigma}_c^2 + \hat{\sigma}_e^2)$ and repeatability was estimated as $t = (\hat{\sigma}_g^2 + \hat{\sigma}_m^2) / (\hat{\sigma}_g^2 + \hat{\sigma}_c^2 + \hat{\sigma}_e^2)$. The lowest heritability was found in Landrace, due mainly to low estimate of additive genetic variance $(\hat{\sigma}_g^2)$.

Table 4.7 Estimates of variances, variance ratios and repeatability (t) estimates for number of pigs born alive per litter (NBA) by breed

Breed	Large White	Landrace	Duroc
$\hat{\sigma}_g^2$	0.97	0.57	1.28
$\hat{\sigma}_m^2$	0.47	0.34	0.36
$\hat{\sigma}_e^2$	6.19	5.46	6.15
h^2	0.13	0.09	0.16
s.e.	(0.024) 1	(0.024)	(0.039)
m^2	0.06	0.05	0.05
s.e.	(0.022)	(0.024)	(0.033)
t	0.19	0.14	0.21

Standard errors of estimates are given in parentheses where available.

These estimates are in agreement with heritability estimates of around 0.10 for number of pigs born alive per litter averaged over several studies (Buytels and Long, 1991; Gu et al., 1989; Haley et al., 1988; Haley and Lee, 1992; Johansson and Kennedy, 1985; Klassen and Long, 1991; Rydhmer et al. (1995), Southwood and Kennedy, 1990, Vangen, 1986). The repeatability between parities ranged from 0.12 to 0.26, with an average of around 0.15 (Buytels and Long, 1991; Gu et al., 1989; Klassen and Long, 1991). The coefficient of variation was high at around 25%.

4.5 Discussion

For animal models, DFREML written by Meyer (1988) was the first public package to implement the derivative-free REML (Smith and Graser, 1986). It became the standard in the field of variance components estimation, and is extensively cited (Misztal, 1994). However, multivariate DFREML algorithms can be computationally expensive, especially if the likelihood function contains many parameters to be estimated. Johnson and Thompson (1994) employed sparse matrix techniques to calculate the elements of the inverse of the coefficient matrix that are required to calculate the first derivatives of the likelihood. Second derivatives of the likelihood are calculated by averaging their observed and expected values. The trace term is cancelled out and the remaining expression is simple to compute (Johnson and Thompson, 1995). This leads to a quasi-Newton algorithm called Average Information REML (AIREML) which is a compromise between the Newton-Raphson and the Fisher scoring algorithms. The univariate animal model method of Johnson and Thompson (1994) was extended by Madsen et al. (1994) to the general multiple trait model with several random effects. The AIREML method was found to be several times faster than the DFREML. For example, using the pig data from this study and the same starting values of the parameters, the AIREML algorithm converged in less than 10 rounds, while DFREML required 20 to 50 times more iterations to converge, with considerably larger amounts of time. Both algorithms gave almost identical parameter estimates. The AIREML method provided estimates of standard errors which were difficult to obtain using the DFREML algorithm. These difficulties are usually found in models with multiple random effects with high sampling correlations between parameters, causing long, narrow ridges on the likelihood surface, so that its shape cannot provide an adequate fit (Meyer, 1991b). Recently, Meyer and Hill (1992) have shown that sampling variances and confidence intervals in a multi-parameter analysis can be estimated one

parameter at a time, using one-dimensional approximation techniques. This method is based on the so-called *profile likelihood*, defined as the likelihood for a subset of parameters of interest with the remaining parameters equal to their maximum likelihood estimates given that parameter. This method was used, for example, in the variance-components estimation for growth traits of Australian beef cattle (Meyer, 1992).

Haley et al. (1988) reviewed published analyses of heritabilities for NBA and found no significant differences in heritability estimates between parities and genetic correlations between adjacent parities approaching unity. However, these individual parity estimates are likely to be biased by the culling of sows based upon earlier litter records. Low heritability and repeatability estimates for NBA indicate the large effect of the temporary environment on this trait. Application of restricted maximum likelihood methods utilising information from all known relatives, inclusion of multiple records on sows, and standardisation of gestation and farrowing environments would be beneficial in the genetic evaluation for NBA.

Litter size includes direct as well as maternal genetic components. The additive maternal effect of a sow is inherited from both her sire and dam, and expressed in her offspring's reproductive performance, i.e. one generation later than the additive direct effect (Willham, 1963; 1972). First-parity records for the number of pigs born alive are more influenced by maternal effects than later parities (Vangen, 1980). Cross-fostering studies have shown that the litter size of gilts reared in large litters can be depressed by around 0.1 piglet for every extra littermate (Van der Steen, 1985). A negative influence of maternal genetic effects on litter size was found in a number of studies, including Nelson and Robinson (1976), Vangen (1980) and Southwood and Kennedy (1990). Recently, Southwood and Kennedy (1990) estimated heritabilities of maternal effects in first-parity records from Yorkshire and Landrace gilts of 0.04 and 0.07,

respectively. They found negative genetic correlation between maternal and direct genetic effects, which indicates that improvements in one effect will lead to reductions in the second. Excluding maternal effects led to a significant underestimation of direct heritability in that study, which may have reduced the overall genetic merit (maternal plus direct). An analysis of the theoretical influence of maternal genetic effects on predicted selection response in litter size, conducted by Roehe and Kennedy (1993), confirmed the reduction in direct response and a negative response in maternal effects due to the negative genetic correlation between direct and maternal effects. They suggested that ignoring maternal effects in the evaluation model may bias estimates of genetic and environmental trends in litter size. Estimates of the contribution of the sire of a litter to the variation in litter size are small and generally can be ignored (Haley et al., 1988; Southwood and Kennedy, 1990; Buytels and Long, 1991).

Correlations between production traits (ADG and BF) and NBA were not estimated. Johansson and Kennedy (1983) found correlations between litter size and performance test traits very close to zero. Similar results were obtained by David et al. (1983) and Lobke et al. (1986). Recent investigation of correlations of litter size with backfat and days to 100 kg conducted by Kennedy and Quinton (1993) confirmed these findings. McKay (1990) reported that litter size did not respond to index selection for reduced backfat thickness and increased growth rate. Gu at al. (1989) found small, negative correlations between litter traits and ADG and BF, though not significantly different from zero. Small, unfavourable genetic correlation of -0.14 between growth rate and NBA was also found by Rydhmer et al. (1992). However, in the recent study Rydhmer et al. (1995) found no correlations between growth rate and NBA and small, negative (i.e. favourable) correlations between BF and litter size. In the recent study of genetic relationships between growth traits and litter size (Short et al., 1994), it was concluded that the accuracy of breeding values for NBA may be increased by including growth traits in the multivariate analysis, provided evaluations are

performed within a specific line and farm. However, if average estimates are used, including growth traits would have little impact on the accuracy of evaluations, since average correlations are near zero. Some genetic evaluation systems, for example Australian Pigblup (Klassen and Long, 1991), assume the correlations between litter size and growth traits to be zero, allowing the production and reproduction analyses to be carried out separately.

4.5.1 Conclusions

The animal model REML techniques can be used to estimate (co)variance components from field data. Estimates of those effects are required to develop efficient selection programmes for growth and reproductive performance traits. Unfavourable correlations between ADG and BF found in this study indicate that improvements in one effect will lead to reductions in the second. Based on available results from literature, the estimated correlations between production traits (ADG and BF) and NBA are generally low and can be ignored. Therefore, where the breeding objectives are litter size and lean growth, a selection index is required to allow simultaneous improvement in the antagonistically correlated ADG and BF, and in the uncorrelated NBA component trait. The estimates of genetic parameters calculated in this study can be utilised in the New Zealand pig improvement programme.

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CHAPTER 5

PREDICTION OF BREEDING VALUES AND ESTIMATION OF GENETIC AND PHENOTYPIC TRENDS WITH AN ANIMAL MODEL

5.1 Abstract

Best Linear Unbiased Prediction (BLUP) of breeding values using an animal model was applied for the genetic evaluation of on-farm tested pigs. The analysis was based on test results of 23,562 Large White, 17,413 Landrace and 5,904 Duroc pigs from 3 New Zealand nucleus herds recorded from 1981 to 1994. Breeding values for the production traits: average daily gain (ADG) and ultrasonically-measured backfat thickness (BF) were estimated for all tested pigs and for base parents and imported animals within each breed, using a multivariate animal model. Fixed effects in the model were herd-year-test and sex with age at measurement as a covariable. Random effects were animals and litters. Inbreeding was taken into account in deriving the inverse relationship matrix. Correlations between production traits (ADG and BF) and number of pigs born alive per litter (NBA) were assumed null, allowing production and reproduction BLUP analyses to be carried out separately. A univariate animal model with repeated records was used to predict breeding values for NBA, with herd-yearseason of farrowing and parity as fixed effects, and random animal (sow) and permanent environmental effects. The reproduction data included 3,106 Large White, 2,500 Landrace and 915 Duroc litter records. The numerator relationship matrix contained all nucleus-born pigs and imported animals. Genetic parameters specified in the models were based on values calculated using restricted maximum likelihood (REML) procedures on the same data, separately for each breed.

Selection in the studied populations was carried for ADG and BF traits using a selection index combining phenotypic deviations from a contemporary (test day) group average. Annual genetic trends for ADG, BF and NBA were derived within breed by weighted regression of mean estimated breeding values on year of test. Environmental trends were estimated from solutions for fixed

effects. Annual phenotypic means were obtained by summing annual genetic and environmental means. Annual gains in ADG and BF for Large White (LW), Landrace (LR) and Duroc breeds were respectively, 2.65 ± 0.09 , 2.13 ± 0.13 , 4.33 ± 0.18 g/day/year for ADG and -0.22 ± 0.02 , -0.21 ± 0.02 and -0.21 ± 0.02 mm/year for BF. The NBA genetic trends were negligible for LW and LR at -0.001 ± 0.005 and 0.001 ± 0.002 pigs/litter/year, respectively, and favourable for Duroc breed at 0.07 ± 0.003 pigs/litter/year. Estimated annual phenotypic trends for LW, LR and Duroc breeds were, respectively, 5.13 ± 1.24 , 5.64 ± 1.26 and -3.12 ± 2.93 g/day/year for ADG, -0.21 ± 0.03 , -0.19 ± 0.05 and -0.49 ± 0.08 mm/year for BF, and 0.02 ± 0.02 , 0.09 ± 0.02 and 0.08 ± 0.08 pigs/litter/year for NBA.

Predicted genetic gains in ADG and BF using a selection index and assuming selection intensity of 1.6 standard deviations and mean generation interval of 1.25 years, were compared to the realised gains derived from the three breeds. The predicted gains of 4.13 g/day/year and -0.88 mm/year for ADG and BF, respectively, were generally substantially higher than those derived from the nucleus data except for Duroc ADG where predicted and actual gains were similar.

5.2 Introduction

Past improvement programmes in pigs have relied on comparing animals within herd and time period, based on a selection index combining performances of growth and carcass traits. In recent years, Best Linear Unbiased Prediction (BLUP) of breeding values using an animal model has become the method of choice for the genetic evaluation of animals (Henderson, 1988). This technique is appropriate for comparing animals with performance records obtained in more than one location or herd environment (Garrick, 1991). The first application of Henderson's Mixed Model Equations (MME) to an animal model was by Henderson (1949). It was later discovered that predictions of random effects from MME are Best, Linear and Unbiased (Henderson et al., 1959; Henderson, 1963; 1973). The application of BLUP technique to multiple traits was first described by Henderson and Quaas (1976). The first routine application of a univariate animal model for the genetic evaluation of on-farm tested pigs in Canada was described by Hudson and Kennedy (1985a). Since then, BLUP implementation to pig improvement was reported in other countries, e.g. in the United States (Schinckel et al., 1986), the United Kingdom (Webb and Bampton, 1988) and Australia (Brandt et al., 1988; Long et al., 1990).

Animal models can readily incorporate all known relationships in the population. Inclusion of all relationships improves the accuracy of evaluation by avoiding biases that result from non-random mating (Tier and Graser, 1991) and by allowing the performance of all relatives to be used for predicting the genetic merit of the individual. There are other benefits connected with genetic evaluation based on the mixed model methodology. Because BLUP's for genetic merit are cumulative over time, they facilitate assessment of genetic change in the population permitting routine auditing of the efficiency of breeding programmes (Kovac and Groeneveld, 1990a). The use of best linear unbiased predictions of

breeding values for the estimation of genetic trenchas been examined by Blair and Pollak (1984) and Belonsky and Kennedy (1984). Hudson and Kennedy (1985b) pointed out that genetic trend, estimated in the population under investigation, allows the effectiveness of livestock improvement strategies to be monitored and can assist in deciding the future emphasis of selection. An acrossherd evaluation allows for identification of superior animals across herds.

Management practices in pig breeding require that estimated breeding values are available to the breeder immediately after pigs complete their test, in order to be used for selection decisions. The estimation of breeding values is done within breed across nucleus farms. Increase in the computational load using BLUP, as compared to the calculation of a traditional selection index, is no longer a problem considering the dramatic advance in computer hardware and improved software algorithms. Pig breeding programmes require weekly evaluations, with only a few records added to each new evaluation. For each weekly run existing BLUP software allows the use of solutions from the previous week's run, thus starting close to the converged solutions for all but the latest crop of animals. This dramatically reduces the number of iterations required to achieve the new convergence (Kovac and Groeneveld, 1990b).

Multiple trait models account for covariances among traits, which should improve the accuracy of estimated breeding values, reducing the prediction error variance (PEV). The gain in accuracy over single trait analyses is due to the use of additional genetic information and an improved data structure (Thompson and Meyer, 1986). However, use of incorrect estimates of covariances may eliminate the advantage of multiple trait analyses (Henderson, 1975). Schaeffer (1984) carried out sensitivity analyses to determine the influence of assumed correlations in multiple trait analysis on the accuracy of ranking animals for genetic merit and found that increases of PEV were almost directly related to differences between

the true and estimated correlations. His recommendation was to use the best available estimates of correlations between traits.

The objective of this study was to examine the application of a multiple trait animal model for the estimation of breeding values of growth performance and reproduction traits of pigs tested on-farm and to investigate the genetic, environmental and phenotypic trends, as well as realised generation intervals and selection differentials in purebred populations of pigs in New Zealand.

5.3 Materials and Methods

5.3.1 Data

Performance records of on-farm tested pigs and sow reproduction records obtained from 3 New Zealand nucleus herds were used in this study. The analysis was based on test results of 23,562 Large White (LW) and 17,413 Landrace (LR) pigs recorded over the period from 1981 to 1994, and 5,904 Duroc records for the 1988 to 1994 period. The reproduction data included 3,106 Large White, 2,500 Landrace and 915 Duroc litter records. Individual on-farm test performance records for average daily gain (ADG, g/day) from birth to test day at average 21 weeks of age and ultrasonically measured backfat thickness (BF, mm) were obtained from weekly tests. On-farm selection occurred the next day after test records were processed. The data structure and distribution of individual performance records by breed are in Table 5.1. All Duroc records were collected on one farm, while LW and LR records each came from two nucleus herds.

Testing methods and information recorded for each pig were as described in Chapter 4 of this study.

Table 5.1 Number of records and data structure for average daily gain (ADG) and backfat_thickness (BF) by breed

Breed	Large White	Landrace	Duroc
Herd	2	2	1
Sex	2	2	2
Test Days 1	763	760	117
Sires	380	357	161
Dams	1,068	881	440
Litters	2,832	2,228	937
Animals ²	23,562	17,413	5,904

One test day each week or fortnight

For reproductive analyses, farrowing seasons with single farrowing records were eliminated. Number of purebred litter records and data structure for number of pigs born alive per litter (NBA) by breed are in Table 5.2.

Table 5.2 Number of purebred farrowing records and data structure for number of pigs born alive per litter (NBA) by breed

Breed	Large White	Landrace	Duroc	
Herds	2	2	1	
Parities	10	8	8	
Farrowing seasons 1	59	59	41	
Sires of dams	305	269	100	
Dams with records	957	777	321	
Litter records	3,106	2,500	915	

³⁻monthly farrowing seasons defined as January to March, April to June, July to September and October to December.

Total number of animals in the model, including base parents (parents with no known ancestors).

The estimated means, phenotypic standard deviations $(\hat{\sigma}_p)$ and coefficients of variation for ADG, BF and NBA by breed are given in Table 5.3. Values of $\hat{\sigma}_p$ are those calculated by the Restricted Maximum likelihood (REML) procedures.

Table 5.3 Means (\bar{x}) , phenotypic standard deviations $(\hat{\sigma}_p)$ and coefficients of variation (CV%) for average daily gain (ADG), backfat thickness (BF) and number born alive per litter (NBA) by breed

Trait		Large White	Landrace	Duroc
ADG (g/day)	\overline{x}	559.11	559.74	517.40
	$\hat{\sigma}_p$	43.89	40.92	49.45
	CV%	7.88	7.33	9.58
BF (mm)	\bar{x}	13.32	14.06	12.80
	$\hat{\sigma}_p$	2.35	2.14	2.28
	CV%	17.54	15.10	17.65
NBA (pigs)	\bar{x}	10.71	9.93	9.27
	$\hat{\sigma}_p$	2.76	2.52	2.80
	CV%	25.79	25.43	30.14

5.3.2 Statistical Models

Separate analyses for performance test and reproduction data were undertaken. This is equivalent to assuming that the phenotypic and genetic correlations between NBA and the production traits (ADG and BF) are zero. For the performance test data, the following mixed model equation was used:

$$y_{ijkl} = h_i + s_j + \beta * p_{ijkl} + c_{ik} + a_{ijkl} + e_{ijkl}$$

where:

y_{iikl} is the ADG or BF observation on the ijklth pig,

 h_i is the fixed effect of the i^{th} herd \times test day,

 s_j is the fixed effect of the j^{th} sex of a pig (male or female),

 β is the (covariate) effect of age at test on y_{ijkl} ,

 p_{ijkl} is the age at test of the l^{th} pig of the j^{th} sex in the i^{th} herd \times test day,

 c_{ik} is the random effect of the k^{th} litter in the i^{th} herd × test day ~ $(0, I\sigma_c^2)$,

 a_{ijkl} is the random additive direct effect of the l^{th} pig of the j^{th} sex in the k^{th} litter $\sim (0, A \sigma_g^2)$,

and

 e_{ijkl} is the random residual (environmental) effect associated with the $ijkl^{th}$ observation ~ $(0, I\sigma_e^2)$.

 σ_g^2 , σ_c^2 and σ_e^2 are the additive direct, litter and residual variances, respectively.

The covariance between additive direct and litter effects was ignored (assumed equal zero). The fixed effect of the i^{th} herd × test day, h_i , was defined

for each animal, based on the weekly or fortnightly test day within the herd in which the pig completed the test. All pigs completed test in the herd of their birth, so all litters were nested within their respective herd of origin. Both parents of all pigs with records were identified and the numerator relationship matrix, A, included all tested pigs and their parents. Only a very small number of animals imported from overseas was introduced into the herd populations in recent years, with their progeny tested during the 1992 and 1993 testing seasons, and grouping of parents of imported animals (Quaas, 1988; Westell et al., 1988), to account for differences in genetic merit of the migrants was not included in the analysis. This may have caused some bias.

For the sow reproductive performance data, a univariate animal model equation with repeated records was assumed:

$$y_{ijkl} = h_i + p_j + m_k + a_{ijkl} + e_{ijkl}$$

where:

y_{iikl} is the observation on the ijklth sow litter size,

 h_i is the fixed effect of the i^{th} herd \times year \times season of birth of the litter,

p, is the fixed effect of the jth parity of the sow,

 m_k is the permanent environmental effect due to k^{th} sow ~ $(0, I\sigma_m^2)$,

 a_{ijkl} is the random direct additive genetic effect of litter record of the k^{th} sow in the i^{th} herd \times year \times season \sim (0, $A\sigma_g^2$),

and

 e_{ijkl} is the random residual (environmental) effect associated with the $ijkl^{th}$ observation $\sim (0, I\sigma_e^2)$.

The permanent environmental effect of sows was fitted as a random effect. It was assumed that permanent effects had the same variances for all sows and were mutually uncorrelated, therefore the variance-covariance matrix of this effect (V_m) was proportional to the identity matrix (I), and assumed uncorrelated to additive genetic effects.

The models described above were used in the prediction of breeding values of animals. They were similar to those used to estimate variance components by restricted maximum likelihood (Chapter 4).

5.3.3 Computing Strategy

A multivariate prediction and estimation software package PEST (Groeneveld and Kovac, 1990) was used to analyse the data. Three types of solvers are available within the *PEST* package. They are: (1) sparse storage of coefficients in memory, (2) Gauss-Seidel/Jacobi iteration on data (Van Vleck and Dwyer, 1985) with complete storage of diagonal blocks, and (3) Gauss-Seidel iteration on data with storage of level elements only. The last solver is the most memory efficient but has the highest CPU requirements. All three types of solvers can be combined in one model run. The algorithms used in PEST and their implementation are described in Groeneveld and Kovac (1990) and Groeneveld et al. (1990). The mixed model equations for the present study were solved by storing coefficients of fixed effects in memory, and using a Gauss-Seidel iteration on data to solve litter and animal effects with a large number of levels. This strategy considerably reduced memory requirements and led to a substantial increase in the rate of convergence, as the fixed effects placed in memory were solved simultaneously in a double block iteration (Groeneveld et al., 1990). The absolute stopping criterion of 0.001 for the iterative process was chosen to assure high level of accuracy in evaluating genetic trends.

Two sets of data files had to be supplied for each breed, one with the pedigree information and date of birth field for each animal in the model, the latter required for taking inbreeding into account, and a second file with animal ID's and the input information for each animal, such as herd, sex, parity, test and litter number, and trait data. A parameter file containing *PEST* commands, description of raw data structure, statistical model description and genetic parameters had to be supplied for each analysis. Genetic parameters specified for each breed were those calculated using the REML procedures (Chapter 4).

Genetic trends for growth performance traits were calculated from means of estimated breeding values (EBV's) for performance-tested pigs, averaged over year of test. For reproduction traits, EBV's were averaged over year of birth for all pigs born alive. Because breeding values are cumulative over time, the average breeding value of all animals at each time period reflects the genetic level of the population at that time for the particular trait (Kovac and Groeneveld, 1990a). Environmental trends for growth traits were calculated from sums of solutions for fixed effects of herd × test day, sex and animal age on test, weighted by the number of animals of a particular sex and age in each test group, and averaged on an annual basis. Environmental trends for NBA were calculated from sums of solutions for fixed effects of herd x year x season of birth and sow parity, weighted by the number of sows in each parity and farrowing season, and averaged on an annual basis. Sums of annual genetic and environmental means in each trait and breed gave the annual phenotypic means. The genetic, environmental and phenotypic means were regressed across years to predict the respective annual trends. The regression was weighted by the number of records in each year. The average breeding values of the base parents (parents with no known ancestors) were set to zero, with all other solutions modified accordingly.

5.3.4 Predicted Rates of Response to Selection

The annual rate of response to selection (ΔT) can be predicted as:

•
$$\Delta T = \bar{i} \sigma_T r_{TI}/L$$
 (Falconer, 1981)

where \bar{i} (the intensity of selection) is the average phenotypic deviation of selected animals from the mean of the population measured in phenotypic standard deviation units and pooled across sexes, σ_T is the additive genetic standard deviation (for single trait selection $\sigma_T = \sqrt{h^2 \sigma_p^2}$ where h^2 is the heritability, and σ_p^2 the phenotypic variance), r_T is the correlation between an individual's breeding value and an estimate of it, which is a measure of the accuracy of prediction, and L is the average generation interval in years pooled across the two sexes. The parameters can be varied in an attempt to maximise ΔT although σ_T is largely beyond the breeder's control (Haley *et al.*, 1988). The age at breeding affects the generation interval, and the size of the parental population and the number of offspring selected affects the intensity of selection. The accuracy of estimation of breeding values can be improved by:

- increasing the number of relatives providing information
- increasing the number of measured traits
- improving the accuracy of trait measurement and data recording.

