Chapter 3

Simulation of a Closed Pig Breeding Herd

3.1 Introduction

Discussion in the previous chapter highlighted several factors which influence response to selection and potential methods available to the breeder for increasing genetic gain. Breeders commonly attempt to maximise genetic gain over the time frame of their breeding program while also avoiding the negative effects of inbreeding. The introduction of advanced on-farm genetic evaluation systems to the Australian pig industry (i.e., PIGBLUP) has provided the means by which breeders may increase within-herd selection response by enhancing accuracy of selection. However, it is well recognised that more efficient use of family information, through BLUP procedures, generally results in elevated rates of inbreeding (eg. Belonsky and Kennedy, 1988; Quinton et al., 1992; Roehe et al., 1993; Wray, 1989). In addition, methods commonly used to control inbreeding may compromise short term genetic gain through decreasing selection differentials.

Elevated rates of inbreeding potentially associated with BLUP procedures raise two major concerns. Firstly, breeders generally recognise that the effects of inbreeding are deleterious, and this concern may hinder the implementation of BLUP methodology within herds. Secondly, although BLUP procedures adequately account for most of the effects of selection and inbreeding, inbreeding depression is not accounted for by the standard animal model (Sorensen and Kennedy, 1983; Kennedy et al., 1988; Uimari and Kennedy, 1990). The parameterisation of Smith and Maki-Tanila (1990) correctly models inbreeding effects. However, their methods are computationally demanding and unlikely to be useful for current genetic evaluation systems. As such, the efficiency of commonly used BLUP procedures is reduced in the presence of inbreeding depression, the effects of which have been observed in several economically important traits (Bereskin et al., 1970; Takahashi et al., 1991). Although it is recognised that the same problem may be true of other evaluation methods, balancing genetic gain with inbreeding may be more difficult with BLUP methodology.

Quinton et al. (1992) compared selection on BLUP estimated breeding values (EBVs) with individual selection at the same level of inbreeding. To achieve comparable levels of inbreeding for alternative selection schemes, more intensive selection was practised for individual selection criteria. The authors found that when compared at low rates of inbreeding (usually less than 2% per year) intensive individual selection yielded greater genetic gain than selection on EBVs. Moreover, where inbreeding depression was assumed present, the elevated rates of inbreeding resulting from EBV selection acted to further reduce selection response. However, the expectation in this work was that inbreeding depression effects were the same for selection alternatives. It is arguable whether or not this will be realised in practice since inbreeding depression is likely to be expressed differently in diverse populations compared at the same level of inbreeding. Regardless of this factor, the authors considered that the extra gain achieved with EBV selection was at the expense of additional inbreeding, and that BLUP genetic evaluation procedures may be suboptimal in situations where low rates of inbreeding are desirable, for example in smaller populations.

The obvious inference from this work was that BLUP may be unsuitable for practical genetic evaluation applications, particularly where it may be most valuable; for sex- or measurement-limited and/or lowly heritable traits, where elevated rates of inbreeding may result from the greater emphasis on use of family information. However, these observations apply to selection within a closed herd, and extrapolation to a national livestock population is hardly possible. For example, computation of coefficients of inbreeding across herds involved in the Canadian Swine Improvement Program, where within-herd genetic evaluation was carried out using an animal model, showed low rates of inbreeding over a ten year period (Hubbard et al., 1990). This result was attributed in part to migration of seedstock between herds. Still, in some herds (and breeds) rates of inbreeding diverged considerably from the national averages calculated, suggesting differences in herd structure and size, breeding policy and selection emphasis. As such, rates of inbreeding in small scale breeding operations are dependent on several factors, and are not solely attributable to choice of genetic evaluation system.

The work of Quinton et al. (1992) only considered changing selection intensities to achieve equivalent rates and levels of inbreeding over time for alternative selection schemes. Additionally, in each scenario, selection was followed by random mating. Several other strategies are available for reducing rates of inbreeding over the short to medium term. For example, rates of inbreeding may be lowered through maintaining a larger number of families (De Vries et al., 1989; Long et al., 1991), reducing variance of family size, reducing the amount of and emphasis placed on family information in genetic evaluation procedures (Toro et al., 1988), avoidance mating systems, and within family selection (Dempfle, 1975). However, these approaches tend to reduce short term response by decreasing selection differentials (refer Section 2.3.4). This is likely the result of the static nature of such approaches, potentially excluding the selection and mating of otherwise desirable individuals which, given the dynamic nature of the breeding operation, would become competitive at certain times.