Possible rates of genetic change in commercial traits and estimates of the parameters for generation intervals and selection intensity were derived by Smith (1984) for pigs, poultry, sheep and beef cattle. The estimated possible genetic response per year in pigs, expressed as a percentage of the mean was 2.7% for weight gain and 1.6% for the lean percentage (Smith, 1984). Values of

parameters used in the above prediction of genetic gain were: generation intervals of one year for both males and females and selection intensities of 1.8 for males and 0.8 for females. Means (\bar{x}) , h^2 , σ_p and r_{77} were 700 g/day, 0.30, 49 g/day and 0.55 for weight gain, and 57%, 0.30, 2.28% and 0.55 for lean percentage, respectively.

In this study, the predicted selection intensity for New Zealand nucleus herds was derived assuming a 100 sow herd, 8 male and 8 female offspring produced per sow per year, and 50% of offspring available for selection after culling for conformation traits such as foot and leg structure, soundness of teats and body and ham structure. The emphasis was on selection of boars and gilts from several families, avoiding selection of litter-mates. The replacement rates for nucleus sires and dams were assumed at 200% and 75%, respectively. That is, a mating ratio of one boar to 10 sows was assumed, with a requirement for 20 replacement sires and 75 replacement females per annum giving respective selection proportions of 5% and 18.8%. Tables of standardised selection differentials indicate that this would amount to $\bar{i} = 1.9$ standard deviations of superiority for sires and $\bar{i} = 1.3$ for dams, with a combined $\bar{i} = (1.9 + 1.3)/2 = 1.6$ standard deviations.

The expected generation interval for boars (that is, the average age of boars when progeny are born), was calculated assuming the age of sires on the birth of progeny conceived from their first mating at about 325 days (210 days + 115 days). Boars were assumed to be in service for 150 days (5 months) on average, by which time they conceived 10 purebred litters. Their last litter was born at 475 days (210 + 150 + 115) of age. Over the boars' life time, the expected average age when progeny are born is then (325 + 475)/2 = 400 days or 1.1 years.

It was assumed that all gilt replacements were selected from the first four parities, with the expected distribution of farrowings by parity, sow age at farrowing and mean litter size at birth as follows:

Table 5.4 Expected distribution of farrowings by parity, sow age at farrowing and mean litter size at birth

Parity	Percent farrowings	Average sow age at	Mean litter size	
of sow	(%)	farrowing (days)	at birth	
1 st	34	339	9.8	
2 nd	31	484	10.6	
3 rd	25	641	11.2	
4 th	10	807	11.4	

The expected generation interval for sows, given the above assumptions, is 514 days or 1.4 years.

The average generation interval (L) obtained from pooling estimates of the generation intervals of boars and sows is (400 + 514)/2 = 457 days or 1.25 years.

The Meat and Livestock Commission (MLC) on-farm selection index (I_{MLC}) used in New Zealand over the last 14 years was as follows:

$$I_{\text{MLC}} = (10.14 * \overline{A}\overline{D}\overline{G}) - (0.0892 * \overline{F}\overline{A}\overline{T}) + (0.002 * \overline{L}\overline{W}\overline{T})$$

where \overline{ADG} , \overline{FAT} and \overline{LWT} are the phenotypic deviations of individual measurements from the contemporary group average for average daily gain from birth to test day (kg), a sum of two ultrasonic fat depth measurements taken 4 cm (C4) and 8 cm (K8) off the mid-line at the position of the last rib (mm), and a test liveweight (kg), respectively.

The approximate accuracy (r_{T}) of the MLC index was 0.308 (Guy, 1985), being the correlation of the index with the MLC objective (T):

$$T = (220 * LTGR) - (15 * DF)$$

where LTGR is the average daily lean tissue deposition (kg) and DF is the average daily feed consumption (kg).

New Zealand pig breeders used the MLC index assuming that genetic parameters for British lines of pigs and the economic weights for traits in the British production/marketing system at the time the index was derived were the same as the New Zealand situation.

The predicted genetic gains in ADG and BF from selection on the MLC index were calculated, using the original MLC index weights and economic values of the objective traits. The REML estimates of genetic and phenotypic parameters for ADG and BF calculated for New Zealand nucleus herds and averaged across breeds were used (Table 5.5).

Table 5.5 Assumed heritabilities (h^2) , means (\bar{x}) , and phenotypic (σ_p) and genetic (σ_g) standard deviations for ADG and BF

Trait	h^2	\overline{x}	σ_p	σ_{g}
ADG (g/day)	0.20	550	43.0	19.2
BF (mm)	0.45	13.5	2.3	1.5

The average genetic and phenotypic correlations between ADG and BF estimated for the analysed New Zealand nucleus herds were 0.35 and 0.40, respectively. For the remaining component traits, New Zealand estimates were not available, and the original MLC parameters were used.

5.4 Results

5.4.1 Trends

The annual genetic, environmental and phenotypic trends for ADG, BF and NBA are presented in Table 5.6 and compared to predicted genetic gains.

Table 5.6 Annual genetic, environmental and phenotypic trends for ADG, BF and NBA traits for Large White, Landrace and Duroc breeds, and predicted genetic gains from selection on the MLC index

Ti	rait: AD	ADG (g/day)		Bl	BF (mm)			NBA (pigs/litter)	
Trend		±s.e.	P^{1}		±s.e.	P^{1}		±s.e.	P^{1}
Large Wh	ite ²								
Genetic	2.65	± 0.09	**	-0.22	± 0.02	**	-0.001	± 0.01	
Environmental	2.49	± 1.22		0.01	± 0.02		0.02	± 0.02	
Phenotypic	5.13	± 1.24	**	-0.21	± 0.03	**	0.02	± 0.02	
Landra	ice ²								
Genetic	2.13	± 0.13	**	-0.21	± 0.02	**	0.001	± 0.002	
Environmental	3.51	± 1.18	*	0.02	± 0.04		0.09	± 0.02	**
Phenotypic	5.64	± 1.26	**	-0.19	± 0.05	**	0.09	± 0.02	**
Dur	oc ³								
Genetic	4.33	± 0.18	**	-0.21	± 0.02	**	0.07	± 0.003	**
Environmental	-7.44	± 2.97		-0.28	± 0.09	*	0.01	± 0.08	
Phenotypic	-3.12	± 2.93		-0.49	± 0.08	**	0.08	± 0.08	
Predicted gains ⁴	4.13	g/day		-0.88	mm		0		

¹ * P < .05; ** P < .01

² 14 years of data (1981 to 1994)

³ 7 years of data (1988 to 1994)

Predicted genetic gains per year of selection on the MLC index, assuming selection intensity, $\bar{i} = 1.6$, and generation interval, L = 1.25 years.

Estimated annual genetic responses in ADG and BF were favourable (P < .01) for analysed Large White (LW), Landrace (LR) and Duroc breeds. In LW and LR, almost no genetic change was observed in ADG and BF between 1981 and 1984 test year (Figures 5.1 and 5.2). In the following 10 years of testing, annual genetic trends calculated for LW and LR were, respectively, 2.78 ± 0.10 and 2.37 \pm 0.14 g/day/year for ADG and -0.28 \pm 0.01 and -0.28 \pm 0.02 mm/year for BF. Annual genetic trends observed in Duroc between 1988 and 1994 were 5.33 ± 0.18 g/day/year for ADG and -0.21 ± 0.02 mm/year for BF. Higher annual genetic progress for ADG found in Duroc, compared to LW and LR, was probably due to lower culling levels of top-rated pigs on physical conformation. LR herds were on average 10% to 20% smaller in size than LW, making it more difficult to find suitable replacements. This may explain lower genetic trends found in LR breed. As expected, the NBA genetic trends for LW and LR were not significantly different from zero, as there was no selection for NBA prior to 1994. Interestingly however, an annual genetic improvement of 0.07 pigs born alive/litter was observed in Duroc. This may be due to a management policy of culling sows producing smaller litters (independent culling levels effect), below a minimum guideline of 9 pigs born alive per litter, and higher than average heritability in NBA of 0.18 estimated for that breed. Annual means of the estimated breeding values for ADG, BF and NBA are shown in Figures 5.1, 5.2 and 5.3, respectively. A small decrease in the LW and LR annual genetic gain observed in the 1992 test season (Figure 5.1) was influenced by the nucleus herd expansion and higher demand for the nucleus replacements to populate the new farm unit.

Figure 5.1 Genetic trends for Average Daily Gain (ADG) for Large White, Landrace and Duroc breed

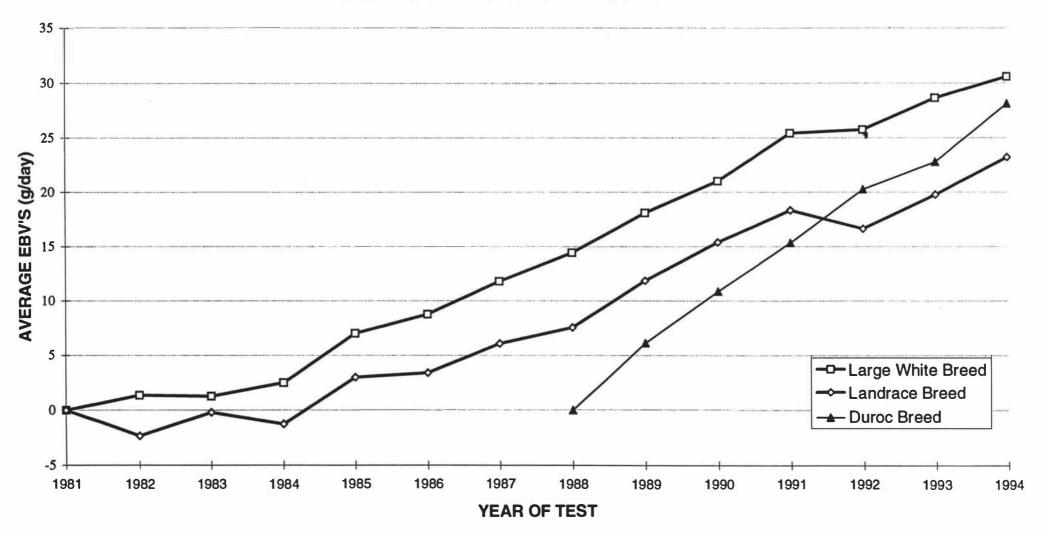


Figure 5.2 Genetic trends for Backfat (BF) for Large White, Landrace and Duroc breed

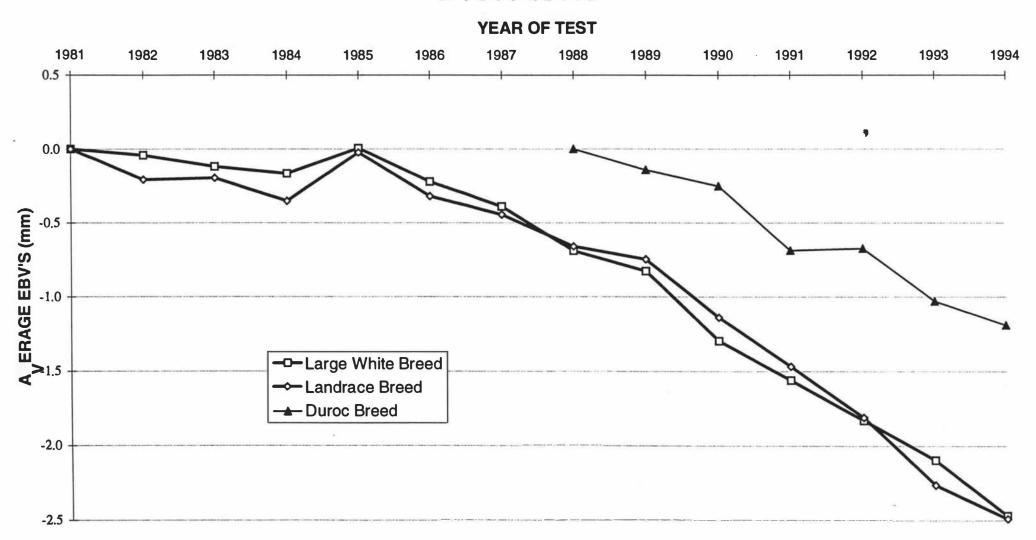
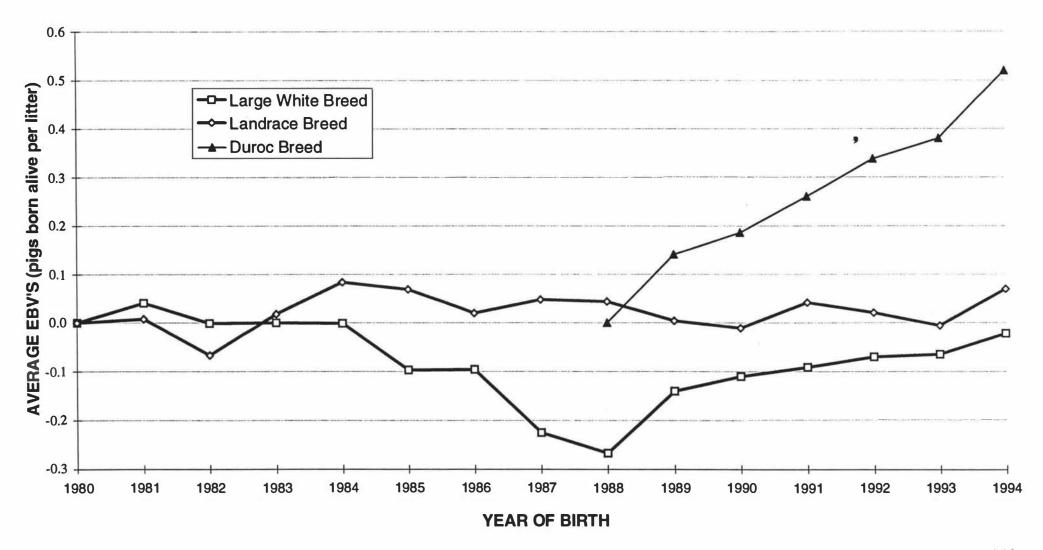


Figure 5.3 Genetic trends for Number Born Alive (NBA) for Large White, Landrace and Duroc breed



Environmental and phenotypic trends observed for ADG in Duroc herd were unfavourable but not significant (Table 5.6), with a large decrease in growth in the 1989 - 1990 test season (Figures 5.4 and 5.7). LW and LR breeds had favourable environmental and phenotypic trends in ADG, with a marked improvement observed in the 1988 - 1990 test season. The overall environmental and phenotypic trends for BF found in Duroc were favourable (Figures 5.5 and 5.8), and no significant environmental change was found in LW and LR. Environmental and phenotypic trends for NBA were positive although not significantly different from zero, with the exception of Landrace breed, which showed a significant improvement in the environmental and phenotypic trends. Duroc herd again demonstrated a severe deterioration in the environmental and phenotypic performance during the 1989 farrowing season. The annual environmental and phenotypic trends for NBA are presented in Figures 5.6 and 5.9, respectively. Observed environmental trends can be attributed to changes in health status, stock management and quality of diets in the respective herds. No significant environmental trends due to seasonal climatic changes were observed.

The realised annual genetic gain for ADG in Duroc exceeded the predictions by about 5%, while observed genetic trends in LW and LR were lower than the predicted genetic gains per year of selection on the MLC index, assuming selection intensity, $\bar{i}=1.6$, and generation interval, L=1.25 years (Table 5.6). Only 24% to 32% of the annual genetic predictions in BF improvement were realised. One of the reasons to such low response may be unfavourable correlations between low backfat levels and physical conformation traits, such as feet and leg soundness. Another factor may be selection from small contemporary batches of pigs, which limits the choice of highly rated, physically sound animals, ultimately reducing the real selection differentials obtained.

Figure 5.4 Environmental trends for Average Daily Gain (ADG) for Large White, Landrace and Duroc breed

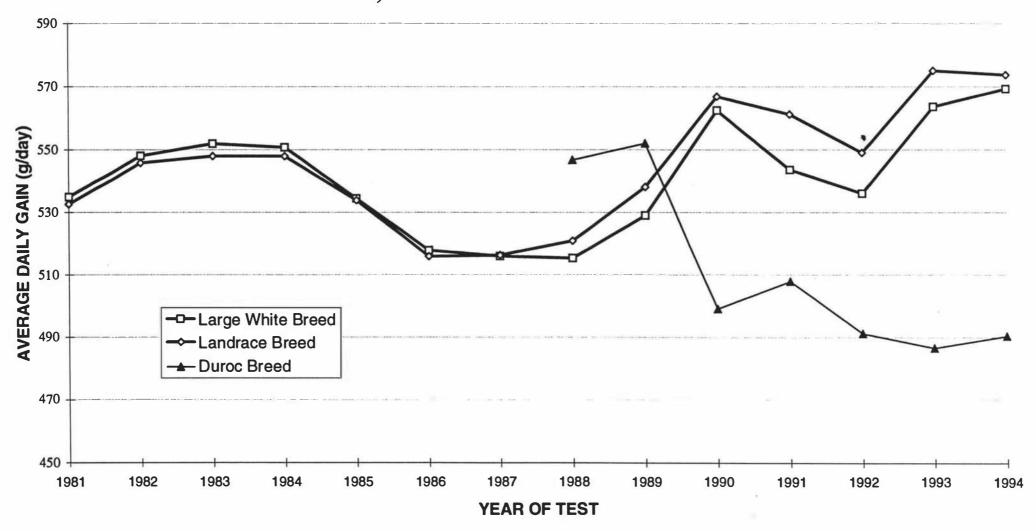


Figure 5.5 Environmental trends for Backfat (BF) for Large White, Landrace and Duroc breed

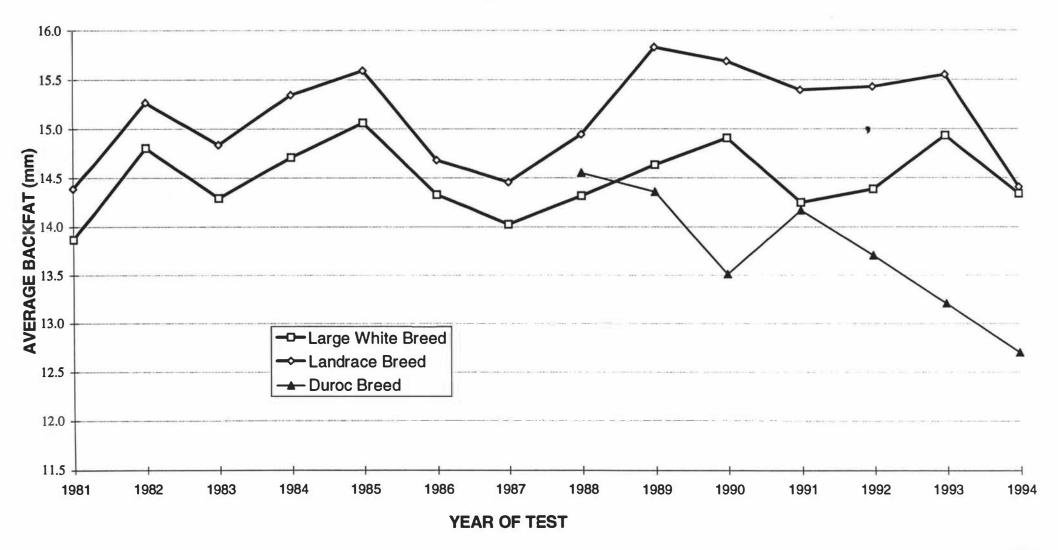


Figure 5.6 Environmental trends for Number Born Alive (NBA) for Large White, Landrace and Duroc breed

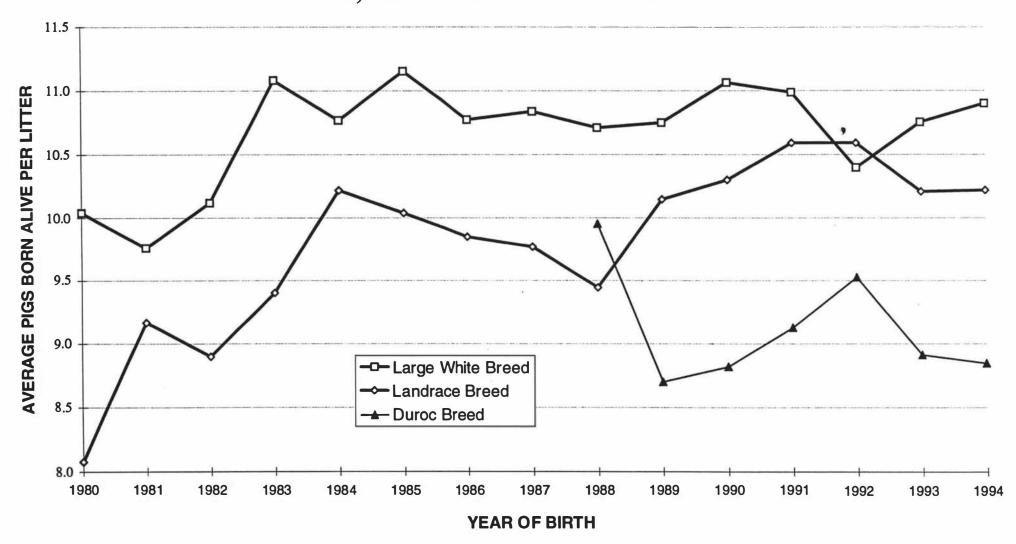


Figure 5.7 Phenotypic trends for Average Daily Gain (ADG) for Large White, Landrace and Duroc breed

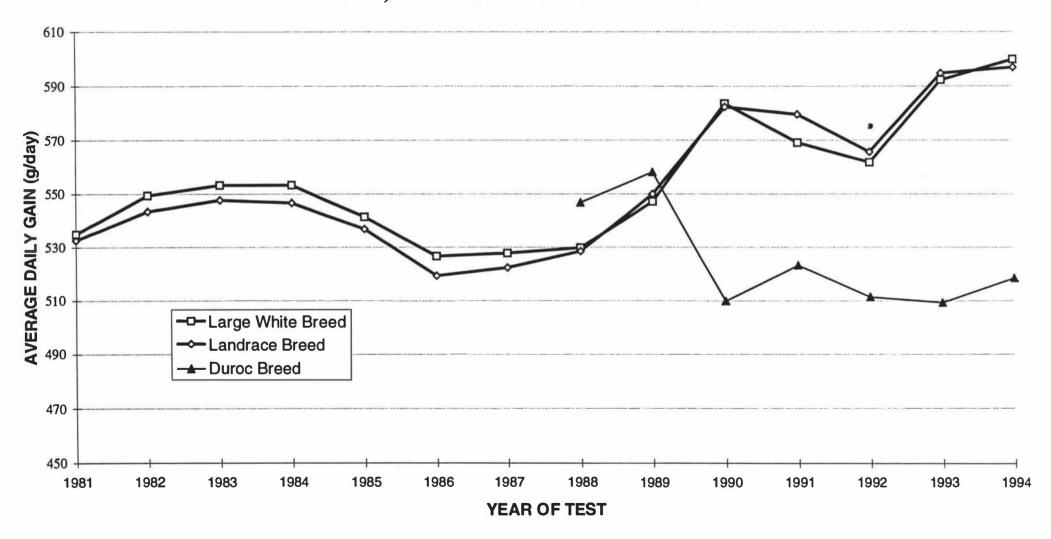


Figure 5.8 Phenotypic trends for Backfat (BF) for Large White, Landrace and Duroc breed

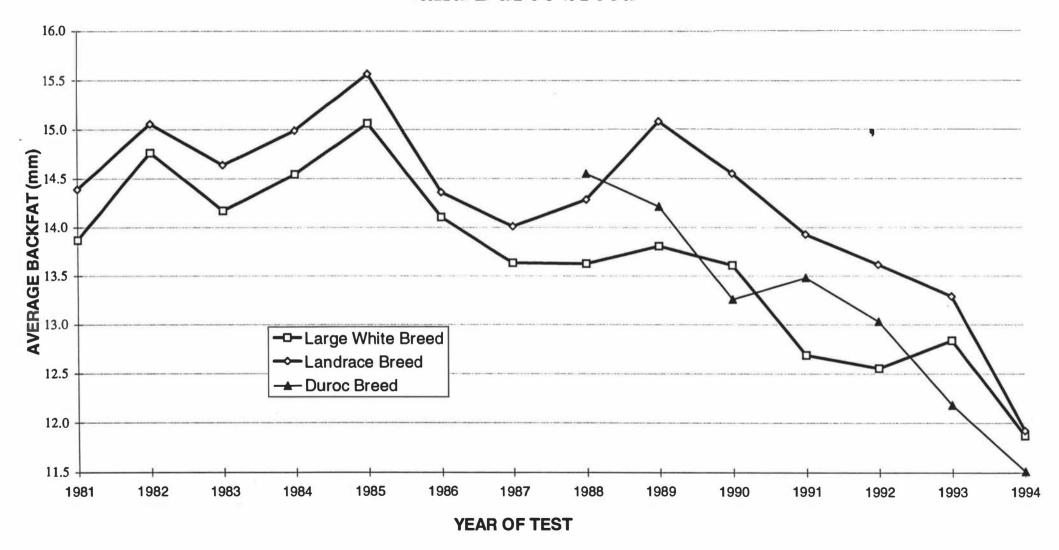
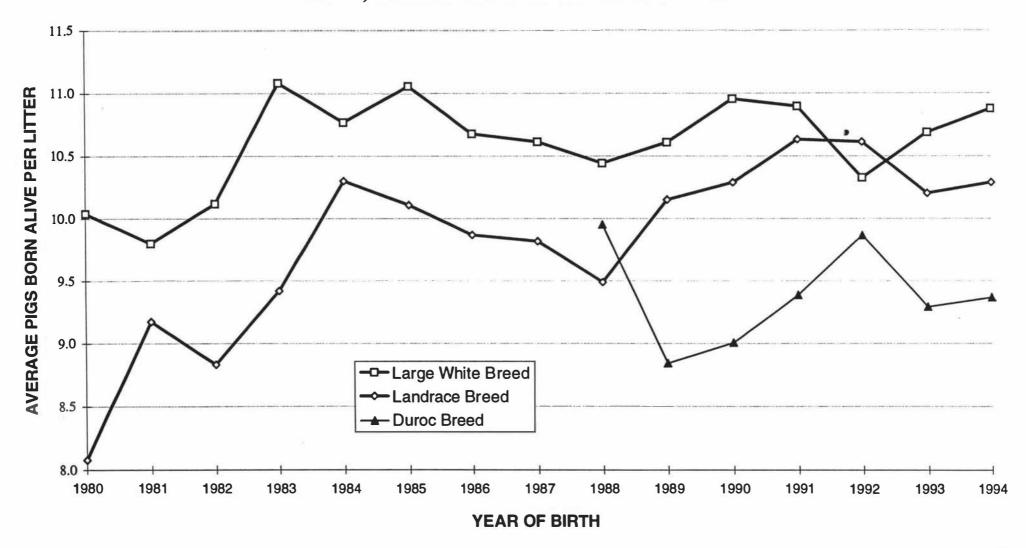


Figure 5.9 Phenotypic trends for Number Born Alive (NBA) for Large White, Landrace and Duroc breed



5.4.2 Generation Intervals

Generation intervals for Large White, Landrace and Duroc boars and sows were calculated as the average age of respective parents on birth of their progeny. The annual generation intervals for boars, sows and combined, averaged over year of birth of progeny are in Figures 5.10, 5.11 and 5.12, respectively. Breed averages are compared with the expected generation intervals of 400 days for boars, 514 days for sows and 457 days (1.25 years) combined. The average realised generation intervals across years by breed are in Table 5.7.

Table 5.7 Generation intervals (L) by breed - realised averages across years

Breed	Boars		So	ws		Combined		
	(days)	(%) 1	(days)	(%) 1	(days)	(years)	(%) ¹	
LW	415	103.9	627	122.0	521	1.43	114.1	
LR	421	105.3	612	119.0	517	1.42	113.1	
Duroc	565	141.3	583	113.3	574	1.57	125.6	
Overall	435	108.7	616	119.9	526	1.44	115.0	
Expected L	400	100.0	514	100.0	457	1.25	100.0	

relative to expected L.

The combined generation intervals for all breeds were about 15% (68 days) higher than the expected ones. The highest generation intervals for the nucleus boars were found in Duroc, exceeding the expected values by about 41%. The sow generation intervals for all three breeds were much higher than expected, ranging from 13% to 22% over the expected guidelines.

Figure 5.10 Generation Intervals for Large White, Landrace and Duroc boars

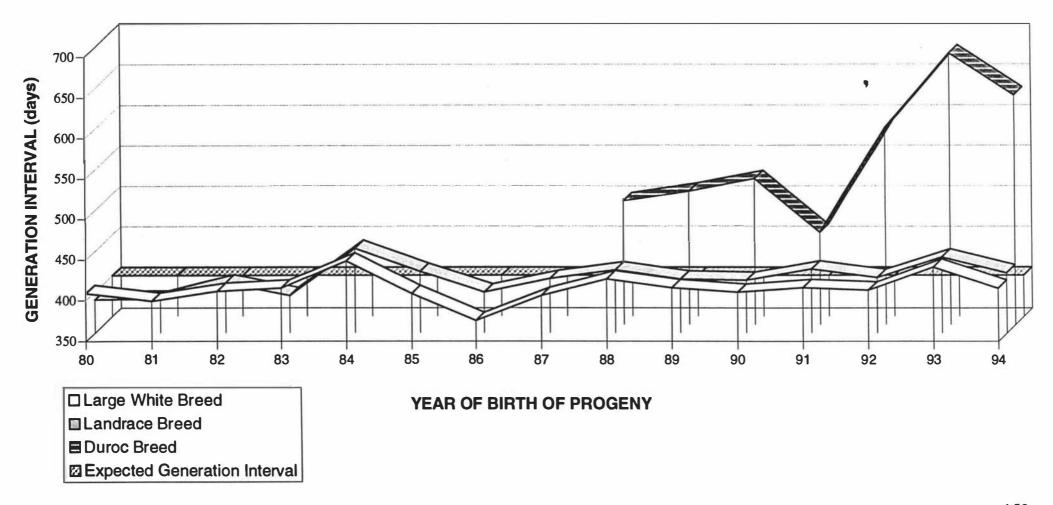


Figure 5.11 Generation Intervals for Large White, Landrace and Duroc sows

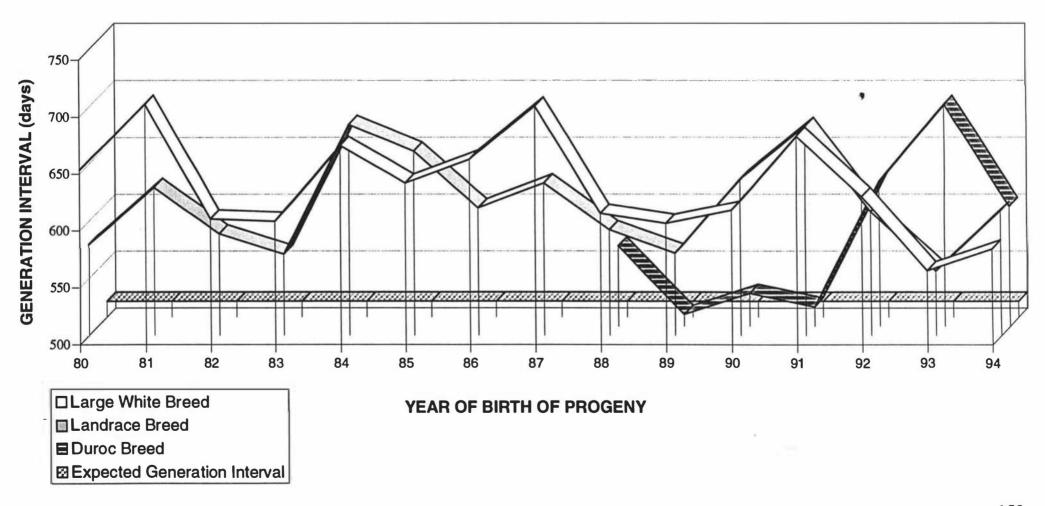
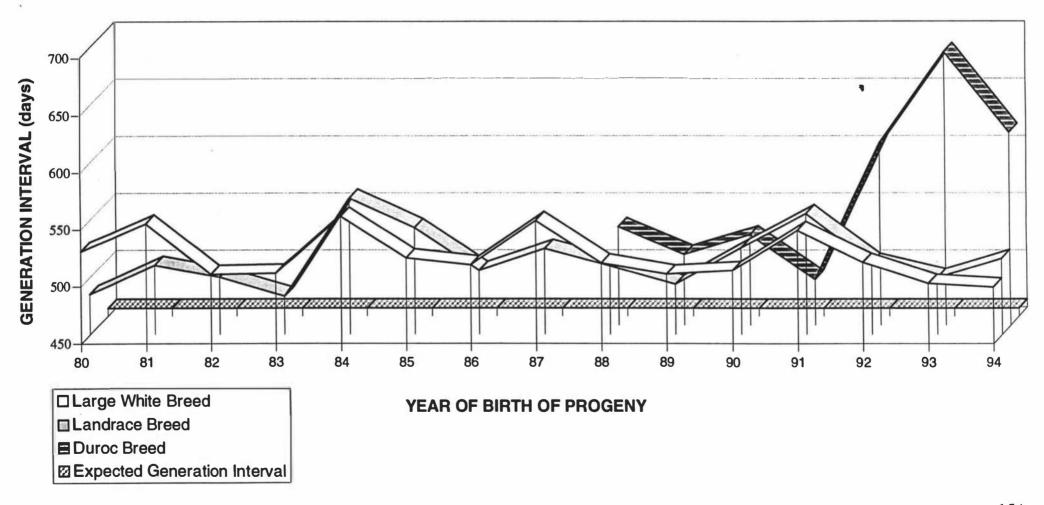


Figure 5.12 Generation Intervals for Large White, Landrace and Duroc (boars and sows combined)



5.4.3 Selection Applied

Selection of Large White, Landrace and Duroc replacements between 1981 and 1994 was based on the MLC selection index. Selection criteria were ADG and BF adjusted for the liveweight taken when the pig was measured. The average realised selection differentials (in actual and standardised units) for ADG and BF, calculated for replacement boars, gilts, and boars and gilts combined, are in Table 5.8.

Table 5.8 Realised selection differentials for ADG and BF traits by breed and sex

					Lander of the second	
		Selection	Selection d	ifferentials		
	I	er generation	Average p	per year 1		
	В	oars	Gi	lts	Boars a	SHIPS TO SHIP SHIPS TO SHIP SHIP SHIP SHIP SHIP SHIP SHIP SHIP
		Standardised		Standardised		Standardised
	(g/day or mm)	units	(g/day or mm)	units	(g/day or mm)	units
Large White						
ADG (g/day)	54.76	1.25	30.98	0.71	30.00	0.68
BF (mm)	-0.27	-0.12	-0.60	-0.26	-0.31	-0.13
Landrace						
ADG (g/day)	52.86	1.29	31.40	0.77	29.77	0.73
BF (mm)	-0.37	-0.17	-0.52	-0.24	-0.32	-0.15
Duroc						
ADG (g/day)	69.04	1.40	36.97	0.75	33.76	0.68
BF (mm)	-0.11	-0.05	-0.37	-0.16	-0.15	-0.07

Mean values for boars and gilts divided by the average generation intervals (in years) taken from Table 5.7.

Selection differentials for each nucleus replacement were calculated as deviations of the selected animal's unadjusted record from the contemporary group (test day) and averaged across all selected animals within breed, sex and trait. The calculated averages represent selection differentials per generation, and the combined average values for boars and gilts were divided by the realised generation intervals (from Table 5.7), to obtain the actual average selection differentials per year. Standardised selection differentials for ADG and BF were obtained by dividing realised selection differentials by the respective phenotypic standard deviations taken from Table 5.3.

Across all breeds, more selection emphasis was placed on ADG in boars than in gilts, despite the same selection index being used for both sexes. On the other hand, higher selection differentials in BF were achieved in gilts compared to boars. Physical conformation played a major part in selection of nucleus replacements. This may explain some of the observed sex differences, as more emphasis was placed on foot and leg structure and body and ham conformation in boars compared to gilts, and soundness of teats was more emphasised in gilt selection. Tested boars were on average leaner than gilts and had higher growth rates.

Selection of replacements was based on index; therefore, selection differentials for individual traits are of secondary importance. Table 5.9 summarises average realised and predicted selection differentials for the MLC index by breed and sex. Phenotypic standard deviations calculated for the MLC Index ranged from 2.1 to 2.2, depending on breed and sex, with the contemporary group index mean equal to zero. The predictions were derived assuming $\bar{i} = 1.6$ standard deviations of superiority, divided by L = 1.25 years, that is, 1.28 standard deviations per year.

Table 5.9 Predicted and realised selection differentials for the MLC index by breed and sex

		Selection d	Selection	Selection differentials		
	pe	er generation	Average	per year 1		
	Boars		Gilts		Boars and gilts combined	
	Realised	Standardised	Realised	Standardised	Realised	Standardised
Large White						
MLC Index	2.80	1.27	1.94	0.89	1.66	0.76
Landrace						
MLC Index	2.79	1.24	1.89	0.88	1.65	0.75
Duroc						
MLC Index	3.35	1.52	2.04	0.97	1.72	0.79
Predictions		1.90 ²		1.30 ²		1.28 ³

Mean values for boars and gilts divided by the average generation intervals (in years) taken from Table 5.7

Proportion of growers selected as replacements ranged from 2.7% to 3.4% for boars and 8.9% to 13.2% for gilts. On average, approximately 0.75 to 0.79 standard deviations of selection for the index were realised per year, being 59% to 62% of the guidelines predicted. Lower than predicted selection differentials in all studied herds may be attributed to not following the proposed breeding programme more closely, particularly in the earlier years of selection. There was not enough emphasis placed on selecting replacements with the highest index values, with too much culling based on physical appearance and conformation traits only. The emphasis on selection of boars and gilts from several families, to avoid selection of litter-mates and potential inbreeding in the relatively small

² Predicted selection intensity, \bar{i} per generation of selection

Pooled selection intensity, $\bar{i} = 1.6$, divided by pooled generation interval, L = 1.25 years.

herds, may have also contributed to low selection intensities. The combined generation intervals were also longer than expected, particularly in the Duroc herd, contributing to the reduction in annual genetic gain. Boars and sows were often kept in breeding much longer than recommended, and several sows were cross-mated in their early parities instead of being pure-mated, contributing to the increase in the generation interval.

Increasing the generation interval can result in less replacements being required, which may theoretically improve the realised selection differentials. The need for less replacements may allow more stringent selection of boars and gilts with higher index values. However, that has not been observed in the analysed herds. As a general rule, to optimise the selection response, ΔT , a balance is needed between the number of replacements which affect the selection intensity, \bar{i} , and the generation intervals.

5.5 Discussion

This study showed desirable changes in performance traits of the analysed nucleus herds. The genetic changes compare favourably to the rate of improvement found in overseas studies. Kennedy (1987) estimated genetic change of age to 90 kg in Canadian populations of Yorkshire, Landrace and Duroc breeds in the range from -0.05 to -0.78 days per year, which is equivalent to a change in ADG of about 0.2 to 2.6 g/day, assuming mean age to 90 kg at 163.5 days (Kennedy *et al.*, 1986). Changes in BF found for these breeds ranged from -0.06 to -0.12 mm per year. The genetic trends found in Polish Large White nucleus herds were small (0.04 g/day/year for ADG and -0.009 mm/year

for BF) and not significant (Kaplon et al., 1991). Higher genetic trends in ADG were estimated by Ferraz and Johnson (1993) for some North American Large White and Landrace herds, averaging at 6.9 g/day/year. However, estimated genetic gains in BF for those herds were low at -0.06 mm/year. Estimates of genetic trends in ADG found for the Swiss Yorkshire and Landrace were 0.54 and 0.86 g/day/year, respectively (Hofer et al., 1992). Genetic responses in daily gain (weaning to test day) for the German Large White and Landrace were estimated at 2.40 and 5.47 g/day/year, respectively (Kovac and Groeneveld, 1990b), and the estimated annual genetic trends of 2.5 g/day for growth rate from birth to slaughter were found by Lundeheim et al. (1994) in the Swedish pig breeding programme.

Some factors may restrict possible rates of genetic change. The intensities of selection may be eroded in practice by other criteria such as appearance or physical soundness. For example, Webb et al. (1991) found that visual selection in a group nucleus consisting of 1300 sows approximately halved the rate of improvement for backfat. Mortality or infertility of selected replacements, errors in selection, inappropriate adjustment for environmental effects and selection from small contemporary batches all tend to reduce the realised selection differentials. Another factor which may reduce the estimated responses by up to 20% is that selection of parents gives rise to a temporary disequilibrium with less genetic variation for selection among offspring (Bulmer, 1971). With continuous long-term selection, there are theoretical limits to selection response. These may be due partly to small population size leading to chance fixation of unfavourable genes, or to unfavourable correlations among selected traits and to loss of reproductive fitness (Smith, 1984). Currently, it is thought that the mean performance in traits such as fertility, leg soundness, longevity and disease resistance decline partly as a result of selection for production traits (Kanis, 1993). Ellis et al. (1988) have found that long-term genetic improvements in backfat thickness have led to a reduction in the additive genetic variation in

fatness and, therefore, diminished rates of response. Another suggestion by Ellis et al. (1988) was that the repeatability and predictive accuracy of ultrasonic backfat thickness measurements are reduced in leaner pigs; therefore, increasing possible errors in the estimation of backfat thickness and contributing to lower response in that trait in latter generations. A recent study of correlation between ultrasonically measured backfat thickness and backfat measurements taken on pig carcasses with an optical Hennessy grading probe suggest this correlation to be as low as 0.6 in some New Zealand nucleus populations (P. Morel personal communication).

Decreasing the average generation interval can theoretically increase the expected annual genetic change. Smith (1984) used generation intervals of one year for boars and for sows in his estimations of predicted genetic response per year in pigs. However, a more realistic pooled generation interval of 1.25 years for New Zealand nucleus pig populations was assumed in this study. This compares with average realised generation intervals ranging from 649 to 830 days (1.8 to 2.3 years) found by Lundeheim *et al.* (1994) for Swedish Landrace and Yorkshire breeds. In this study, the actual generation intervals of approximately 1.4 years were found for New Zealand breeds.

It appears that during the first 4 years of selection (1981 – 1984) no attention was paid to the performance index selection in LW and LR and too much emphasis was placed on other characteristics, such as physical appearance (Garrick, 1985). The following 10 years of selection produced consistent, almost linear genetic trends in ADG and BF in both breeds.

Selection objectives for LW and LR herds were re-defined in early 1994 and an additional trait of NBA was included in the selection index. Also in early 1994, a DNA test for the presence of the halothane gene - "HAL-1843-nm" (Fujii et al., 1991) was introduced to screen nucleus stock against this undesirable

gene. Pigs carrying the mutant HAL gene on both chromosomes are called affected. Affected pigs are prone to the porcine stress syndrome and liable to sudden death in response to any form of stress. The gene is also the main cause of low water-holding capacity by pork, leading to PSE (pale, soft, exudative meat). However, the presence of the halothane gene increases carcass lean content and killing-out percentage (Simpson and Webb, 1989). Animals carrying one copy of the HAL gene are called carriers and appear to show intermediate levels of leanness and stress susceptibility between the normal (HAL gene-free) and affected pigs. The HAL gene test allows identification of both the affected as well as carrier pigs. Currently, the disadvantages of the HAL gene are considered to outweigh its advantages, and all affected as well as carrier pigs are culled, irrespective of their breeding value. Reduced selection emphasis on growth and backfat (less pigs to select from) and the removal of (potentially leaner) HAL gene carriers may slow down the rate of genetic improvement in these traits, particularly in the LR breed, which was found to have much higher frequency (44%) of the halothane gene carriers and affected pigs, compared to 5% for LW.

Improved accuracy and elimination of selection bias in the estimation of fixed effects, attributed to selection using BLUP rather than the traditional selection index, as well as larger nucleus populations will at least partially compensate for the above deficiencies. Several studies (Belonsky and Kennedy, 1988; Keele *et al.*, 1988; Sorensen, 1988; Wray, 1988; Mabry and See, 1990; Long *et al.*, 1991) have demonstrated the opportunity for higher genetic and economic gains in pig breeding by using BLUP, when compared to the traditional index selection. The reported advantages ranged between 10% ($h^2 = 0.60$) and 55% ($h^2 = 0.10$) of gain in response by using BLUP. Use of artificial insemination to allow across-herd BLUP estimates increased the response to selection by another 38% (Mabry and See, 1990). One of the major advantages of BLUP over selection index is in the comparison of animals from different

generations or those born in different years. This allows "sequential culling", that is, selection of animals with the highest breeding values, regardless of age (Hagenbuch and Hill, 1978; Keele *et al.*, 1988). The BLUP simulation study of Wray (1988) suggested additional selection responses of 10% to 15% per annum from sequential culling on a trait with heritability 0.4 to 0.6.

Several researchers (Belonsky and Kennedy, 1988; Toro et al., 1988; de Vries et al., 1990; Bunter and Long, 1991) have found selection using BLUP in closed herds is associated with increased inbreeding and reduced genetic variance. However, these negative effects were more than offset by the increased accuracy of selection under BLUP. Most breeders would occasionally introduce immigrants to their herds and this can markedly reduce the average level of inbreeding.

The accuracy of estimated genetic trends calculated from estimated breeding values is dependent on the assumed heritabilities, as demonstrated by Blair and Pollak (1984) and Sorensen and Kennedy (1984). If assumed heritability is less (greater) than true heritability, then genetic trend is under (over) estimated (Sorensen and Kennedy, 1984). In this study, estimates of (co)variance components, genetic and phenotypic correlations and common environmental effects of traits were obtained for different breeds by REML procedures, and used to estimate breeding values and calculate genetic and phenotypic trends in the studied populations of pigs.

5.6 Conclusions

The genetic gains demonstrated in this study for Large White, Landrace and Duroc pigs have been achieved through selection decisions based on a selection index that combines ADG and BF traits. Since the index used was not optimised for the breeding objective and production and marketing systems of New Zealand, this almost certainly resulted in sub-optimal selection response towards an appropriate breeding goal.

The predicted annual selection intensity (\bar{i}) for boars and gilts combined was 1.28 standard deviations of selection for the index, assuming $\bar{i}=1.6$ standard deviations per generation of selection and the pooled generation interval (L) of 1.25 years. The annual realised selection differentials ranged from 0.75 to 0.79 standard deviations. They were obtained for each breed using the selection differentials achieved from selection on the MLC index, divided by the average realised generation intervals. The combined actual generation intervals for all breeds were about 15% (68 days) higher than expected. Therefore, the realised selection response was between 59% and 62% of that predicted.

The estimated annual genetic gains ranged from 2.1 to 4.3 g/day for ADG and -0.2 to -0.3 mm for BF. The observed genetic trends in ADG and BF were compared with the respective predicted gains of 4.13 g/day/year and -0.88 mm/year, calculated using the original MLC index weights and economic values, and assuming \bar{i} and L as above. The predicted genetic gains were generally substantially higher than those derived from the nucleus data except for Duroc ADG where predicted and actual gains were similar. Overall, the actual genetic changes in ADG and BF compared favourably with the rate of improvement found in similar overseas studies. The NBA genetic trends were negligible for

Large White and Landrace, but favourable (+0.07 pigs/litter/year) for Duroc breed.

This study provided estimates of genetic, environmental and phenotypic trends, realised selection differentials and generation intervals, which can be used to evaluate the effectiveness of the breeding programme. Further improvement in ΔT can be achieved by increasing the intensity of selection, decreasing the generation intervals, and improving the accuracy of estimation of breeding values. The first two tasks can be accomplished by optimising (balancing) the number of replacements and the age at breeding. The size of the parental population and its ratio with the number of offspring selected will directly affect the selection intensity.

Application of BLUP methodology for the estimation of breeding values of growth performance and reproduction traits of pigs tested on-farm was examined and across-herd evaluation was used to study the realised genetic gains and the effect of environment on performance. Further improvements in selection response are expected from the routine use of BLUP and AI technologies, allowing more accurate prediction of genetic merit of individual animals, providing comparisons between animals born and tested in different management regimes, time periods, and subjected to different amounts of prior selection, and allowing determination of genetic and environmental trends in the selected populations.

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CHAPTER 6

GENETIC CONNECTEDNESS BETWEEN

MANAGEMENT UNITS

6.1 Abstract

An across-herd genetic evaluation by Best Linear Unbiased Prediction using an individual animal model requires that animals in different management units are genetically related. A degree of genetic connectedness between herd-year units is influenced by the number of common (reference) animals used.

The genetic drift variance and the variance of estimates of management-unit effects methods have been used to estimate measures of connectedness between two nucleus Large White and between two nucleus Landrace herds, and to determine the implications of increasing the number of reference sires.

The estimated measures of connectedness for the studied nucleus populations had small values, indicating a high degree of genetic connectedness. Large White herds were more tightly connected than Landrace. Increasing the number of reference sires had favourable effect on the degree of genetic connectedness, improving the accuracy of genetic evaluation. Ten additional reference sires increased the degree of connectedness by up to 22%. However, excessive numbers of selected sires may have detrimental effect on selection differential and on the overall selection response. The presence of reference sires was found necessary to provide genetic links between herds to ensure that the nucleus units are genetically connected and that estimated breeding values are reliably comparable across herds included in the genetic evaluation.

6.2 Introduction

Genetic evaluation by Best Linear Unbiased Prediction (BLUP) and use of animal models (Henderson, 1973; Henderson and Quaas, 1976) opened new possibilities for across-herd genetic evaluation. BLUP can account for herd and management effects, but genetic links or connectedness between herds are required to assist in separating genetic and environmental effects. These links can be provided by the exchange of breeding stock amongst herds or management units. Artificial insemination (AI) provides a useful tool for establishing genetic links between herds, allowing utilisation of paternal half-sib relationships (Garrick, 1989). The genetic ties across environments and selection years are established by including relationships between animals in the Mixed Model Equations (MME) (Blair and Pollak, 1984). A high degree of connectedness between management units improves the accuracy of genetic comparison of animals in different herds and decreases errors in selection (Kennedy and Trus, 1993).

Considerations of connectedness in relation to genetic evaluation under sire models were discussed by Foulley *et al.* (1990). However, genetic evaluation utilising animal models, with all genetic relationships between animals taken into account, has recently become the method of choice (Henderson, 1988). Kennedy and Trus (1993) demonstrated that the most appropriate measure of connectedness is the average prediction error variance (PEV) of differences in estimated breeding values between animals in different management units. They have shown that PEV of differences is influenced by average genetic relationship between and within management units. PEV can be derived from the diagonal elements of the inverse of the coefficient matrix in the MME (Meyer, 1989). However, PEV of differences can be difficult to compute for large numbers of animals. Approximations suggested for large data sets (Misztal and Wiggans,

1988; Meyer, 1989) do not provide off-diagonal elements of the PEV matrix, which are required for comparisons of differences between specific animals.

Alternative measures of genetic connectedness have been suggested by Foulley et al. (1992) and Kennedy and Trus (1993) for situations when the computation of the off-diagonal elements of the PEV matrix is not possible. Methods based on genetic drift variance and a variance of estimates of management-unit effects investigated by Kennedy and Trus (1993) were found to be highly correlated with PEV, with respective correlations of 0.924 and 0.995.

These last two methods were applied in the present study to estimate measures of connectedness between two nucleus Large White and between two nucleus Landrace herds, and to determine the implications of increasing the number of reference sires.

6.3 Methods and Results

6.3.1 Measures of Connectedness between two Herds

Two New Zealand nucleus Large White and Landrace populations were studied. Each population had breeding stock produced in two different locations, with both breeds present in each location. The South Island nucleus herd was established recently (in 1992), to service the local multipliers and commercial producers, to increase the total nucleus size, and to minimise the potential risk of a disease outbreak in a single nucleus farm. All South Island nucleus animals originated from the North Island nucleus herd. Since then, a small number of live boars and gilts have been transferred between the two herds (in both directions). The nucleus structure requirement was to operate North and South Island farms as one herd, using BLUP to calculate estimated breeding values (EBV's) across herds, and to use AI to provide genetic links between the locations.

The genetic drift variance (GDV) and a variance of estimates of management-unit effects (VMU) as proposed by Kennedy and Trus (1993) were used to measure connectedness between the two herds. The GDV method was based on calculating the average relationships among animals with records, within and between the management units. Elements of the numerator relationship matrix (A) were used in calculations. This method did not require identifying base parents or ancestors within any particular herd. Firstly, the matrix X'ZAZ'X, which measures the sum of genetic relationships within and between management units, had to be computed. X and Z were incidence matrices for management units and animals with records, respectively. A lower triangular matrix L, such that LL' = A, was computed following the rules given by Henderson (1976) and Quaas (1976). Inbreeding was taken into account. The average relationships between and within management units were obtained by

dividing diagonal elements of matrix X'ZAZ'X by the square of the number of records in the unit and off-diagonal elements by the product of the number of records in each of the units.

The VMU method required calculation of the variance-covariance matrix of management-unit estimates:

$$[X'X - X'Z(Z'Z + A^{-1}\lambda)^{-1}Z'X]^{-1}\sigma^{2}$$

where $\lambda = \sigma_e^2/\sigma_a^2 = (1 - h^2)/h^2$, and σ_e^2 and σ_a^2 are residual and additive genetic variances, respectively. The variance of estimated differences between management units effects was the difference of the sums of the diagonal and off-diagonal elements of the variance-covariance matrix. The positive off-diagonal elements were the result of genetic relationships between animals in the different units, and they contributed to the reduction in the variance between herds, i.e. increased connectedness. The VMU method was dependent on the trait heritability (h^2) and the estimates of connectedness were obtained for different heritability levels from 0.1 to 0.7 (Table 6.1).

The GDV and VMU methods of computing the genetic connectedness between management units were implemented using the Matlab® programming language.

Table 6.1 Measures of connectedness between two herds for Large White and Landrace breeds (base level)

Measure	h^2	Large White	Landrace	
Total number of sire and dam records		731	653	
in the nucleus (base level)				
Genetic drift variance (GDV)		0.0501	0.0962	
Variance of management unit effects	0.1	0.0185	0.0286	
(VMU) for different heritability (h^2)	0.3	0.0267	0.0425	
levels	0.5	0.0370	0.0586	
	0.7	0.0543	0.0844	

The estimated measures of connectedness for the present nucleus populations (base level) had small values, indicating a high degree of genetic connectedness. Large White herds were more tightly connected than Landrace. This may be explained by the Large White having larger population size in both farms and higher number of related (between herds) nucleus sires and dams available for mating.

6.3.2 Simulation

Increasing the degree of connectedness was simulated by adding 2, 6 or 10 sires with progeny records in both herds to the current (base level) nucleus. Each herd unit provided half of the sires and each sire had five matings with randomly selected sows in its own herd and five matings with sows in the alternate herd (a total of 10 matings per sire). Full-sib and half-sib matings were not permitted. Additionally, a breeding structure was simulated, by adding five sires with 10 matings each to sows from within their own herd only (10 additional sires in

total). The simulations were performed separately for each breed. Change in the genetic connectedness between the two herds was estimated for each of the simulated situations using the genetic drift variance method (Table 6.2).

Table 6.2 Effect of adding different number of reference sires on the change in genetic connectedness between two nucleus herds

	Large	White	Landrace			
	GDV measure ¹	% change ²	GDV measure ¹	% change ²		
Base level (current nucleus	s) 0.0501		0.0962			
Base + 2 sires ³	0.0486	-3.0	0.0941	-2.2		
Base + 6 sires 3	0.0460	-8.2	0.0830	-13.7		
Base + 10 sires ³	0.0413	-17.6	0.0749	-22.1		
Base + 10 sires ⁴	0.0592	+18.2	0.1015	+5.5		

¹ Genetic drift variance (GDV) as a measure of connectedness

The level of connectedness between the two herd units increased with the number of reference sires. Ten additional reference sires increased the genetic connectedness by 17.6 % and 22.1 % for Large White and Landrace, respectively, as compared to the current (base) level. On the other hand, an additional 10 sires mated to sows within their own herds caused a decrease in genetic connectedness between two herds by 18.2% and 5.5 % for Large White and Landrace breeds, respectively (Figure 6.1).

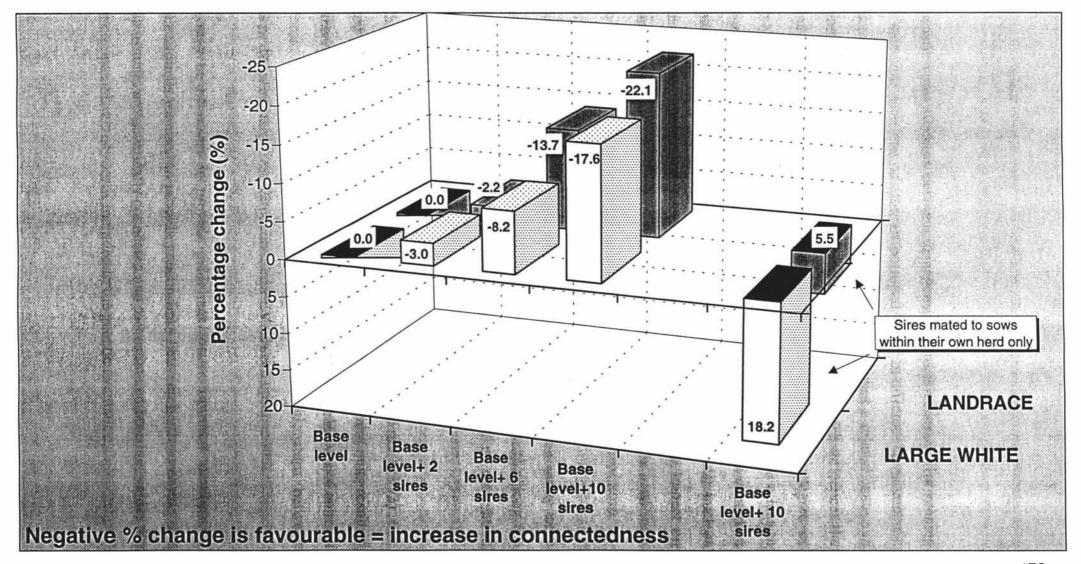
Percentage change in the measure of herd connectedness compared to base level situation (negative % change is favourable - increase in connectedness)

Each sire mated to 10 sows (five matings in their own herd and five in the opposite herd)

⁴ Five additional sires per herd. Each sire mated to 10 sows within their own herd only (no additional reference sires).

Figure 6.1 CHANGE IN GENETIC CONNECTEDNESS BETWEEN TWO HERDS

Effect of a different number of reference sires



6.4 Discussion

Genetic connectedness between management units is necessary for making reliable selection decisions on animals born and tested in different environments. The increase in the average prediction error variance implies a related change in the variance-covariance matrix of estimated breeding values which influences the accuracy of EBV's (Foulley et al, 1992). The reduction in the degree of connectedness is expected to alter the accuracy of selection leading to a loss in genetic progress. However, the improvement in genetic connectedness should be achieved using the optimal number of sires, as required for a particular nucleus size. Excessive numbers of selected sires would have a negative impact on selection differential and on the overall selection response. Hence, a need for a balance between the number of reference sires and the optimal sow/boar ratio.

The two methods of Kennedy and Trus (1993) applied in this study were also used by Hofer (1994) to measure the degree of connectedness among the station-tested pigs in Switzerland. He also found high degree of correlation between these methods and the PEV of EBV comparisons.

This study confirmed the findings of Kennedy and Trus (1993) that increased genetic relationships among animals within management units result in the increased prediction error variance of comparisons between EBV's of animals in different management units. However, increased relationships between animals in different herds result in decreased PEV of such comparisons.

It may be necessary to provide guidelines for the optimum numbers of reference animals required to provide genetic links between herds to ensure that the nucleus units are genetically connected and that estimated breeding values are reliably comparable across herds included in the genetic evaluation.

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CHAPTER 7

ECONOMIC INDICES USING BREEDING VALUES PREDICTED BY BLUP

7.1 Abstract

Economic indices were developed for a range of pig genotypes using relative economic values obtained by means of a computer model simulating life cycle production of a breeding sow and growth performance of her offspring under ad libitum feeding. Different selection strategies were investigated and predicted genetic gains in growth performance and reproduction traits following index selection using previously derived economic values were estimated. The effect of different sets of selection criteria on the efficiency of selection, use of restricted selection indices, and sensitivity to changes in the economic values and in the structure of future costs and returns were studied, and the effects of these changes on the predicted selection response were analysed.

The increase in profit resulting from further selection was lower in pig populations representing improved genotypes, as a result of lower predicted genetic gains in growth and carcass traits. This reduced rate of increase in profit was partially offset by the increase in predicted genetic gains in reproductive performance. For improved genotypes, the predicted increase in profit per gilt life cycle after one generation of selection ranged from \$26 to \$98 for one standard deviation of index selection with a selection intensity of 1. For unimproved genotypes, higher genetic gains in growth and carcass traits resulted in profits exceeding \$120 per generation of selection. Reductions in relative selection efficiency from using reduced and restricted indices were observed ranging from 13% to 43%. Indices with genetic gains in digestible energy intake restricted to zero produced higher predicted genetic gains in growth and reproduction traits. An increase in the economic value of lean tissue growth rate had a favourable effect on predicted gains in growth and carcass traits, while slowing down the decrease in the genetic level of feed intake. Greater economic emphasis on litter size resulted in lower predicted genetic gains in growth and carcass traits.

7.2 Introduction

The objective of selection in animal and plant breeding is usually to increase the mean, economically weighted, genotypic value of several traits. The information on more than one trait can be combined by a special use of Fisher's (1936) discriminant function, as proposed by Smith (1936) and extended by Hazel (1943) for the selection of individuals in animal populations. The resulting selection index maximises improvement in economic merit, and therefore is often called an economic selection index. Hazel (1943) defined the net economic merit or aggregate genotype as a linear function of additive genetic values, each weighted by the relative economic value. The statistical properties of the selection index were given by Henderson (1952), Williams (1962) and Henderson (1963).

For practical reasons, aggregate genotype is often limited to heritable traits of high economic importance. The production objective, defined as the overall goal of a breeding programme in terms of its maximum efficiency, is usually broader than the maximum profit optimised by the aggregate genotype (Gibson, 1992). Some of the production objective traits (e.g. meat quality, physical soundness, aggressiveness) may not be included in the aggregate genotype, and their improvement may depend on subjective selection decisions or independent culling methods (Brascamp and de Vries, 1992; de Vries and Kanis, 1994). In this study, the breeding objective term was used as equivalent to the aggregate genotype. To predict the value of an individual for its aggregate genotype, variables are measured on the individual itself, on its relatives, or both. These measurable characters, often called selection criteria, can be combined in a selection index, upon which animals are ranked and the best selected for breeding. The selection criteria used to predict the breeding values (BV's) in the

index can differ from traits in the aggregate genotype, although some overlap usually occurs and is likely to be desirable (Schneeberger et al., 1992).

Selection index can be designed to maximise genetic gain in the aggregate genotype of a subset of traits while holding the genetic response of other traits to zero. The idea of imposing restrictions on selection indices was introduced by Kempthorne and Nordskog (1959). Tallis (1962) extended it by setting the response of some traits by a fixed amount while maximising genetic gains in the remaining traits. A similar approach has been used by Pesek and Baker (1969) to achieve genetic gains in each index trait at a specified rate. The last type of selection index is known as desired gains index, where the relative genetic change in two or more traits is predetermined. Other types of constrained selection indices were proposed by Rao (1962), James (1968), Cunningham *et al.* (1970), Harville (1974, 1975), Niebel and Van Vleck (1983), Brascamp (1984), Itoh and Yamada (1988), and others.

Pig breeding programmes giving relatively high weighting to improved feed efficiency and lean content at the expense of growth rate on ad libitum feeding are showing a correlated decline in voluntary feed intake (Mitchell et al., 1982; Brandt et al., 1985; McPhee, 1989). Kreiter and Kalm (1986) discussed several alternatives to prevent further decline in daily feed intake (DFI). One of the methods was to use the restricted selection index with response in DFI restricted to zero change. Another alternative was to increase the economic weight of growth traits, such as average daily gain (ADG), or to select for lean tissue growth rate (LTGR). It remains uncertain whether the added expense of measuring individual feed consumption leads to a worthwhile increase in genetic improvement (Webb and Curran, 1986). However, it is well established that selection on the basis of improved growth rate and reduced ultrasonic backfat measurements lead to correlated improvement in feed efficiency.

There is growing evidence that some lines of pigs may be approaching the optimal levels of backfat thickness, especially in countries without castration and with low carcass weights. When this optimum is reached, further genetic improvement in feed efficiency by substituting lean for fat will not be possible (Ollivier et al., 1990). As a result, breeding programmes are likely to turn to other traits, such as litter size and meat quality, to improve overall efficiency of the production system. However, these traits are less heritable and less easy to measure, compared to growth and carcass traits. Therefore, they can benefit from applying new techniques, such as comparisons across environments and generations, utilisation of all possible genetic relationships, and use of Best Linear Unbiased Prediction (BLUP) technology. BLUP combines the ability of a selection index to incorporate multitrait information from relatives with the facility to take account of fixed environmental effects and genetic change when predicting breeding values. Estimated Breeding Values (EBV's) predicted by BLUP for measurable selection criteria can be combined into an index to predict an aggregate genotype made up of economically important traits and their associated economic values. The index weights depend on the genetic variances and covariances among the selection criteria and the traits in the aggregate genotype, and on the economic values of these traits.

The objective of the present study was to investigate predicted genetic gains in growth performance and reproduction traits using selection indices based on economic values derived for a range of improved and unimproved genotypes. A study of the effect of different sets of selection criteria on the efficiency of selection, use of restricted selection indices, and sensitivity analyses of changes in the economic values and in the structure of future costs and returns were also conducted.

7.3 Methods

7.3.1 Selection Indices for a Range of Pig Genotypes

Economic indices have previously been derived for a wide range of pig genotypes, using relative economic values obtained by means of a computer model simulating life cycle production of a breeding sow and growth performance of her offspring. Traits in the breeding objective were upper limit to body protein deposition rate (Pd_{max}, g/day), mean daily ad libitum digestible energy intake (DEi, MJ/day), minimum lipid (Ld) to protein (Pd) deposition ratio (R_{min}), and number born alive per litter (NBA, pigs/litter). A testing system with ad libitum feeding was assumed. Selection criteria included average daily gain (ADG, g/day) from birth to test day at around 70 to 90 kg liveweight, ultrasonically measured backfat depths (BF, mm), representing a measurement taken at P₂ position (6.5 cm off the mid-line at the position of the last rib), obtained immediately prior to selection, average ad libitum daily feed intake (DFI, g/day) measured over the growth period from transfer (around 20 kg liveweight) to slaughter, and number born alive per litter (NBA).

Only one set of genetic and phenotypic parameters was used for all studied genotypes to demonstrate selection effects. In practice, a set of parameters estimated for a specific pig improvement programme would be required. The restricted maximum likelihood approach (REML) was used to estimate genetic parameters for ADG, BF and NBA in selected New Zealand nucleus herds. Assumed heritabilities (h^2), common environmental (litter) effects (c^2), phenotypic standard deviations (σ_p), and genetic (r_g) and phenotypic (r_p) correlations were averages of the parameters obtained for Large White, Landrace and Duroc breeds (see also Tables 4.3, 4.5 and 4.7 in Chapter 4). Estimates of heritabilities used for DFI and DEi and their correlations with other growth and

carcass traits were rounded averages from literature sources (McPhee et al., 1979; Wyllie et al., 1979; Vangen, 1980; Foster et al., 1983; Brandt et al., 1985; Knap et al., 1985; Standal and Vangen, 1985; Kreiter and Kalm, 1986; Johansson et al., 1987; Cameron et al., 1990; Kanis and de Vries, 1992; Mrode and Kennedy, 1993).

For Pd_{max} and R_{min} , no direct information about parameters is available, and the assumptions proposed by Kanis and de Vries (1992) were used. They assumed $h^2 = 0.2$ for both Pd_{max} and R_{min} and a correlation between these traits of -0.4. Standard deviations (σ_p) for Pd_{max} and R_{min} were taken as one-sixth of their respective ranges simulated in this study (0.8 to 1.2 and 120 g/day to 200 g/day) (Whittemore, 1983). Genetic correlations for DFI, Pd_{max} , DEi and R_{min} were assumed equal to phenotypic correlations. For Pd_{max} and R_{min} , correlations of 0.5 and -0.5 with ADG, -0.6 and 0.6 with BF, and -0.1 and 0.30 with DFI and DEi, respectively, were assumed (Cöp, 1974; Kanis, 1990; Kanis and de Vries, 1992).

Correlations between production traits and number born alive per litter were ignored (assumed zero) (see discussion in Chapter 4). The parameters used for NBA were: $h^2 = 0.11$, permanent environmental variance (m^2) = 0.05, and σ_p = 2.6. The complete set of parameters used in this study for production traits is in Table 7.1.

Table 7.1 Assumed heritabilities (h^2) , common environmental (litter) effects (c^2) , phenotypic standard deviations (σ_p) , and genetic $(r_g)^1$ and phenotypic $(r_p)^2$ correlations for production traits

	ADG (g/day)	►BF (mm)	DFI (g/day)	Pd _{max} (g/day)	DEi (MJ/day)	R _{min} (ratio)
ADG		0.35	0.70	0.50	0.70	-0.50
BF	0.40		0.30	-0.60	0.30	0.60
DFI	0.70	0.30		-0.10	0.90	0.30
Pd_{max}	0.50	-0.60	-0.10		-0.10	-0.40
DEi	0.70	0.30	0.90	-0.10		0.30
R_{\min}	-0.50	0.60	0.30	-0.40	0.30	
h^2	0.20	0.45	0.30	0.20	0.30	0.20
c^2	0.11	0.06	0.15	0.00	0.00	0.00
σ_p	43.0	2.3	170.0	15.0	2.5	0.1

genetic correlations above the diagonal

The index weights for the predicted breeding values of the selection criteria and estimated genetic gains in both the traits in the breeding objective and the selection criteria in the index were computed using classical methods introduced by Hazel (1943), and extended by Kempthorne and Nordskog (1959), Lin (1990) and Schneeberger *et al.* (1992), to cover restricted indices and breeding values predicted by BLUP.

Economic values (EV's) of reproduction and growth performance traits, calculated per gilt life cycle for a selection of unimproved and improved genotypes (Table 7.2), were used in the economic index. The predicted genetic gains per generation of selection were compared to study the effectiveness of selection at each mean level of performance in the selected populations (Table 7.3).

² phenotypic correlations below the diagonal.

Table 7.2 Mean levels of performance in selected population and economic values for traits in the breeding objective calculated for a range of unimproved (1 to 2) and improved (3 to 9) genotypes

	Mean levels of performant Traits in the breeding objective				nance in selected population Selection criteria			Economic values for traits in the breeding objective (\$/gilt life cycle)			
	Pd _{max}	DEi	R_{min}	NBA ¹	ADG	BF	DFI	Pd _{max}	DEi	R_{\min}	NBA
Genotype	(g/day)	(MJ/day)	(ratio)	(pigs)	(g/day)	(mm)	(g/day)				
1	120	30.0	1.0	10.8	590	18.6	2397	16.3	-67.1	-898.5	11.8
2	120	30.5	1.2	10.8	593	19.1	2326	19.4	-59.9	-868.0	7.1
3	140	30.6	1.0	10.8	629	16.8	2186	13.1	-62.5	-578.9	48.7
4	160	33.3	0.8	10.8	675	16.2	2653	7.6	-87.7	-93.4	55.4
5	180	24.2	0.9	10.8	567	12.2	1729	1.8	-6.1	-546.0	85.1
6	180	27.1	1.0	10.8	625	13.2	1935	4.2	-18.6	-305.0	86.7
7	180	30.0	1.0	10.8	669	14.0	2224	5.6	-39.8	-60.5	84.1
8	200	24.2	1.1	10.8	549	14.1	1730	0.5	20.6	-319.6	72.7
9	200	27.1	1.0	10.8	627	13.3	1936	0.7	-9.4	-53.3	87.2

¹ NBA as breeding objective trait and selection criterion character.

7.3.2 Review of Index Theory

The aggregate genotype or net merit (T) and selection index (I) are defined as

$$T = v'g$$

and

$$I = b' y$$

where g is a vector of additive genetic values for the m traits included in the aggregate genotype,

- v is a vector of economic values for those traits,
- y is a vector of n phenotypic values expressed as deviations from their respective means, and
- b is a vector of weighting factors to be used in the index.

The selection index equations (Hazel, 1943) in matrix notation are:

$$P b = G_{12} v$$
 [7.1]

where P is an $n \times n$ phenotypic covariance matrix among the n characters in the selection index, and

 G_{12} is an $n \times m$ genotypic covariance matrix among the n characters in the selection index and the m traits in the aggregate genotype.

The optimum set of selection index weighting factors (b) is that which maximises the correlation (r_{T}) between the selection index (I) and the aggregate genotype (T), or equivalently, minimises the prediction error variance.

Thus, given P, G_{12} , and v, b can be derived as

$$b = \mathbf{P}^{-1} \mathbf{G}_{12} \mathbf{v}. \tag{7.2}$$

The variance of the index, the variance of the aggregate genotype and the covariance of index and aggregate genotype are, respectively

$$\sigma_I^2 = b' P b$$

$$\sigma_T^2 = v' G_{22} v$$

$$\sigma_{TI} = b' G_{12} v = b' P b$$

where G_{22} is an $m \times m$ matrix of genotypic covariances among the m traits in the aggregate genotype.

If the characters measured are the phenotypic expressions of the traits in the objective then n = m and G_{12} and G_{22} are identical (Lin, 1978). The following equalities exist:

$$\sigma_{TI} = \sigma_I^2$$

$$b_{TI} = \sigma_{TI}/\sigma_I^2 = 1, \text{ and}$$

$$r_{TI} = \sigma_{TI}/\sigma_I \sigma_T = \sigma_I^2/\sigma_I \sigma_T = \sigma_I/\sigma_T,$$

with b_{TI} defined as the regression of breeding values on index values.

The square of the correlation r_{TT} expresses the fraction of the additive variance that is accounted for by the measurements combined in the index, i.e., $r_{TT}^2 = \sigma_I^2/\sigma_T^2$ (Falconer, 1981). This is often known as the reliability.

When selection is on I, the response to selection or genetic gain in the aggregate genotype (T) is the mean breeding value of the selected parents, predicted from the regression of breeding values on index values as

$$\Delta T = \mathbf{b}_{TI} S = \bar{i} \mathbf{r}_{TI} \sigma_{T} = \bar{i} \sigma_{I}$$

were $S = \bar{i} \sigma_I$, is the selection differential of index values, and \bar{i} is the selection intensity. The genetic gain in T is proportional to r_{TI} which is a maximum when $b = P^{-1} G_{12} v$. The annual selection response, $\Delta T/\text{year}$, is the objective criterion to maximise (Niebel and Van Vleck, 1983).

The predicted genetic gain in the objective traits due to selection on I is

$$\Delta G = G_{12}$$
' $b(\bar{i}/\sigma_I)$

where ΔG is a column vector of genetic gains corresponding to each trait in the objective.

Alternatively, ΔT can be expressed as a linear combination of the genetic gains in the objective traits, each weighted by its relative economic value (Lin, 1978; Falconer, 1981):

$$\Delta T = v' G_{12}' b (\bar{i} / \sigma_I) = v' \Delta G.$$

The percentage of gain ($\Delta G\%$) contributed by each of the objective traits is obtained from

$$\Delta G\% = G_{12}$$
' $b (100 v \bar{i} / \sigma_I^2)$.

Estimated breeding values for animal i, for the n characters in the index, can be obtained from

$$\hat{u}_i = B' y$$

assuming known fixed effects in the estimation of EBV's (i.e. using the Best Linear Predictor, BLP), where \hat{u}_i is a vector of the estimated breeding values for animal i, for the characters in the index, B is a matrix consisting of vectors with index weights for each EBV to be predicted, and y is a vector of observed phenotypes. Index weights in B are derived from

$$B = P^{-1} G_{11} [7.3]$$

where G_{11} is an $n \times n$ genotypic covariance matrix among the characters in the index.

7.3.3 Economic Indices Using EBV's Predicted by BLUP

Estimated breeding values (EBV's) predicted using BLUP animal models (Henderson, 1973 and 1988; Henderson and Quaas, 1976) can be combined into an economic index to predict the aggregate genotype. Information from relatives is accounted for through the numerator relationship matrix (A). As in the prediction of EBV's by BLP, the information required to calculate index weighting factors, to allow prediction of the aggregate genotype, comprises economic values of traits in the aggregate genotype, genotypic variances and covariances among the selection criteria in the index, and the genotypic covariances among the selection criteria and the aggregate genotype traits.

The unrestricted genetic index (I_g) considered here is defined as

$$I_g = v' \hat{g} \tag{7.4}$$

where \hat{g} is a vector of estimated breeding values for the objective traits in T and v is a vector of known economic values for those traits.

The Mixed Model Equations (MME) of Henderson (1973) can be expanded to include \hat{g} as well as \hat{u} , the vector of the estimated breeding values for the characters in the index:

$$\begin{bmatrix} X' R^{-1} X & X' R^{-1} Z & 0 \\ Z' R^{-1} X & Z' R^{-1} Z + A^{-1} * G_{11} & A^{-1} * G_{12} \\ 0 & A^{-1} * G_{21} & A^{-1} * G_{22} \end{bmatrix} \begin{bmatrix} \hat{\beta} \\ \hat{u} \\ \hat{g} \end{bmatrix} = \begin{bmatrix} X' R^{-1} y \\ Z' R^{-1} y \\ 0 \end{bmatrix}$$
 [7.5]

where

X and Z are known incidence matrices relating the observations to the fixed effects and EBV's, respectively,

R = var(e), and e is a vector of random residuals,

A, G_{11} , G_{12} , G_{22} are as previously defined, and G_{12} ' = G_{21} ,

$$var\begin{bmatrix} u \\ g \end{bmatrix} = A * \begin{bmatrix} G_{11} & G_{12} \\ G_{21} & G_{22} \end{bmatrix} = G$$
, and

 $\hat{\beta}$ is a vector of predicted fixed effects.

From the last row of [7.5], the EBV's for animal i, for the traits in T, can be estimated (Henderson, 1977):

$$\hat{g}_i = G_{21} G_{11}^{-1} \hat{u}_i, ag{7.6}$$

and an index b_u ' \hat{u}_i can be used to predict the aggregate genotype $v'g_i$, where b_u is a vector of index weights applied to the estimated breeding values for the selection criteria in the index. Replacing \hat{g}_i from [7.6] in $v'\hat{g}_i$, it follows that

$$b_{u}'\hat{u}_{i} = v'\hat{g}_{i} = v'G_{21}G_{11}^{-1}\hat{u}_{i},$$

and

$$b_{u} = G_{11}^{-1} G_{12} v. ag{7.7}$$

The index weights can be computed without any knowledge of the population structure, and the same b_u vector can be used for all animals, as long as the same set of predicted EBV's is available for each animal. From [7.7], the vector of index weights depends only on the economic values for the traits in the aggregate genotype and on the genetic variances and covariances among the selection criteria and the traits in the net merit (Schneeberger *et al.*, 1992).

7.3.4 Reduced Selection Indices

The relative contribution of each variable in the index to the overall net merit can be determined in order to decide the actual set of traits to be measured. The cost of including that variable can be measured against its effectiveness in the index. The usual method of finding the value of a particular variable in the index is to construct a reduced index from which that variable has been excluded

(Cunningham, 1969). The efficiency of the i^{th} reduced index relative to the original index can be measured as the ratio of the rates of genetic progress in T:

$$\frac{\Delta T_i}{\Delta T} = \frac{\sigma_{I_i}}{\sigma_{I}},$$

provided the same \bar{i} and the same generation intervals are applied.

The comparison of standard deviations of the index, σ_I , provides a simple measure of the relative efficiencies of different indices in terms of genetic progress.

The effectiveness of using reduced indices relative to the original index was studied for one of the improved genotypes representing current 'nucleus level' growth performance of New Zealand Large White, Landrace and Duroc breeds. The relative efficiency of the i^{th} reduced index was calculated as a ratio of its σ_I to σ_I of the original index:

$$\frac{\sigma_{I_i}}{\sigma_I} \times 100$$
.

The value of the i^{th} source of information in the original index was calculated as the percent reduction in genetic progress which would result if that variate was omitted:

$$\left(1-\frac{\sigma_{I_i}}{\sigma_I}\right)\times 100$$
.

7.3.5 Restricted Selection Indices

The restricted selection index provides a way to manipulate genetic changes in component traits. To impose the restriction that the index shall produce no change in the additive genetic value of the j^{th} trait (g_j) , the index equations [7.1] are solved subject to

$$cov(g_i, I) = b' G_i = 0$$

where cov (g_j, I) is the covariance between I and g_j , and G_j is the j^{th} column of G_{12} .

The method of Kempthorne and Nordskog (1959) and of Tallis (1962) incorporated this restriction by introducing a Lagrange multiplier into the expression to be maximised (r_{TI}) and solved the resulting equations directly for b^* , where b^* is a vector of solutions for the restricted index:

$$b^* = [\mathbf{I} - \mathbf{P}^{-1} \mathbf{G}_i (\mathbf{G}_i' \mathbf{P}^{-1} \mathbf{G}_i)^{-1} \mathbf{G}_i'] \mathbf{P}^{-1} \mathbf{G}_0 \mathbf{v}_0$$

or its equivalent

$$b^* = P^{-1}[I - G_i(G_i, P^{-1}G_i)^{-1}G_i, P^{-1}]G_0v_0$$

where G_0 is a submatrix of G_{12} corresponding to the traits without constraints, such that $G_{12} = [G_0 : G_j]$, and v_o is a subvector of v for non-constrained traits in the aggregate genotype (Brascamp, 1984).

For b^* , which is proportional to b, $\sigma_{I^*}^2 = b^*$, $P b^* = b^*$, $G_0 v_0$, and the predicted genetic gain in the component traits due to selection on I^* is

$$\Delta G^* = G_{12}' b^* (\bar{i} / \sigma_{I*}).$$

7.3.6 Derivation of Implied Economic Weights

Application of restricted methods in computing the index weights for different selection indices results in a different objective criterion, T, for each index composed of a new set of restricted relative economic values (v^*) (Niebel and Van Vleck, 1983). The knowledge of v^* allows redefinition of T and use of Hazel's optimal linear index in deriving the index coefficients.

Gibson and Kennedy (1990) have shown that there exists a set of implied linear economic weights for the constrained indices. If the selection index coefficients, b^* , are known, the economic weights, v^* , which would have led to these coefficients can be derived. For n variables in the selection index and m traits in the aggregate genotype, when $n \ge m$, then from equation [7.1]:

$$G_{12}' G_{12} v^* = G_{12}' P b^*$$

hence

$$v^* = (G_{12}, G_{12})^{-1} G_{12}, P b^*.$$
 [7.8]

When m > n, unique solutions can only be found if m - n or more values of v^* can be predetermined. Solutions can then be calculated by adding a matrix of Lagrange multipliers (L) to G_{12} and a vector of predetermined economic weights (a) to $P b^*$, so that

$$v^* = \begin{bmatrix} G_{12} \\ L \end{bmatrix}^{-I} \begin{bmatrix} Pb^* \\ a \end{bmatrix}.$$
 [7.9]

7.3.7 Restricted Index Weights for BLUP EBV's

The restricted genetic index (I_g^*) can be expressed as

$$I_{g}^{*} = v^{*}, \hat{g}$$
 [7.10]

where v^* is a vector of unknown economic weights for the objective traits and \hat{g} is the same as defined in [7.4]. Provided the implied v^* can be derived as previously described, the vector of restricted index weights, b_u^* , applied to the estimated breeding values can be calculated as follows

$$b_{\mu}^{*} = G_{11}^{-1} G_{12} v^{*}$$

Alternatively, b_u^* can be derived from equations [7.1] and [7.7] as

$$b_u^* = G_{11}^{-1} P b^*. ag{7.11}$$

Note that this last equation does not require any knowledge of the implied economic weights.

7.3.8 Sensitivity of Selection Indices to Changes in Economic Values

Alternative situations were studied to test the sensitivity of selection indices to changes in the economic values (EV's) of the objective traits. The analyses were performed for the improved genotype [6] from Table 7.2, representing current 'nucleus level' performance of New Zealand pigs, with economic values derived from the life cycle simulation model. The predicted genetic gains, percentage of gain contributed by each of the objective traits and index

parameters $(\sigma_I, \sigma_T, r_T)$ were calculated for each of the studied indices (with and without constraints and with different combinations of measured characters). The predicted annual genetic gains in the breeding objective traits (Pd_{max}, DEi, $R_{\rm min}$ and NBA), assuming index selection with $\bar{i} = 1.6$ standard deviation units of index and mean generation interval of 1.25 years, were used to calculate the difference in the overall life cycle profit expressed as an Annualised Present Value (APV, see Chapter 2 and 3 for calculation details). For example, the difference in APV for the base index I_1 was calculated by simulating life cycle production of a breeding sow and growth performance of her offspring for genotype [6], using mean base performance levels of Pd_{max} = 180 g/day, DEi = 27.1 MJ/day, $R_{min} = 1.0$, and NBA = 10.8 pigs/litter, and the respective performance levels of 180+4.1 g/day, 27.1-0.44 MJ/day, 1.0-0.03, and 10.8+0.22 pigs/litter, which represent predicted genetic gains in these objective traits after one year of selection (see Table 7.4 B). The calculated difference in APV for the above example was +\$33.75 per year of selection. Responses from selection using four different indices were studied: I_1 and I_2 indices without constraints, and I_5 and I_6 indices with the predicted genetic gain in DEi restricted to zero (Table 7.4).

The effects of doubling the economic values of Pd_{max} and NBA (each in turn with economic values of other objective traits unchanged) on the predicted genetic gains and on the overall response to selection were analysed for I_1 , I_2 , I_5 and I_6 indices. Using the above example for index I_1 , the predicted annual genetic gains from Table 7.5 B, when Pd_{max} EV was doubled, were used to calculate the increase in APV after one year of selection, with the respective performance levels for $Pd_{max} = 180+4.8$ g/day, DEi = 27.1-0.4 MJ/day, $R_{min} = 1.0-0.04$, and NBA = 10.8+0.16 pigs/litter. The calculated difference in APV for genotype [6] using the sub-optimal set of economic values was +\$33.0 per year of selection, which is equivalent to 2.2% decrease in selection response, compared to the original (I_1) selection index. To study the effects of doubling the

economic value for NBA, the predicted annual genetic gains from Table 7.6 B for I_1 , I_2 , I_5 and I_6 indices were used. The predicted percentage decrease in annual response from selection using the four studied indices was plotted to compare the effects of changes in economic values on the overall index efficiency.

7.3.9 Sensitivity of Selection Indices to Changes in Feed Prices, Pigmeat Returns and Non-Feed Costs

Alternative situations were studied to test the sensitivity of selection indices to future changes in three main areas of costs and returns affecting the net profit of the commercial pig breeding enterprise. These areas were identified as feed costs, pigmeat returns and non-feed costs, such as labour, management, housing costs, health, cost of power and other general expenses. The approach similar to testing the sensitivity to changes in the economic values was adopted. calculations were performed using the life cycle simulation model and assuming mean base performance levels for genotype [6]. The predicted annual genetic gains from Table 7.4 B for the four studied indices: I_1 , I_2 , I_5 and I_6 were used to calculate the difference in APV as a result of one year of selection, assuming current prices and production circumstances. The differences in APV were also calculated by independently changing the base feed costs, pigmeat returns and non-feed costs by +30%, +20%, +10%, -10%, -20% and -30%. The resultant changes in the life cycle APV from one year of selection, assuming the above % changes in costs and returns, were expressed as a percentage change in the index efficiency, relative to the base (current) situation. The effects of changes in feed costs, pigmeat returns and non-feed costs on the index efficiency were plotted.

7.4 Results

7.4.1 Economic Indices for a Range of Pig Genotypes

Mean levels of performance and economic values for traits in the breeding objective calculated for a small selection of unimproved (1 to 2) and improved (3 to 9) pig genotypes are presented in Table 7.2. The predicted genetic gains per generation, percentage of gain contributed by each of the objective traits, selection index parameters, and BLUP index weights for each of the selected pig genotypes are in Table 7.3. The economic values for each objective trait are in \$/gilt life cycle, hence the values of the predicted genetic gains are calculated in terms of the gilt life cycle improvement.

The predicted genetic gains per generation of selection, with the intensity of selection equal to one standard deviation of the index ($\bar{i} = 1$), are compared to study the effectiveness of selection for each genotype representing different genetic levels of performance in the selected populations. Figure 7.1 shows the predicted genetic gains in the breeding objective traits, Pd_{max} , DEi and R_{min} , for the nine studied genotypes. The mean genetic levels of performance at each base population before and after one generation of selection are represented in the 3-D scatter chart by the respective data point markers. For example, a marker labelled I for the first genotype has the coordinates of 120.0, 30.0 and 1.0 for Pd_{max} , DEi and R_{\min} , respectively, and the marker I' represents the same genotype after one generation of selection, with the respective coordinates of 123.96, 29.58 and 0.969. Because the data point markers are "floating" in three-dimensional space, tie lines and grid lines are used to visually help gauge the values of each data point. Different shapes of markers are used for different groups of genotypes. Additionally, the genetic changes calculated for each genotype are presented in the form of a magnified 3-D box, to clearly demonstrate the magnitude and

direction of the predicted genetic gains in each objective trait. The walls of each 3-D box are proportionately scaled, relative to each other, based on the values of the predicted gains.

Effects of selection at different base genetic levels varied significantly. The highest predicted gains in Pd_{max} were found for unimproved genotypes (1 and 2), and only a third to a quarter of those levels were predicted in the highly improved pigs, with $Pd_{max} > 180$ g/day. Negative economic values for DEi resulted in a proportional decrease in the predicted gains for DEi and DFI. Positive EV for DEi (genotype 8) resulted in the increase in DEi and DFI genetic gains, and a significant increase in ADG gain. The remaining genotypes were predicted to decrease their ADG gains. Level of changes in Pd_{max} and DEi gains coincided with the amount of change in body composition, with the least improved genotypes showing the highest potential for BF decrease. R_{min} had the lowest predicted gains in the highly improved genotypes (8 and 9), which produced lean carcasses, with sufficient amounts of metabolisable energy available both for protein and lipid deposition. Overall selection response, measured by σ_I and r_{II} , was the highest for unimproved genotypes, and gradually declined as the base populations become more improved.

Predicted genetic gains in NBA appear to be closely related to economic values for that trait relative to other traits. The highest predicted gains for NBA were found for improved genotypes, which correspondingly had low genetic gains in the production traits. Predicted genetic gains in NBA calculated for one standard deviation of selection for a range of unimproved and improved genotypes are presented in Figure 7.2.

Table 7.3 Predicted genetic gains calculated for one standard deviation of selection and selection index parameters for unimproved (1 to 2) and improved (3 to 9) genotypes. Selection criteria are: ADG, BF, DFI and NBA

		edicted dex sel	_	_				contri	entage buted object	by eac	ch of	Selection	on index	x parar	neters	BL.	UP inde	ex weig	ghts
	Breedi	ng obje	ctive ti	aits	Select	ion cri	teria												
Genotype	Pd _{max} (g/day)	DEi MJ/day		NBA ² (pigs)		BF (mm)	DFI (g/day)	Pd _{max} (%)	DEi (%)	R _{min} (%)	NBA	σ_i (\$/gene	σ_r	r _{TI}	r^2_{TI}	ADG	BF	DFI	NBA
1	4.0	-0.42	-0.03	0.01	-1.8	-0.8	-33.7	53.3	23.5	23.1	0.1	121.0	172.8	0.70	0.49	10.4	-80.9	-2.2	11.8
2	4.1	-0.39	-0.03	0.00	-1.3	-0.8	-30.9	61.0	17.8	21.2	0.02	129.6	182.5	0.71	0.50	11.8	-91.3	-2.3	7.1
3	3.8	-0.45	-0.03	0.04	-2.2	-0.8	-35.7	51.2	28.9	17.9	2.0	97.6	148.8	0.66	0.43	7.7	-61.7	-1.8	48.7
4	2.8	-0.60	-0.02	0.06	-4.8	-0.7	-46.4	26.7	66.5	2.8	4.0	79.2	145.0	0.55	0.30	3.1	-30.7	-1.5	55.4
5	3.1	-0.24	-0.02	0.19	-0.2	-0.6	-19.9	15.4	4.1	35.9	44.6	36.4	81.1	0.45	0.20	2.8	-19.4	-0.5	85.1
6	3.2	-0.34	-0.03	0.17	-1.4	-0.6	-27.3	31.9	15.2	18.2	34.7	42.1	88.8	0.47	0.23	2.9	-22.6	-0.6	86.7
7	2.9	-0.48	-0.02	0.14	-3.3	-0.7	-37.3	33.6	39.1	3.0	24.3	48.8	101.1	0.48	0.23	2.5	-22.2	-0.8	84.1
8	1.5	+0.26	-0.01	0.23	+4.2	-0.2	+18.4	2.9	20.5	11.1	65.6	25.7	68.7	0.37	0.14	1.6	-9.1	0.03	72.7
9	1.0	-0.20	-0.01	0.27	-1.5	-0.2	-15.8	2.7	7.2	1.8	88.3	26.5	76.7	0.35	0.12	0.4	-3.9	-0.2	87.2

Genetic gains calculated in terms of the gilt life cycle improvement

² NBA as breeding objective trait and selection criterion character.

Figure 7.1 Predicted Genetic Gains in Production Traits *

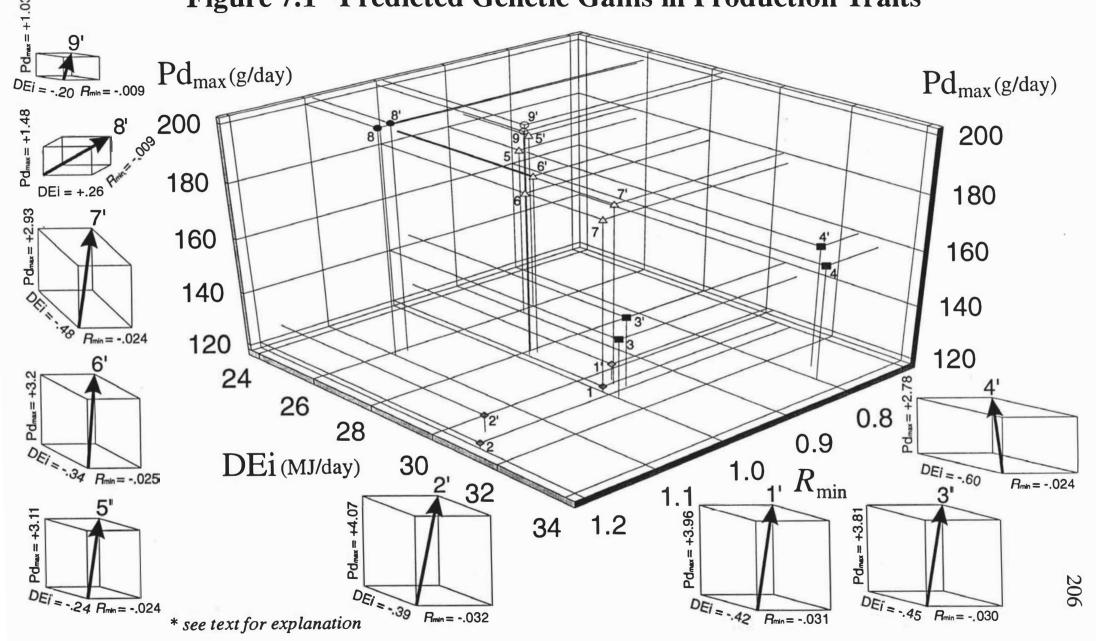
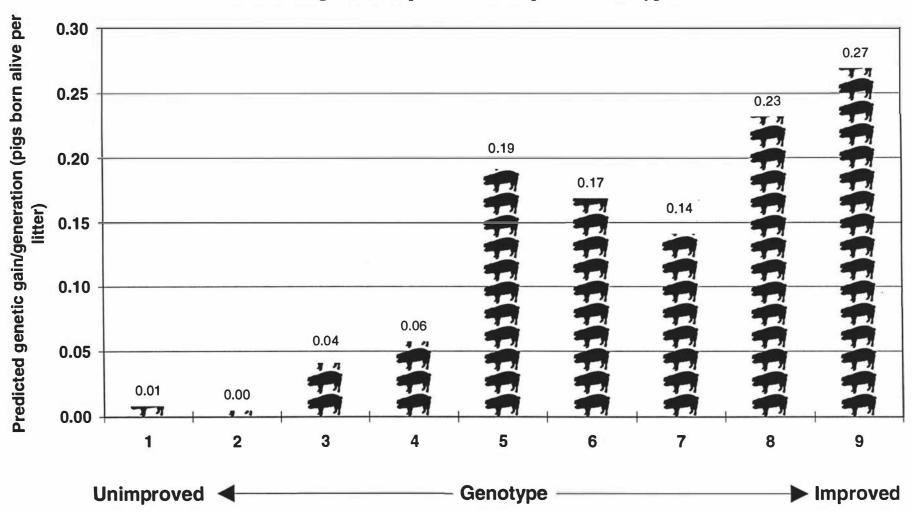


Figure 7.2 Predicted Genetic Gains in NBA

Calculated for One Standard Deviation of Selection For a Range of Unimproved and Improved Genotypes



7.4.2 The Relative Efficiencies of Reduced Selection Indices

Four indices (I_i) with different sets of characters as selection criteria were compared. The studied indices included the following measurable components:

 I_1 : ADG, BF, DFI, and NBA

I₂: ADG, BF, and NBA

 I_3 : ADG, BF, and DFI

 I_4 : ADG and BF.

These traits are typically measured in testing programmes of varying degrees of sophistication, depending on the breeding direction assumed for a particular line of pigs and the testing resources available.

Index I_1 , referred here as the original index, was derived using the same economic values and genetic parameters, and the same selection criteria as the index previously obtained for genotype [6] (Table 7.2 and 7.3). Indices I_2 , I_3 , and I_4 are reduced indices relative to the original index, and their predicted efficiencies and genetic gains in the component traits are compared in Table 7.4 (indices I_1 to I_4). The BLUP index weights for each of the four indices are given in Part B of Table 7.4.

The reduction in the relative efficiency of the index as a result of omitting a particular selection criterion can be seen by comparing the values in the last three columns in Part B of Table 7.4. The largest reduction, estimated at 41.6%, is predicted when both DFI and NBA are excluded as selection criteria. The annual response to selection or the absolute value of the aggregate genotype, $\Delta T/\text{year}$, provides an indication of the potential \$ loss from not measuring some of the index variables.

7.4.3 The Relative Efficiencies of Restricted Selection Indices

Table 7.4 shows the predicted responses to selection when DEi is restricted to zero change in the genetic value of that trait. The restriction was applied to four indices with different sets of selection criteria traits (indices I_5 to I_8). The effect of restriction on genetic gains in component traits and on the overall index efficiency can be seen by comparison to the respective indices I_1 to I_4 without constraints. The implied economic values for DEi and the BLUP index weights, derived for each of the four restricted indices, are also given in Table 7.4.

Restricting DEi genetic gain to zero reduced the relative efficiency of I_5 by 13.5%, relative to the original index, I_1 . However, the efficiency reductions for I_6 versus I_2 , and I_8 versus I_4 , were small, at about 1% and 2%, respectively. The highest loss in efficiency was found for I_7 , when compared to I_3 , at about 22%.

The predicted genetic gains in Pd_{max} were higher for restricted indices, when compared to their respective reduced indices, with the exception of I_5 . An improvement in the genetic gain for NBA was observed for I_5 versus I_1 , and significant improvements were found in ADG for all restricted indices. The predicted responses in ADG changed from negative (unfavourable) to positive, favourable gains for all restricted indices. Small reductions in genetic gains were found for BF, and the predicted reduction in DFI was significantly smaller for all restricted indices, when compared to their unconstrained counterparts.

The restriction was achieved at the expense of the overall genetic response as compared with the unrestricted indices. However, since the restricted index meets the requirements of the new aggregate genotype, the reduction in genetic response may be justified.

Table 7.4 A Effect of using different selection criteria on the index parameters and predicted genetic gains

Efficiencies for reduced and restricted indices relative to the original index

I

A. Selection index parameters and predicted genetic gains per generation, assuming selection intensity, $\bar{i}=l$

	Choice	of sele	ection	criteria		Econom	nic values			Predic	ted gene	tic gain	per gene	ration 3		Percen	tage of g	ain cont	ributed	Selec	tion inde	x param	eters
	(Mea	surable	chara	cters)		(\$/gilt li	ife cycle)		Bree	ding obj	ective tra	its	Select	ion Crit	егіа	by eac	h of the	objective	e traits	•			
	ADG	BF	DFI	NBA	Pd_{max}	DEi	R_{\min}	NBA	Pd_{max}	DEi	R_{\min}	NBA ²	ADG	BF	DFI	Pd_{max}	DEi	R_{\min}	NBA	σ,	σ_{τ}	r_{Tl}	r^2_{TI}
Index					(g/day)	MJ/day	(ratio)	(pigs)	(g/day)	MJ/day	(ratio)	(pigs)	(g/day)	(mm)	(g/day)	(%)	(%)	(%).	(%)	(\$/gene	ration) 3		
	Selec	tion ii	ndices	with	out con	ıstraint	'S																
I_1	+	+	+	+	4.2	-18.6	-305.0	86.7	3.2	-0.34	-0.03	0.17	-1.4	-0.6	-27.3	31.9	15.2	18.2	34.7	42.1	88.8	0.47	0.23
I_2	+	+		+	4.2	-18.6	-305.0	86.7	2.6	-0.06	-0.02	0.20	-0.5	-0.7	-4.3	31.2	3.4	15.1	50.4	34.9	88.8	0.39	0.16
I_3	+	+	+		4.2	-18.6	-305.0	86.7	4.0	-0.43	-0.03	0.00	-1.8	-0.8	-33.8	48.9	23.3	27.9	0.0	34.0	88.8	0.38	0.15
I_4	+	+			4.2	-18.6	-305.0	86.7	3.7	-0.09	-0.03	0.00	-0.7	-1.0	-6.1	62.8	6.8	30.4	0.0	24.6	88.8	0.28	0.08
	Resti	ricted	indice	es with	n predi	icted ge	enetic go	in in	Digest	ible En	ergy in	take (D	Ei) res	tricted	to zero								
I_5	+	+	+	+	4.2	12.2	-305.0	86.7	3.1	0.00	-0.02	0.19	2.4	-0.5	-1.5	35.4	0.0	18.3	46.4	36.4	83.2	0.44	0.19
I_6	+	+		+	4.2	-7.4	-305.0	86.7	2.7	0.00	-0.02	0.21	0.7	-0.7	0.0	32.7	0.0	15.8	51.4	34.6	84.4	0.41	0.17
I_7	+	+	+		4.2	12.2	-305.0	86.7	4.2	0.00	-0.03	0.00	3.3	-0.7	-2.0	65.9	0.0	34.1	0.0	26.7	83.2	0.32	0.10
I_8	+	+			4.2	-7.4	-305.0	86.7	3.9	0.00	-0.03	0.00	1.1	-0.9	0.0	67.4	0.0	32.6	0.0	24.1	84.4	0.29	0.08

The original selection index (I₁) calculated for improved genotype [6], with mean performance levels for Pd_{max} = 180 g/day, DEi = 27.1 MJ/day, R_{min} = 1.0 and NBA = 10.8 pigs/litter and with all selection criteria included and measured

² NBA as breeding objective trait and selection criterion character

Genetic gains calculated in terms of the gilt life cycle improvement.

Table 7.4 B Effect of using different selection criteria on the index parameters and predicted genetic gains

Efficiencies for reduced and restricted indices relative to the original index

I

B. Index efficiencies and predicted genetic gains per year, assuming selection intensity, $\bar{i} = 1.6$, and generation interval, L = 1.25 years

	Choice of selection criteria					Pr	edicted g	enetic ga	in per y	ear ³		В	LUP inde	x weigh	its	Index e	fficiency	Reduction
	(Mea	surable	charac	ters)	Bro	eding obj	jective tra	aits	Select	ion Crit	егіа					Absolute	Relative	in
	ADG	BF	DFI	NBA	Pd_{ma}	DEi	R_{min}	NBA ²	ADG	BF	DFI	ADG	BF	DFI	NBA	value	efficiency	efficiency
Index					(g/day) MJ/day	(ratio)	(pigs)	(g/day)	(mm)	(g/day)					(\$/year) ³	(%)	(%)
	Selec	tion in	ndices	without con	straints													
I_1	+	+	+	+	4.1	-0.44	-0.03	0.22	-1.8	-0.8	-35.0	2.9	-22.6	-0.6	86.7	53.9	100	
I_2	+	+		+	3.3	-0.08	-0.02	0.26	-0.6	-0.9	-5.5	0.9	-25.0		86.7	44.7	83	17
I_3	+	+	+		5.1	-0.54	-0.04	0.00	-2.3	-1.0	-43.3	2.9	-22.6	-0.6		43.5	81	19
I_4	+	+			4.7	-0.11	-0.03	0.00	-0.9	-1.3	-7.8	0.9	-25.0			31.5	58	42
	Resti	ricted	indice	s with predi	cted genetic gain in Dige.	tible Er	nergy in	take (D	Ei) res	tricted	to zero							
I_5	+	+	+	+	3.9	0.00	-0.03	0.25	3.1	-0.7	-1.9	3.2	-22.2	-0.3	86.7	46.6	87	13
I_6	+	+		+	3.5	0.00	-0.02	0.26	1.0	-0.8	0.0	1.4	-24.4		86.7	44.3	82	18
I_7	+	+	+		5.4	0.00	-0.04	0.00	4.2	-0.9	-2.5	3.2	-22.2	-0.3		34.1	63	37
I_8	+	+			5.0	0.00	-0.03	0.00	1.4	-1.2	0.0	1.4	-24.4			30.8	57	43

The original selection index (I₁) calculated for improved genotype [6], with mean performance levels for Pd_{max} = 180 g/day, DEi = 27.1 MJ/day, R_{min} = 1.0 and NBA = 10.8 pigs/litter and with all selection criteria included and measured

NBA as breeding objective trait and selection criterion character

Genetic gains calculated in terms of the gilt life cycle improvement.

Restricting the genetic gain in NBA to zero produced the same results as in the respective I_3 , I_4 , I_7 and I_8 indices, with NBA variables not being measured. This equivalence was expected, since the genetic and phenotypic correlations between production traits and NBA were assumed to be zero.

7.4.4 Effects of Changes in Economic Values on the Predicted Genetic Gains and on the Efficiency of Index Selection

Economic values of Pd_{max} and NBA were doubled (each in turn), and the predicted genetic gains, percentage of gain contributed by each of the objective traits and index parameters $(\sigma_I, \sigma_T, r_{\pi})$ were calculated for each of the studied situations. Results are presented in Tables 7.5 and 7.6.

Doubling the economic value of Pd_{max} produced higher (more favourable) predicted genetic gains in growth and carcass traits (Pd_{max} , R_{min} , ADG and BF), lower predicted gains in NBA, and smaller reductions in DEi and DFI traits (Table 7.5), compared to the respective indices in Table 7.4. Relative efficiencies of the reduced indices decreased between 10% and 29%, compared to the basic (I_1) index, with the lowest efficiencies predicted from indices with NBA and DFI not measured. Placing more emphasis on the genetic gain in Pd_{max} may be desirable in some specialised sire lines, with less importance given to reproductive performance, and in lines of pigs where further decline in the genetic level of appetite, as determined by the *ad libitum* DEi, is undesirable.

The predicted changes in genetic gains and index parameters from doubling the economic value of NBA are presented in Table 7.6. Only indices with the NBA trait as a measurable selection criterion were applicable. A significant improvement in the NBA genetic gain was observed, despite its low heritability,

while the predicted genetic gains in the remaining production traits were lower, compared to the respective indices in Table 7.4. Relative efficiencies of the reduced indices were lower, compared to the basic (I_1) index. However, only 6% to 8% reduction in efficiency was observed when DFI was excluded as a criterion or when DEi gain was restricted to zero. Placing more emphasis on the genetic gain in NBA may be desirable in some specialised dam lines, where the main goal is to maximise the genetic improvement in the reproduction traits, and the growth and carcass traits are of secondary importance.

The effects of doubling the economic values of Pd_{max} and NBA on the annual response to selection were studied. The predicted percentage decreases in the overall index efficiency relative to the base level situations are presented in Figure 7.3 for the four studied indices. Doubling the economic values of Pd_{max} decreased the index efficiency by about 2% for indices without constraints and about 4% decrease in efficiency was observed for indices with DEi genetic gain restricted to zero. Relatively small decrease in efficiency (-0.3% to -0.4%) was found for unconstrained indices when NBA EV was doubled, and much higher loss in efficiency ranging from -3.1% to -5.7% was calculated for restricted indices.

Table 7.5 A Effect of relative changes in the economic values on the index parameters and predicted genetic gains.

The economic value for Pd_{max} is doubled, with no change in economic values of other objective traits

Efficiencies for reduced and restricted indices relative to the basic index 1

A. Selection index parameters and predicted genetic gains per generation, assuming selection intensity, $\bar{i}^9 = 1$

	Choice	of sel	ection o	riteria		Econom	ic values			Predic	ted gene	tic gain	per gene	ration 3		Percen	age of g	ain conti	ributed	Selec	tion inde	x param	eters
	(Mea	surable	charac	cters)		(\$/gilt li	fe cycle)		Bree	ding obj	ective tra	aits	Select	ion Crit	eria	by eac	h of the	objective	e traits				
	ADG	BF	DFI	NBA	Pd_{max}	DEi	R_{min}	NBA	Pd_{max}	DEi	R_{min}	NBA ²	ADG	BF	DFI	Pd_{max}	DEi	R_{min}	NBA	σ ,	σ_{τ}	\mathbf{r}_{TI}	r^2_{TI}
Index		(g/day) MJ/day (ratio) (pi							(g/day)	MJ/day	(ratio)	(pigs)	(g/day)	(mm)	(g/day)	(%)	(%)	(%)	(%)	(\$/gene	ration) 3		
	Selec	tion ir	ndices	with	out cor	ıstraint	S								> -								
I_1	+	+	+	+	8.4	-18.6	-305.0	86.7	3.8	-0.31	-0.03	0.12	-0.7	-0.7	-25.0	55.4	10.1	15.4	19.0	56.9	103.5	0.55	0.30
I_2	+	+		+	8.4	-18.6	-305.0	86.7	3.3	-0.03	-0.02	0.15	0.4	-0.8	-1.7	57.7	1.0	14.0	27.4	47.4	103.5	0.46	0.21
I_3	+	+	+		8.4	-18.6	-305.0	86.7	4.2	-0.34	-0.03	0.00	-0.8	-0.8	-27.8	68.4	12.5	19.1	0.0	51.2	103.5	0.49	0.24
I_4	+	+			8.4	-18.6	-305.0	86.7	3.8	-0.03	-0.03	0.00	0.5	-1.0	-2.1	79.4	1.4	19.2	0.0	40.4	103.5	0.39	0.15
	Restr	ricted	indice	es with	h predi	icted ge	enetic go	in in	Digest	ible En	ergy in	take (D	Ei) res	tricted	to zero								
I_5	+	+	+	+	8.4	18.9	-305.0	86.7	3.7	0.00	-0.03	0.14	2.8	-0.6	-1.7	60.5	0.0	15.6	23.9	50.7	98.7	0.51	0.26
I_6	+	+		+	8.4	-12.4	-305.0	86.7	3.3	0.00	-0.02	0.15	0.9	-0.8	0.0	58.4	0.0	14.1	27.4	47.3	100.9	0.47	0.22
I_7	+	+	+		8.4	18.9	-305.0	86.7	4.2	0.00	-0.03	0.00	3.2	-0.7	-1.9	79.5	0.0	20.5	0.0	44.3	98.7	0.45	0.20
I_8	+	+			8.4	-12.4	-305.0	86.7	3.9	0.00	-0.03	0.00	1.1	-0.9	0.0	80.5	0.0	19.5	0.0	40.3	100.9	0.40	0.16

Basic selection index (I_1) , with economic value of Pd_{max} doubled, calculated for improved genotype [6], with mean performance levels for $Pd_{max} = 180$ g/day, DEi = 27.1 MJ/day, $R_{min} = 1.0$ and NBA = 10.8 pigs/litter and with all selection criteria included and measured

NBA as breeding objective trait and selection criterion character

³ Genetic gains calculated in terms of the gilt life cycle improvement.

Table 7.5 B Effect of relative changes in the economic values on the index parameters and predicted genetic gains. The economic value for Pd_{max} is doubled, with no change in economic values of other objective traits Efficiencies for reduced and restricted indices relative to the basic index ¹

B. Index efficiencies and predicted genetic gains per year, assuming selection intensity, $\bar{i} = 1.6$, and generation interval, L = 1.25 years

	Choice	of sel	ection o	riteria			Pre	dicted g	enetic ga	in per ye	ear 3		В	LUP inde	x weigh	its	Index ef	ficiency	Reduction
	(Mea	surable	charac	eters)		Bree	ding obj	ective tra	aits	Select	ion Crit	eria					Absolute	Relative	in
	ADG	BF	DFI	NBA		Pd_{max}	DEi	R_{\min}	NBA ²	ADG	BF	DFI	ADG	BF	DFI	NBA	value	efficiency	efficiency
Index						(g/day)	MJ/day	(ratio)	(pigs)	(g/day)	(mm)	(g/day)					(\$/year) ³	(%)	(%)
	Selec	tion ii	ndices	without con	nstraints														
I_1	+	+	+	+		4.8	-0.40	-0.04	0.16	-0.9	-0.9	-32.0	4.9	-37.8	-0.9	86.7	72.8	100	
I_2	+	+		+		4.2	-0.03	-0.03	0.19	0.5	-1.1	-2.2	2.1	-41.1		86.7	60.7	83	17
I_3	+	+	+			5.3	-0.44	-0.04	0.00	-1.0	-1.0	-35.5	4.9	-37.8	-0.9		65.5	90	10
I_4	+	+				4.9	-0.04	-0.03	0.00	0.6	-1.2	-2.6	2.1	-41.1			51.7	71	29
	Restr	ricted	indice	s with pred	icted genetic gain in	Digest	ible En	ergy in	take (D	Ei) res	tricted	to zero							
15	+	+	+	+		4.7	0.00	-0.03	0.18	3.6	-0.8	-2.1	5.3	-37.4	-0.4	86.7	64.9	89	11
I_6	+	+		+		4.2	0.00	-0.03	0.19	1.2	-1.0	0.0	2.4	-40.8		86.7	60.6	83	17
I_7	+	+	+			5.4	0.00	-0.04	0.00	4.1	-0.9	-2.4	5.3	-37.4	-0.4		56.6	78	22
I_8	+	+				5.0	0.00	-0.03	0.00	1.4	-1.2	0.0	2.4	-40.8			51.6	71	29

Basic selection index (I₁), with economic value of Pd_{max} doubled, calculated for improved genotype [6], with mean performance levels for Pd_{max} = 180 g/day, DEi = 27.1 MJ/day, R_{min} = 1.0 and NBA = 10.8 pigs/litter and with all selection criteria included and measured

NBA as breeding objective trait and selection criterion character

Genetic gains calculated in terms of the gilt life cycle improvement.

Table 7.6 Effect of relative changes in the economic values on the index parameters and predicted genetic gains The economic value for NBA is doubled, with no change in economic values of other objective traits Efficiencies for reduced and restricted indices relative to the basic index 1

Selection index parameters and predicted genetic gains per generation, assuming selection intensity, $\bar{i}=1$

	Choice	of sel	ection	criteria		Econom	nic values			Predic	cted gene	etic gain	per gene	ration 3		Percen	tage of g	ain cont	ributed	Selec	ction inde	x param	eters
	(Mea	surable	e chara	cters)		(\$/gilt li	ife cycle)		Bree	ding obj	ective tr	aits	Select	ion Crit	eria	by eac	h of the	objectiv	e traits				
	ADG	BF	DFI	NBA	Pd_{max}	DEi	R_{\min}	NBA	Pd_{max}	DEi	R_{\min}	NBA ²	ADG	BF	DFI	Pd_{max}	DEi	R_{min}	NBA	σ,	σ_{τ}	r_{TI}	r^2_{TI}
Index					(g/day)	MJ/day	(ratio)	(pigs)	(g/day)	MJ/day	(ratio)	(pigs)	(g/day)	(mm)	(g/day)	(%)	(%)	(%)	(%)	(\$/gene	ration) 3		
	Select	ion in	dices 1	withou	t const	raints																	
I_1	+	+	+	+	4.2	-18.6	-305.0	173.4	2.2	-0.24	-0.02	0.24	-1.0	-0.5	-19.1	15.6	7.4	8.9	68.0	60.1	157.0	0.38	0.15
I_2	+	+		+	4.2	-18.6	-305.0	173.4	1.6	-0.04	-0.01	0.26	-0.3	-0.5	-2.7	12.4	1.3	6.0	80.3	55.4	157.0	0.35	0.12
	Restr	icted i	indices	with p	predict	ed gene	tic gain	in Dige	estible .	Energy	intake (DEi) re	stricted	to zero)								
<i>I</i> ₅	+	+	+	+	4.2	12.2	-305.0	173.4	2.0	0.00	-0.01	0.25	1.6	-0.3	-0.9	14.8	0.0	7.7	77.6	56.3	153.9	0.37	0.13
16	+	+		+	4.2	-7.4	-305.0	173.4	1.7	0.00	-0.01	0.26	0.5	-0.4	0.0	12.9	0.0	6.2	80.9	55.1	154.6	0.36	0.13

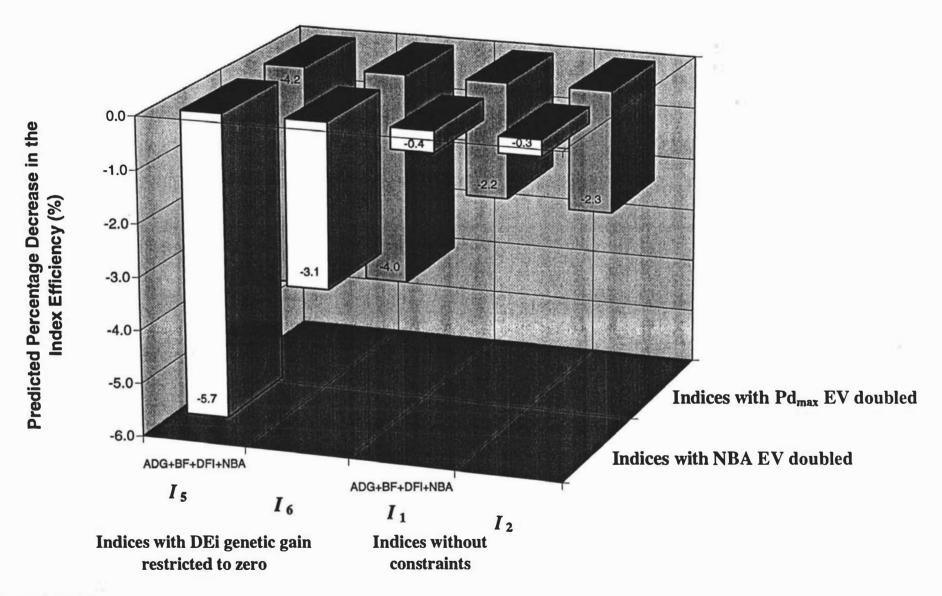
	Choice of selection criteria						Pre	dicted g	enetic ga	in per ye	ear 3		В	LUP inde	x weigh	its	Index el	ficiency	Reduction
	(Measurable characters)						ding obj	ective tra	aits	Select	ion Crit	eria					Absolute	Relative	in
	ADG	BF	DFI	NBA	1	Pd _{max}	DEi	R_{\min}	NBA ²	ADG	BF	DFI	ADG	BF	DFI	NBA	value	efficiency	efficiency
Index					()	g/day)	MJ/day	(ratio)	(pigs)	(g/day)	(mm)	(g/day)					(\$/year) ³	(%)	(%)
	Selec	tion i	ndices	vithout	constraints														
I_1	+	+	+	+		2.9	-0.31	-0.02	0.30	-1.3	-0.6	-24.5	2.9	-22.6	-0.6	173.4	77.0	100	
I_2	+	+		+		2.1	-0.05	-0.01	0.33	-0.4	-0.6	-3.5	0.9	-25.0		173.4	70.9	92	8
Restricted indices with predicted genetic gain in Digestible Energy intake (DEi) restricted to zero																			
I_5	+	+	+	+		2.5	0.00	-0.02	0.32	2.0	-0.4	-1.2	3.2	-22.2	-0.3	173.4	72.1	94	6
16	+	+		+		2.2	0.00	-0 .01	0.33	0.6	-0.5	0.0	1.4	-24.4		173.4	70.6	92	8

Basic selection index (I_1) , with economic value of NBA doubled, calculated for improved genotype [6], with mean performance levels for Pd_{max} = 180 g/day, DEi = 27.1 MJ/day, $R_{min} = 1.0$ and NBA = 10.8 pigs/litter and with all selection criteria included and measured

NBA as breeding objective trait and selection criterion character

Genetic gains calculated in terms of the gilt life cycle improvement.

Figure 7.3 Effect of Changes in Economic Values on the Index Efficiency *



7.4.5 Effects of Changes in Feed Prices, Pigmeat Returns and Non-Feed Costs on the Efficiency of Index Selection

Sensitivity of selection indices to future changes in feed costs, pigmeat returns and non-feed costs was analysed for several alternative situations. The difference in APV as a result of one year of selection was calculated for the four studied indices: I_1 , I_2 , I_5 and I_6 , using predicted annual genetic gains from Table 7.4 B. The APV differences were obtained for each of the simulated percentage increases (or decreases) in production costs and returns and compared to the respective selection responses calculated for the current prices and production circumstances. The increase or decrease in feed costs, pigmeat returns or non-feed costs by the same percentage produced similar absolute responses in respective indices.

Figure 7.4 shows the effect of changes in feed prices on the predicted percentage change in the index efficiency. Increase in feed prices by 10%, 20% or 30% from the current level was expected to reduce the response to selection by about 4%, 8% or 12%, respectively. Decrease in feed prices produced similar in magnitude improvement in the overall index efficiency.

The changes in pigmeat returns had much higher effect on the index efficiency, with respective 10%, 20% and 30% increases in pigmeat prices resulting in approximately 16%, 32% and 48% increase in the selection response (Figure 7.5). Similar but negative responses were predicted from decreasing the pigmeat returns. Indices without constraints were generally more affected by the changes in pigmeat prices, compared to restricted indices.

Changes in non-feed costs produced relatively the lowest responses in the index efficiency, ranging from 3% to 8% change for 10% to 30% increase/decrease in costs (Figure 7.6). Increase in non-feed costs caused the

reduction in selection response compared to the base (current) level. Indices without constraints were more affected by the changes in non-feed costs than the restricted indices.

In future pig production systems, feed prices will probably increase, while pigmeat returns and non-feed costs are likely to be reduced. However, the direction of these changes and their magnitude for individual commercial pig enterprises are difficult to predict. It appears, that the percentage change in pigmeat returns will have much larger effect on the index efficiency than the comparable percentage changes in feed and non-feed costs.

Figure 7.4 Effect of Changes in Feed Prices on the Index Efficiency *

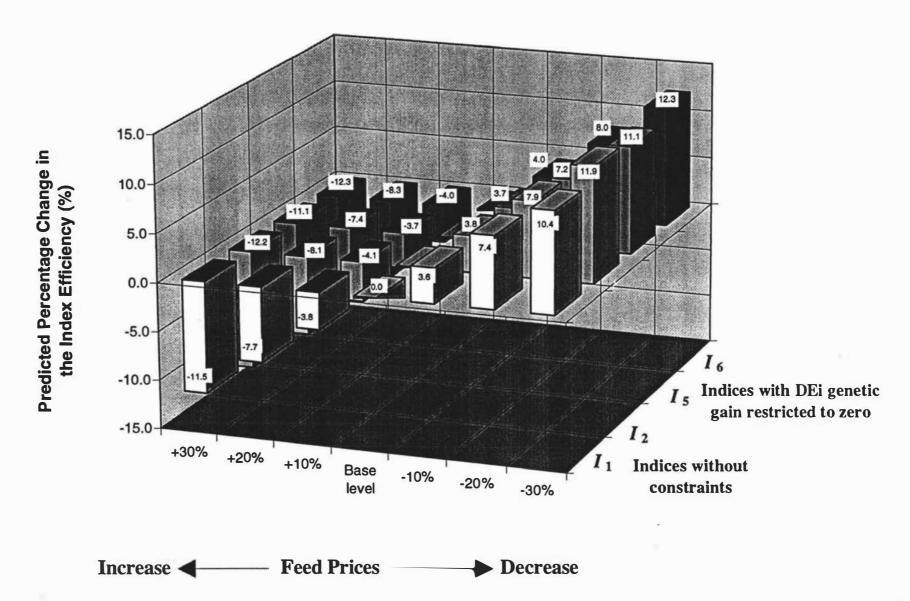


Figure 7.5 Effect of Changes in Pigmeat Returns on the Index Efficiency *

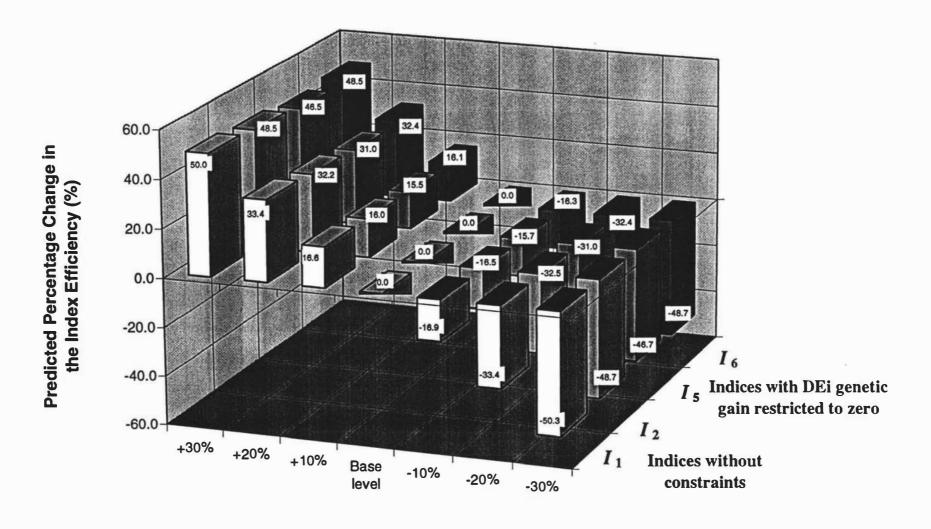
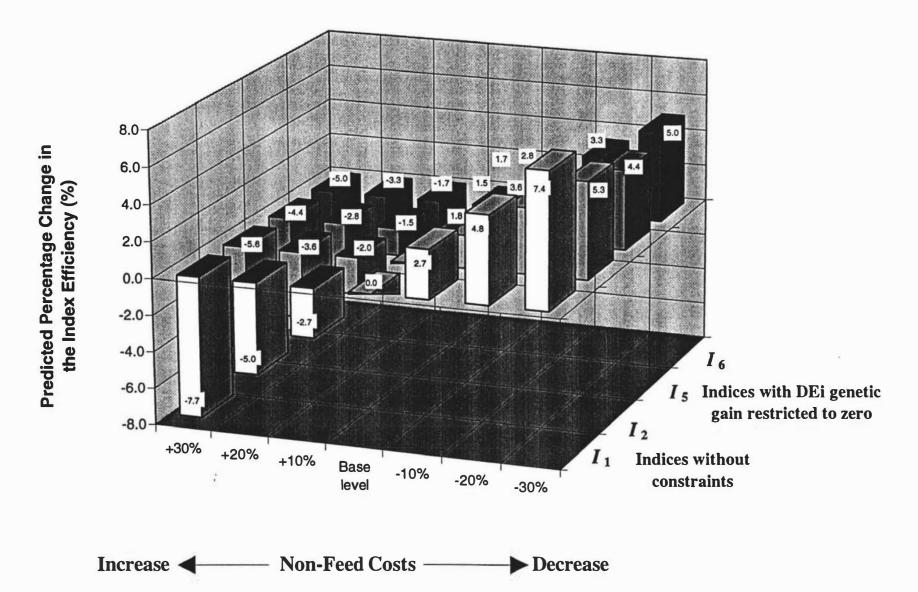




Figure 7.6 Effect of Changes in Non-Feed Costs on the Index Efficiency *



7.4.6 Concluding Remarks

This study demonstrated that selection using indices with DEi genetic gain restricted to zero is expected to produce higher genetic gains in Pd_{max} and NBA, small reductions in genetic gain for BF, significant improvements in ADG genetic gains changing from negative to positive (favourable) responses, and much smaller, or close to zero, reductions in DFI, compared to indices without constraints. The restriction was achieved at the expense of the overall economic response as compared with the unrestricted indices. However, since the restricted index meets the requirements of the long-term objective of maintaining pig's appetite, this reduction in response may be justified.

For specialised dam lines, where the main goal is to maximise genetic improvement in the reproduction traits, the recommended indices to use in the breeding programme are I_5 or I_6 from Table 7.6. These indices would permit a significant improvement in the NBA genetic gain, with only small reductions (3% to 6%) in the overall index efficiency, compared to the base level selection index. When individual measurement of DFI is too expensive or impractical, then I_6 is the index of choice.

Placing more emphasis on the genetic gain in Pd_{max} may be desirable in some specialised sire lines, with less importance given to reproductive performance. Indices I_5 or I_6 from Table 7.5 would be recommended, permitting higher expected gains in growth and carcass traits, but still maintaining desired genetic change in reproductive performance. Index I_6 , without DFI being measured, offers lower genetic gains in Pd_{max} and ADG but more favourable genetic responses in BF and NBA, and zero decrease in DFI genetic gain, compared to I_5 . Index I_6 is the likely choice for the sire line improvement programme, with individual measurements of DFI being too costly or impractical to implement. The reductions in the overall index efficiency for I_5 and I_6 from

Table 7.5 were small, around 4%, compared to the base level selection index. Small (around 2%) decrease in efficiency was found for unconstrained indices when Pd_{max} EV was doubled, indicating the robustness of the studied indices to changes in the economic values. Indices with DEi genetic gain restricted to zero were found to be generally less affected (more robust) by the possible future changes in pigmeat prices and production costs, compared to indices without constraints.

7.5 Discussion

7.5.1 Assumptions

The genetic and phenotypic parameters required for the construction of selection indices can differ, depending on the base level of performance, production circumstances, and feeding regime, i.e. restricted or *ad libitum* (Standal and Vangen, 1985; Webb and Curran, 1986; Cameron *et al.*, 1990). In this study, only one set of parameters for all studied genotypes was used, and r_g equal to r_p was assumed for some of the component traits, for which direct information about the genetic parameters was not available. This was an acceptable simplification, which eliminated the confounding effect of different sets of parameters on the economic weights, and allowed direct comparison of selection effects. However, more accurate set of genetic parameters would be required to derive selection indices for a specific pig improvement programme.

7.5.2 Effect of Changes in Economic Weights on Selection Response

It has been demonstrated that different sets of economic values required for the construction of selection indices for distinct genotypes lead to different responses to selection in the component traits and in the aggregate genotype. The selection indices derived in this study can be used to optimise short-to-medium term selection in the respective base populations. However, they may be sub-optimal in the long term, as demonstrated by Kanis and de Vries (1992). Instead of changing the breeding objective after some generations of selection, they proposed to use a desired gains index as a preferred method to optimise selection in the long term. It was also suggested by Webb (1986), that index selection, while maximising short-term economic gain is not always in line with the biological optimum in the long term.

The increase in profit resulting from further selection was found to decline in pig populations representing improved genotypes, as a result of lower predicted genetic gains in growth and carcass traits. One of the reasons was the need to maintain or even increase the genetic level of voluntary feed intake in the improved genotypes, confirming the findings of Kanis and de Vries (1992). This reduced rate of increase in profit was partially offset by the increase in predicted genetic gains in reproductive performance.

Benefits of concurrent selection for litter size and lean growth depend on relative economic values, accuracies of selection, genetic variation and the genetic correlation among growth and reproductive traits. Webb (1991) argued that when breeding objectives include litter size and lean growth, maximum improvement will be obtained by dividing the populations into sire and dam lines. With zero genetic correlation between lean growth and litter size, the benefit of selection for litter size and lean growth in a dam line was estimated by Webb and Bampton (1988) at 5%, relative to genetic improvement from index selection for a single objective, lean growth. With an unfavourable genetic correlation of -0.2 between lean growth and litter size, these benefits would be enlarged to 6%. At ideal backfat levels, they estimated a relative improvement in the annual selection response (in financial terms) at around 15% and 22%, respectively, assuming the genetic correlations of zero and -0.2. Webb and Bampton (1988) also found that use of family records in specialised dam lines can improve the accuracy of selection for litter size by as much as 50%. Estimated correlations between production and reproduction traits vary greatly between studies (e.g. Morris, 1975; Johansson and Kennedy, 1983; Haley et al., 1988; Short et al., 1994; Rydhmer et al., 1995). In selection for production only, e.g. in specialised sire lines, responses in reproductive traits may depend on the relative emphasis placed on growth rate and leanness in the breeding evaluation, assuming the correlations among growth and litter traits differ significantly from zero (Rydhmer et al., 1992). Reproduction traits are now commonly incorporated into selection indices

and multitrait BLUP evaluations, and their correlations with production traits are often ignored (e.g. Stewart et al., 1990; Long et al., 1990a; Klassen and Long, 1991; Short et al., 1994). By assuming that the correlation between growth and litter traits is zero, separate BLUP evaluations for growth and reproduction traits are undertaken, and the estimated breeding values are then combined in an index using appropriate economic values.

The effects of changing economic weights on the efficiency of index selection in pigs were studied by Morris $et\ al.\ (1978)$, Smith $et\ al.\ (1983)$, Kreiter and Kalm (1986) and Kanis and de Vries (1992). They carried out sensitivity analyses to changes in the response to selection, by altering the economic values of component traits. Similar analyses were performed in the present study. However, as pointed out by Morris $et\ al.\ (1978)$, the change in the relative economic values of the objective traits produces different standard deviations of the objective (σ_T), and the resultant r_T values may not be directly comparable.

In this study, the relative changes in genetic gains of the component traits and in the efficiency of selection were relatively small, compared to the large changes (+200%) in some economic values, confirming the findings of Fowler et al. (1976), Vandepitte and Hazel (1977) and Morris et al. (1978). However, suboptimal breeding objectives are likely to reduce the efficiency of the genetic improvement scheme, as shown by Smith (1983) and Smith et al. (1983). This is particularly important with unfavourably correlated traits in the aggregate genotype. Gjedrem (1972) recommended that all traits with known economic values should be included in the aggregate genotype. However, in practice the number of traits actually considered by breeding organisations is often limited only to those with well defined genetic and economic parameters, and with non-trivial values of $(v \times h^2)$ factors (Smith, 1983). Fast genetic improvement in some traits may have brought them to nearly optimal levels (e.g. BF). Other traits may have remained unchanged (e.g. NBA) or shown deleterious changes

(e.g. DEi). More emphasis placed on the latter would then appear to be justified (Ollivier et al., 1990). Similar recommendation came from Nordskog (1986), who suggested assigning economic weights only to the minimum number of (primary) traits most directly controlling efficiency of production and then using the genetic and phenotypic parameters of other (secondary) traits and their genetic correlations with the primary traits to derive the optimal weighting for the traits to be included in a selection index.

7.5.3 Genetic Evaluation using BLUP Index

Henderson (1963) introduced a modification to Hazel's (1943) selection index which separated application of the selection index into two steps. The first step is estimation of individual breeding values (\hat{g}) for each trait included in the definition of the aggregate genotype. The second step is application of the relative economic values (ν) to calculate $I_g = \nu'$ \hat{g} (see also equation [7.4]). This separation permits use of more accurate BLUP techniques to estimate individual breeding values of traits, including adjustment for differing amounts of information (Henderson, 1963; 1973), and it then allows the economic values applied to vary with differing breeding objectives, without recalculating breeding values (Hazel *et al.*, 1994). This simplifies continuous updating of trait information on all relatives and allows for variation in the relative economic weights most appropriate for individual breeds or breeders.

The economic advantages of selection based on BLUP EBV's over traditional selection index have been demonstrated in several studies (e.g. Belonsky and Kennedy, 1988; Keele et al., 1988; Wray, 1988; Mabry and See, 1990; Long et al., 1991). For a balanced data structure, the weighted EBV index will have a higher accuracy than the traditional selection index, because it uses information on relatives as well as information from other traits. Long et al.

(1990b) found, that although BLUP is affected to a greater degree by pedigree errors, it still provides better response to selection than selection based on a phenotypic index.

Some of the BLUP evaluation systems (e.g. Stewart et al., 1990; Long et al., 1990a) use two sub-objectives of the pig's life cycle (the growing-finishing sub-objective and the sow sub-objective). These sub-objectives are defined separately, using economic, production and marketing information supplied by the breeder. The two sub-objectives are then combined with appropriate emphasis into a single value, on which selection is based. This concept permits development of selection criteria for a subset of the overall breeding objective, and allows breeders to exploit the complementary effect associated with specialised maternal and paternal lines (Stewart et al., 1988).

In the context of BLUP, the amount and source of available information can be different for each animal, influencing the variance-covariance matrix among the estimated breeding values, $Var(\hat{u}_i)$, and the estimates of predicted genetic gains from selection on the index. The $Var(\hat{u}_i)$ depends on the inbreeding coefficient and on the prediction error variance (PEV) of the EBV's. The accuracy of EBV's is defined as the correlation between an estimated breeding value and the true breeding value and is a measure of the value of the information on the animal and its relatives used to compute the EBV. The methods to calculate approximations of the prediction error variances and covariances of the estimated breeding values were reported recently by Misztal and Wiggans (1988) and Tier et al. (1991). Crow et al. (1991) evaluated the use of an estimate of $Var(\hat{u}_i)$, calculated for a group of animals available for selection, using mean squares and mean cross products of their EBV's. Another approximation, based on the assumption that EBV's for a "standard" animal are predicted from only one record on the animal itself, was used by Schneeberger et al. (1992) to calculate the estimated variance of the index and the predicted genetic gains.

This simplification might be sufficient to give an indication of the direction in which the population will move under selection.

7.5.4 Importance of Voluntary Feed Intake

Recently, there is concern that present methods of performance testing may need to be revised to prevent further decline in feed intake. Unfavourable genetic correlations between feed intake and lean meat content, meat-to-fat ratio and backfat thickness (Brandt et al.,1985; Kreiter and Kalm, 1986; Webb and Curran, 1986), and relatively high economic values placed on carcass leanness and food conversion ratio compared with that for daily gain may result in a decrease in food intake capacity and limit further improvement in lean growth rate and sow productivity (Fowler et al., 1976; Smith and Fowler, 1978; Webb, 1989; Smith et al., 1991; Kerr and Cameron, 1994). Long-term economic improvement is expected to come from increase in the rate of lean tissue deposition (LTGR), accompanied by the increase in appetite (Fowler, 1986; Webb, 1986; Ollivier et al., 1990). The optimal system of performance testing appears to be based on ad libitum feeding, allowing monitoring of voluntary feed intake and full expression of LTGR. Recording of individual feed intake may be desirable, providing a measure of genetic differences in maintenance requirements which cannot be predicted from either growth rate or backfat. However, the value of this additional information would have to exceed the costs of measuring individual feed consumption. According to Cunningham (1969), the cost-effectiveness of the index can be improved by removing those variables for which the proportion of the total recording cost is much greater than their relative contribution to the rate of genetic gain.

Brandt *et al.* (1985) and Kreiter and Kalm (1986) proposed restricting genetic gains in daily feed intake to zero, to prevent further decline in appetite. They found a decrease in the predicted genetic gain in lean meat content and backfat thickness, and a significant improvement in average daily gain. Kreiter and Kalm (1986) concluded that at present, the simplest way to control feed intake under *ad libitum* feeding is to place more emphasis on growth rate. This was confirmed here, by studying the effect of doubling the economic value of Pd_{max} on other component traits. The result was higher (more favourable) predicted genetic gains in growth and carcass traits and lower rate of feed intake decrease. Placing more emphasis on Pd_{max} and/or restricting genetic gain in DEi to zero may be applicable in some specialised sire lines to prevent further decline in voluntary feed intake, as demonstrated in this study.

7.5.5 Summary and Conclusions

For optimal selection response, correct relative economic values for traits in the aggregate genotype are important. The actual genotypic levels of Pd_{max} , DEi, R_{min} and reproductive performance traits in combination with management circumstances determine the EV's required. The life cycle production model incorporating biological pig growth simulation was applied in this study to obtain the EV's for different base genotypes. The resultant EV's optimised the change in voluntary feed intake in relation to other growth and reproductive performance traits. The increase in profit resulting from further selection was lower in pig populations representing improved genotypes, despite the fact that assumed variance parameters were identical for different genotypes. This reduced rate of increase in profit resulted from lower gains in growth and carcass traits, partially offset by an increase in predicted genetic gains in reproductive performance. For improved genotypes, the predicted increase in profit per gilt life cycle after one generation of selection ranged from \$26 to \$98 for one standard deviation of

index selection with a selection intensity of 1. For unimproved genotypes, higher genetic gains in growth and carcass traits resulted in profits exceeding \$120 per generation of selection.

The selection response for pigs may be modified by applying restriction to the index or by using a desired gains approach to prevent decrease in DEi for the long-term perspective. Future improvement in the aggregate genotype from reduction in fatness and in voluntary feed intake is expected to be limited. Reduction in the genetic level of DEi, and subsequently DFI, may not be desirable for some improved lines of pigs with already low levels of appetite. The indices designed to further reduce DEi in those genotypes would negatively affect genetic gains in Pd_{max}, ADG and NBA, as demonstrated in this study. The indices with DEi genetic gain restricted to zero were found to be generally less affected by the possible future changes in pigmeat prices and production costs, compared to indices without constraints.

It was shown that for specialised dam lines, where the main goal is to maximise genetic improvement in reproduction traits, the recommended indices are those where more emphasis is placed on NBA, permitting larger genetic gains in litter size, with only small reductions (3% to 6%) in overall index efficiency. Placing more emphasis on genetic gain in Pd_{max} may be desirable in some specialised sire lines, with less importance given to reproductive performance. This would permit higher predicted genetic gains in growth and carcass traits, but still maintaining desired genetic change in reproductive performance. The efficiencies of derived indices were relatively robust to changes in the economic values for Pd_{max} or NBA.

Considering the likely reduction in expected genetic gains in growth and carcass traits, more attention should be paid to the inclusion of litter size and meat quality traits in the selection objective. BLUP methodology permits more

accurate selection for litter size in larger multi-herd populations. Other reproductive traits, such as sow longevity, rebreeding interval and piglet survival, are likely to gain importance in the future.

The challenge for the future is to create an animal with a large appetite, but which can convert the food eaten into lean meat with high efficiency. In addition to economic values, knowledge of genetic parameters is required for estimation of individual breeding values and for derivation of selection indices for a specific pig improvement programme. Further research is needed to develop routine methods of estimating genetic levels of Pd_{max} , DEi and R_{min} for individual pigs, thereby allowing for direct selection on these traits.

7.6 References

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GENERAL DISCUSSION

The first step in this development of an improved selection programme was to choose the method of derivation of relative economic values of traits in the breeding objective. Different approaches were considered, including economic and biological indices and methods using life cycle production modelling. The model approach was chosen as the most appropriate method for deriving relative economic values for New Zealand pig production systems. The main advantages of using a life cycle pig production model included:

- ability to account for the whole life cycle production efficiency
- incorporation of nutrient partitioning and simulation of pig growth
- simultaneous derivation of REV's for production and reproduction traits
- ability to account for the effects of genetic changes in performance and differences in production systems.

Economic values of reproduction and growth performance traits were estimated at the commercial level of production, with efficient production of slaughter pigs as the main goal. However, as pointed out by de Vries (1989b), this may not always be optimal for a breeding organisation, where the value of improvement of a trait is determined by its impact on saleability of the breeding stock. There is a need for appropriate definition of a breeding objective for average production conditions of each country, to ensure that short-term interests of breeding organisations do not compromise overall long-term response (Ollivier et al., 1990). The parameters used in this study represented current average performance of New Zealand commercial pig farms.

Differences in selection responses to alternative selection regimes could lead to "selection regime by production system" interaction (Webb and Curran, 1986). Selection environments of breeding organisations are sometimes chosen

to maximise accuracy of measurement, and in the past this involved central testing stations, individual penning and feed recording. However, commercial production takes place in a wide range of environments, with different feeding systems and husbandry conditions, which may result in lower than expected genetic correlations between performance in testing station and farm environments (Groeneveld et al., 1984; Ollivier et al., 1984; Webb and Curran, 1986). Another concern is the existence of genotype by feeding level interaction (ad libitum versus restricted) and the reduction in voluntary feed intake (appetite) in programmes emphasising feed conversion efficiency (Webb, 1989). results of the recent study on correlated responses in performance test traits with ad libitum feeding (Cameron and Curran, 1994) confirm previous findings (e.g. Mitchell et al., 1982; Brandt et al., 1985; McPhee, 1989) that selection for lean growth rate can improve the overall efficiency by increasing growth rate and maintaining or increasing daily feed intake, while selection on lean food conversion improves efficiency of lean growth primarily by a reduction in daily feed intake.

The biological interactions between voluntary feed intake and growth and carcass traits have been accommodated in the computer model simulating life cycle pig production developed in this study. The concepts of nutrient partitioning and the linear/plateau relationship between daily protein deposition and digestible energy intake (Kielanowski, 1969; Whittemore and Fawcett, 1976) were incorporated in the biological growth model, which was part of the life cycle model (Chapter 2). By changing the genetic levels of the three variables controlling growth: upper limit to body protein deposition rate (Pd_{max}), mean daily ad libitum digestible energy intake (DEi), and minimum lipid to protein deposition ratio (R_{min}), it was possible to simulate effects of genetic changes in several biological components and calculate economic values of growth and reproduction traits for several pig genotypes (Chapter 3). Based on these relative economic values, selection indices were developed that optimised selection for

growth, voluntary feed intake and reproduction, and predicted genetic gains were investigated for a range of improved and unimproved genotypes (Chapter 7).

One of the unique features of the model developed in this study was the utilisation of a wide range of grower diets in pig growth simulation, in recognition that food is the major item of expenditure on the pig unit and different least-cost diets are needed to optimise growth in various pig genotypes. Another implementation was the inflation-free discount rate (Smith, 1978) used to calculate the decrease in value of the future net returns to account for time preference of consumption. Current genetic improvement schemes are concerned with present economic needs and discounting includes some allowance for risk and uncertainty about future husbandry-marketing requirements (Smith, 1988). It is also open to discussion which commercial environment should be considered in the calculation of REV's. Should it be that of today's average herd, or that of the better performing 10% of the herds as an indication of future environments? Brascamp and de Vries (1992) suggest that partial answer to this question lies in the results of recently completed experiment (Webb and Curran, 1986; Cameron and Curran, 1994), which provided information on the genetic relationships between components of efficient lean growth rate. According to Long (1992), the breeders should consider the average economic values that are valid over the next 3 to 5 years as this is the target to breed for, to meet the requirements of their customers. Breeders must determine the type of commercial producers they want to develop their breeding stock for, as this will influence the process of developing breeding objectives and the allocation of resources needed for the pig breeding operation. In the present study, a farrow-to-finish management system producing bacon pigs was assumed. The assumption was also made that the farm production system was operating at an optimum, and environmental and management factors such as temperature of the grower shed, herd disease status, and the number of sows (herd size) had no effect on the estimation of relative economic values of traits, calculated as a change in profit per gilt life cycle.

Until recently, it was regarded that the omission of reproductive performance traits from the index which includes growth and carcass traits, would result in only small losses in economic improvement (Avalos and Smith, 1987). The current opinion is that litter size has become an important trait in the breeding objective, and new statistical technology together with highly prolific Chinese breeds offer the potential for rapid genetic improvement (Webb, 1991). It has been shown that selection for litter size can be successful particularly when selecting within specialised dam lines (Webb and Bampton, 1988; Treacy, 1989). The coefficient of variation for litter size is high, at around 0.25, which compensates for the low heritability and for the fact that expression of the trait is sex-limited. Optimisation of the breeding programme requires that traits which contribute to the breeding objective must be identified and their relative economic worth quantified. Inclusion of reproductive performance in the models of Tess et al. (1983a), de Vries (1989a), and in the present model, allowed simultaneous derivation of REV's for production and reproduction traits. The whole life cycle production efficiency was accounted for which permitted the interactions between reproduction and growth performance traits to be established. Reproduction traits were found to depend on the overall life cycle profit, as influenced by the genotype. Inclusion of sow productivity traits in the breeding objective was important for populations of improved genotypes, confirming similar findings by Tess et al. (1983b).

Choice of the optimum breeding objective depends on knowledge of genetic parameters of the traits in the aggregate genotype and characters used as selection criteria. Accurate phenotypic and genetic parameters are needed for the development of selection indices and for the prediction of breeding values. Restricted Maximum Likelihood procedures have several desirable statistical properties and are widely used for genetic parameter estimation. REML algorithms utilise all available records, account for the loss in degrees of freedom due to fixed effects in the model and maximise only that portion of the likelihood

which is invariant to the fixed effects (Patterson and Thompson, 1971). Multivariate REML methods were employed in this study to provide more accurate estimates of heritabilities and genetic correlations for the analysed nucleus pig populations (Chapter 4). Simulation work suggests that estimates of variances obtained using the mixed model equations are not noticeably biased by selection (Sorensen and Kennedy, 1984). Also, if REML estimates are obtained from the data and used in the mixed model equations, the resulting estimates of breeding values are unbiased over repeated sampling (Sorensen and Kennedy, 1986). The desirable statistical properties of REML make it the method of choice for genetic parameter estimation in animal breeding.

Mixed Model Equations (MME), originally developed by C.R. Henderson for predicting random effects without assuming parameter values of fixed effects to be known, are now routinely used for genetic evaluation in several animal species including pigs. It was later discovered that predictions of random effects from MME are Best, Linear and Unbiased (BLUP) (Henderson et al., 1959, Henderson, 1963). The BLUP method has several important advantages, discussed in Chapters 5 and 7, over the traditional selection index. If selection is practised across years and herds, then BLUP is the technique of choice (Garrick, 1991). BLUP can account for herd effects and, therefore across-herd analyses can be performed if adequate genetic ties or connectedness exist between herds (Chapter 6). These genetic links are provided via the exchange of stock and/or use of artificial insemination (AI). In the past, selection among small privatelyowned nucleus herds has been achieved by providing a standard environment via a central testing station. Use of traditional selection index in the central testing environment allowed estimation of individual performance only, without taking into account progeny performance. The growing emphasis on selection for litter size and use of relatives' records from dam and sire families brings the requirement for large multi-herd populations tested on farm. Concentration of nucleus pig improvement in the hands of large breeding companies and the

increase in health control requirements, together with the availability of BLUP and AI technologies, makes central testing stations practically redundant. It has been argued that the investment in central test stations should now be switched to AI centres to assist in providing genetic links across herds (Webb, 1991).

Application of BLUP for the estimation of breeding values of pigs tested on farm allowed determination of genetic and environmental trends in the studied populations (Chapter 5). This was essential in evaluating the efficiency of past selection decisions. The analyses employed in this study to monitor genetic, environmental and phenotypic trends can be used to estimate future genetic gains in reproduction and growth performance traits, permitting retrospective evaluations of the effectiveness of the breeding programmes in purebred populations of pigs.

Main Conclusions

- The breeding objective should be based on biological and economic efficiency of sow reproductive ability and growth performance of her offspring.
- The optimisation of the pig breeding programme requires accurate knowledge
 of the relative economic values of reproduction and production traits. The
 model developed in this study can be used for this purpose.
- Results demonstrated EV's of traits depended on the average genetic merit in the pig herd and its interaction with management circumstances (level of feeding, nature of the diet, life cycle length). EV's for DEi were negative for unimproved genotypes and became positive for improved genotypes with insufficient amounts of metabolisable energy to realise their Pd_{max} genetic potentials. Pd_{max} EV's were lower for improved genotypes and became zero when full expression of Pd_{max} was restricted by insufficient digestible energy intakes. The present model accommodates biological interactions between voluntary feed intake and growth and carcass traits and accounts for the increasing importance of pig's appetite in the estimations of economic values of traits. The methods developed here can be used to re-evaluate breeding objectives in pig populations.
- The importance of litter size as a breeding objective trait depends on the overall life cycle profit and increases with the improved genotypes.
- The statistical technology applied in this study facilitates accurate estimation
 of genetic parameters and breeding values, and allows comparisons of genetic
 merit of pigs performing in different herds and time periods.
- The analyses employed to monitor genetic and environmental trends provided a check on the efficiency of past selection decisions. Realised genetic gains in ADG and BF varied between breeds and were, respectively, 52% to 105% and 24% to 32% of those theoretically possible. The realised selection response, based on actual selection differentials and generation intervals, was between

- 59% and 62% of that predicted.
- Predicted genetic gains from selection on different economic indices were
 calculated using genetic parameters and relative economic values obtained in
 this study. The increase in profit resulting from further selection was lower in
 pig populations representing improved genotypes, as a result of lower
 predicted genetic gains in growth and carcass traits. This reduced rate of
 increase in profit was partially offset by the increase in predicted genetic gains
 in reproductive performance.
- Further research is needed to develop routine methods of estimating genetic levels of Pd_{max} , DEi and R_{min} for individual pigs, thereby allowing for direct selection on an objective incorporating these traits.

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Zusammenfassung

Zuchtziele und Zuchtwertschätzung als Mittel zur Verbesserung der Profitabilität in der Schweineproduktion

Die optimale Zuchtplanung in der Schweineproduktion basiert auf der Wahl eines geeigneten Zuchtziels, wirtschaftlicher Gewichte für objektive Messgrössen, Selektionskriterien und den daraus folgenden genetischen und phänotypischen Parametern, Selektionsindizes und erwarteten Züchtungsfortschritten, sowie einer geeigneten Populationsstruktur.

Um die wirtschaftlichen Gewichte (EV) von Merkmalen der Fortpflanzungsund Wachstumsleistung zu schätzen, wurde ein Computermodell, das die Lebensleistung einer Zuchtsau, sowie die Wachstumsleistung ihrer Nachkommen simuliert, entwickelt. Bestandteil dieses Lebensleistungs-Modell war ein biologisches Wachstumsmodell, das, mit Hilfe der linear-plafonierten Beziehung zwischen der täglichen Stickstoffeinlagerung und der täglichen Aufnahme an verdaulicher Energie, die Verdauung und den Stoffwechsel von Energie und Stickstoff aus dem Futter simuliert. Es wurde angenommen, dass die Wachstumsfähigkeit von Schweinen hauptsächlich durch genetische Faktoren, wie Obergrenze für die Einlagerung von Körperprotein (Pdmax), durchschnittliche ad libitum Aufnahme von verdaulicher Energie (DEi), und minimales Verhältnis zwischen Fett- und Proteineinlagerung (R_{min}), bestimmt wird. Indem man die Auswirkungen genetischer Veränderungen mehrerer biologischer Komponenten in einem kombinierten Produktionssystem (Vermehrung und Mast) bei ad libitum Fütterung simulierte, wurden die wirtschaflichen Gewichte pro Lebensleistung einer Jungsau berechnet. In Tieren mit geringem genetischen Potential (dh. Pd_{max} < 140 g/Tag, DEi > 30 MJ/Tag, $R_{min} \ge 1$) wurden wirtschaftliche Gewichte von \$12 zu \$22 für eine Erhöhung von Pd_{max} um 1 g/Tag, von \$-20 zu \$-123 für eine Zunahme von DEi um 1 MJ/Tag, von weniger als \$-500 für eine Erhöhung von

R_{min} um eine Einheit, und von weniger als \$12 für jedes zusätzlich lebend geborene Ferkel pro Wurf berechnet. In Genotypen mit hohen Potential wurde das wirtschaftliche Gewicht für Pdmax bei einer Erhöhung um eine Einheit auf \$14 berechnet, und für hohe Pd_{max}-Werte von über 180 g/Tag, wenn die Auswirkungen von Pd_{max} durch ungenügende Aufnahme an verdaulicher Energie eingeschränkt waren, näherte es sich null. Die wirtschaflichen Gewichte für DEi in Genotypen mit hohem Potential und ungenügendem Angebot an verwertbarer Energie waren positiv. Während Schweine mit hohem genetischem Potential hohe wirtschafliche Gewichte für die Anzahl lebend geborener Ferkel pro Wurf aufwiesen (> \$70 pro zusätzliches Ferkel), waren die EVs pro Einheit Zunahme in anderen Fortpflanzungsmerkmalen, wie Alter der Jungsau beim ersten Oestrus, Zeitspanne zwischen Absetzen und Oestrus, und Ferkelsterblichkeit während der Säugezeit, leicht negativ. Die Resultate zeigen, dass die wirtschaftlichen Gewichte vom genetischen Potential der entsprechenden Herde, sowie dessen Interaktion mit Management-Faktoren des Betriebes (Fütterungsintensität, Art des Futters, Verbleib der Sauen im Produktionssystem) abhängen.

Zur Schätzung der (Co) Varianzen, Heretabilitäten, genetischen Korrelationen und gemeinsamen Umwelteffekte für Merkmale der Fortpflanzungs- und Wachstumsleistung von feldgeprüften Schweinen der Rassen Edelschwein, Landrasse und Duroc, wurden Mehrmerlemals-Tiermodelle und Restricted Maximum Likelihood (REML)-Methoden verwendet. Best Linear Unbiased Prediction (BLUP)-Methoden, die die Bestimmung von genetischen, umweltbedingten und phänotypischen Trends in den untersuchten Populationen erlauben, wurden zur Schätzung der Zuchtwerte eingesetzt. Die realisierten Züchtungsfortschritte pro Jahr variierten von 2.1 zu 4.3 g/Tag Lebendtageszunahme und von -0.2 zu -0.3 mm für Rückenspeckdicke. Die realisierten genetischen Trends für Lebendtageszunahme und Rückenspeckdicke waren vergleichbar mit publizierten Resultaten aus ähnlichen Studien, aber erheblich geringer als die entsprechenden erwarteten Werte von 4.13 g/Tag/Jahr und -0.88 mm/Jahr. Einzig in der Durocrasse waren der realisierte und der

erwartete Züchtungsfortschritt in Lebendtageszunahme vergleichbar. Während in den Duroc ein positiver genetischer Trend für die Anzahl lebend geborener Ferkel (+0.07 Ferkel/Wurf/Jahr) gefunden wurde, waren die entsprechenden Werte in der Landrasse und den Edelschweinen vernachlässigbar klein. Dank Mixed-Model Techniken (BLUP and REML) wurden, unter Einbezug aller verfügbarer Informationen über Verwandtschaften, Messgrössen und Umwelteffekte, effiziente und genaue Voraussagen der Zuchtwerte und Schätzungen der genetischen Parameter erzielt.

Mit Hilfe von Indizes, die von einer Reihe von Tieren mit hohem und genetischen Potential berechnet wurden, wurden verschiedene Selektionsstrategien untersucht und die erwarteten genetischen Zuchtfortschritte geschätzt. Die Effekte verschiedener Kombinationen von Selektionskriterien auf den Selektionserfolg, der Einsatz von Selektionsindizes mit Restriktionen, und die Empfindlichkeit gegenüber Aenderungen der wirtschaftlichen Gewichte und der Struktur zukünftiger Kosten/Nutzen Verhältnisse wurden untersucht. Im weiteren wurden die Auswirkungen dieser Veränderungen auf den erwarteten Selektionserfolg analysiert. Als Ergebnis eines geringeren erwarteten Züchtungsfortschritts in Merkmalen der Wachstums- und Schlachtleistung, war der zusätzlich erzielte Gewinn durch fortlaufende Selektion in Genotypen mit hohem Potential geringer als in solchen mit geringem Potential. Diese geringe Gewinnzunahme wurde durch einen erhöhten erwartenen Zuchtfortschritt in Fortpflanzungsleistung wettgemacht. In Genotypen mit hohem Potential betrug der erwartete Gewinnzuwachs für die Lebensleistung einer Jungsau nach einer Generation Selektion zwischen \$26 und \$98 pro Standardabweichung des Selektionsindex mit einer Selektionsintensität von 1. Ein Gewinnzuwachs von mindestens \$120 pro Generation Selektion wird von Genotypen mit geringem Potential, und daher erhöhtem erwarteten Zuchtfortschritt in Merkmalen der Wachstums- und Schlachtleistung, erwartet. Wird der Wurfgrösse ein höheres wirschaftliches Gewicht zugemessen, reduziert sich der erwartete Zuchtfortschritt für Wachstums- und Schlachtleistung.

Résumé

Objectifs de sélection et évaluation génétique pour améliorer le profit des porcheries

L'établissement d'un programme optimal de sélection porcine nécessite le choix d'un objectif de sélection et de valeurs économiques relatives pour chaque caractère; le choix de critères de sélection et de leurs paramètres génétiques et phénotypiques; la détermination d'indices de sélection et du progrès génétique prédit ainsi que le choix d'une structure de la population.

Un modèle informatique simulant les cycles de production à vie d'une cochette et les performances de croissance de ses descendants a été développé pour estimer les valeurs économiques relatives (EV's) des performances de reproduction et d'engraissement. Un modèle de croissance biologique simulant la digestion et le métabolisme de l'énergie et des protéines ingérées chez le porc à l'engrais était intégré dans le modèle de production à vie. Dans ce modèle de croissance biologique, la relation entre la quantité d'énergie digestible ingérée et la quantité de protéine déposée est une relation linéaire avec un plateau. On supposa que les principaux facteurs génétiques qui contrôlent la croissance des porcs étaient la limite supérieure pour la quantité journalière de protéine déposée (Pd_{max}), la consommation volontaire journalière d'énergie digestible (DEi) et le rapport minimum entre les dépôts lipidiques et protéiques (R_{min}). Les valeurs économiques relatives ont été calculées en simulant des changements génétiques au niveau de différents critères biologiques, et ce pour un naisseur-engraisseur alimentant ses porcs à volonté.

Pour des porcs ayant un faible potentiel génétique ($Pd_{max} < 140 \text{ g/j}$, DEi > 30 MJ/j, $R_{min} \ge 1$), les EV's suivantes ont été calculées: \$12 à \$22 par gramme de

Pd_{max} en plus, \$-20 à \$-123 par MJ/j ingérée en plus, et moins de \$-500 pour une augmentation d'une unité du rapport R_{min} . Les EV's pour le nombre de porcelets nés vivants par portée (NBA) étaient inférieures à \$12 par porcelet supplémentaire.

Dans le cas de génotypes améliorés, les EV's pour Pd_{max} avaient des valeurs inférieures à \$14 et devenaient nulles pour des Pd_{max} supérieurs à 180 g/j. Au dessus de 180 g/j la quantité d'énergie ingérée devient le facteur limitant de la quantité de protéines déposées tandis que les EV's pour DEi deviennent positives. Les EV's pour NBA étaient supérieures pour les génotypes améliorés (> \$70 par porcelets en plus). Les EV's calculées pour d'autres caractères de reproduction: âge à la première ovulation, intervalle entre sevrage et saillie-fécondante, et pourcentage de mortalité pré-sevrage, étaient relativement basses. Ces résultats montrent que les EV's dépendent du niveau génétique du troupeau et du système de gestion appliqué (intensité d'alimentation, composition de la ration, longueur du cycle de vie).

La procédure du maximum de vraisemblance (REML) et des modèles animaux multicaractères ont été utilisés pour estimer les héritabilités, variances, covariances, corrélations génétiques et les effets commun dûs à l'environnement pour les performances de reproduction et de croissance chez des porcs Grand Porc Blanc, Landrace et Duroc.

On a recouru à la méthode d'évaluation génétique BLUP pour estimer les valeurs d'élevage dans les populations analysées. Les progrès génétiques annuels réalisés variaient de 2.1 à 4.3 g/j pour le gain journalier (ADG), et de -0.2 à -0.3 mm pour l'épaisseur du lard dorsale mesurée avec des ultrasons (BF). Ces progrès génétiques annuels réalisés sont comparables à ceux rapportés dans des études réalisées à l'étranger. Toutefois, à l'exception de ADG chez le Duroc, ils étaient inférieurs aux progrès génétiques prédits, 4.13 g/j/an et -0.88 mm/an. Les

tendances génétiques pour NBA étaient négligeables chez le Grand Porc Blanc et le Landrace, et favorables (+0.07 porcelets/portée/an) chez le Duroc.

Des indices de sélection, dérivés d'une variété de génotypes, ont été utilisés pour simuler différentes stratégies de sélection et les progrès génétiques prédits ont été estimés. Les effets des différents critères de sélection sur l'efficacité de la sélection, l'utilisation d'indice assorti de restrictions, les changements de valeurs économiques et la structure des futurs coûts et revenus ont été étudiés. On a examiné les effets de ces changements sur la réponse à la sélection prédite. L'accroissement du profit résultant de la sélection était inférieur pour les génotypes améliorés, ceci en raison des faibles progrès génétiques prédits pour les performances de croissance et de carcasse. Toutefois, cette réduction de l'accroissement du profit était partiellement compensée par les progrès génétiques prédits pour les performances de reproduction.

Après un génération de sélection (intensité de sélection = 1), l'accroissement prédit du profit par cycle de vie d'une cochette variait de \$26 à \$98 par écart type de l'indice de sélection pour les génotypes améliorés et de plus \$120 pour les génotypes d'un faible niveau génétique. Une augmentation de l'importance économique accordée aux critères de reproduction débouche sur une diminution du progrès génétique prédit pour les performances de croissance et de carcasse.