An alternative is to define the problem of optimising genetic gain, while maintaining low rates of inbreeding, at the level of the individual or mating pair. In this scenario changes in the genetic relationships between selected individuals may be accounted for. Goddard and Smith (1990), suggested that knowledge of an individual's average relationship with other animals in the breeding herd may be valuable for comparing selection candidates. Other more dynamic methods considered at the level of the mating pair have also been proposed (Smith and Hammond, 1987b; Toro and Nieto, 1984; Toro and Pérez-Enciso, 1990). However, the effectiveness of alternative methods to achieve high rates of genetic gain and lower rates of inbreeding are dependent on constraints such as the structure of the breeding population, the genetic determination of the trait(s) of interest, and the joint effects of selection, mating and testing procedures. Current procedures evaluated to reduce rates of inbreeding may not be optimal in terms of overall genetic gain.

The objective of this chapter, therefore, was to evaluate alternative selection and mating policies for optimising genetic gain while considering rates of inbreeding over the short to medium term. The effects of inbreeding depression were not simulated, although this does not imply that these are unimportant. Studies in this chapter have been based on the development of a stochastic simulation program which models a closed pig herd undergoing directional selection. The development of simulation procedures is discussed in Section 3.2. Simulation results are presented and discussed in Sections 3.3 and 3.4. A concluding discussion is presented in Section 3.5.

3.2 Simulation Procedures

A general simulation program was designed to enable a variety of population structures to be modelled by varying number of sows, number of sows per boar, maximum number of parities per sow, number of litters per sow per year, number of pigs born alive per litter, percentage of pigs born available for selection per week, and the maximum number of litters per boar. The above parameters defined a system in which a continuous cycle of performance testing, evaluation for selection, mating and the generation of future records was carried out. Further, the simulation modelled an average pig production system characterising the environment to which these events and decisions were confined. Consequently, the population consisted of overlapping generations constrained within a particular age group structure and production environment. Simulated breeding values for the trait of interest and coefficients of inbreeding were of principal interest. A single set of these parameters characterised the population used in this study.

All pigs generated within the simulation were performance tested in batches, confined to the management group of their contemporaries at birth. A single performance test record was then available for the trait of interest, defined for several heritabilities. Selection was solely for this trait, the selection criterion being either individual performance (I) or an estimated breeding value (EBV) obtained using BLUP procedures. After entry to the breeding herd no additional culling on performance occurred, although general reproductive failure (eg. sows failure to conceive on two successive matings) and other unavoidable reasons for culling (eg. loss of soundness) were simulated. Mating of selected individuals was one of three types: at random, positive assortative (pairs allocated according to their merit for the selection criterion), and mate selection procedures. The time frame in which selection and mating decisions were made was one week. The length of the breeding program, therefore, was defined by weeks of selection carried out.

In Figure 3.1 the sequence of events occurring for a single replicate is represented, where each cell contains the computer subroutine used and its primary functions. Details of simulation procedures follow, with reference made to computing subroutines noted in Figure 3.1 where appropriate. For the small population size investigated, it was envisaged that the simulated population was only part of a complete operation, since continuous production cycles imply a population size large enough to use fixed resources (eg. farrowing and bacon sheds). Interest in the consequences of alternative breeding programs on genetic gain and rates of inbreeding was confined to this population alone.

3.2.1 Parameters Defining the Simulated Herd

Several parameters were integral for defining the size of the breeding operation simulated, the sequence of events occurring for each individual throughout the duration of the breeding program, and characteristics of the trait of interest. Parameters common to all breeding programs simulated, and used to define size and operational aspects are described as follows:

NSOWS*: number of sows. Defines the **expected** size of the female breeding herd.

NSPB: number of sows per boar. Used for calculating the number of boars in service concurrently, **NBOARS**, which influences the total number of boars required annually.

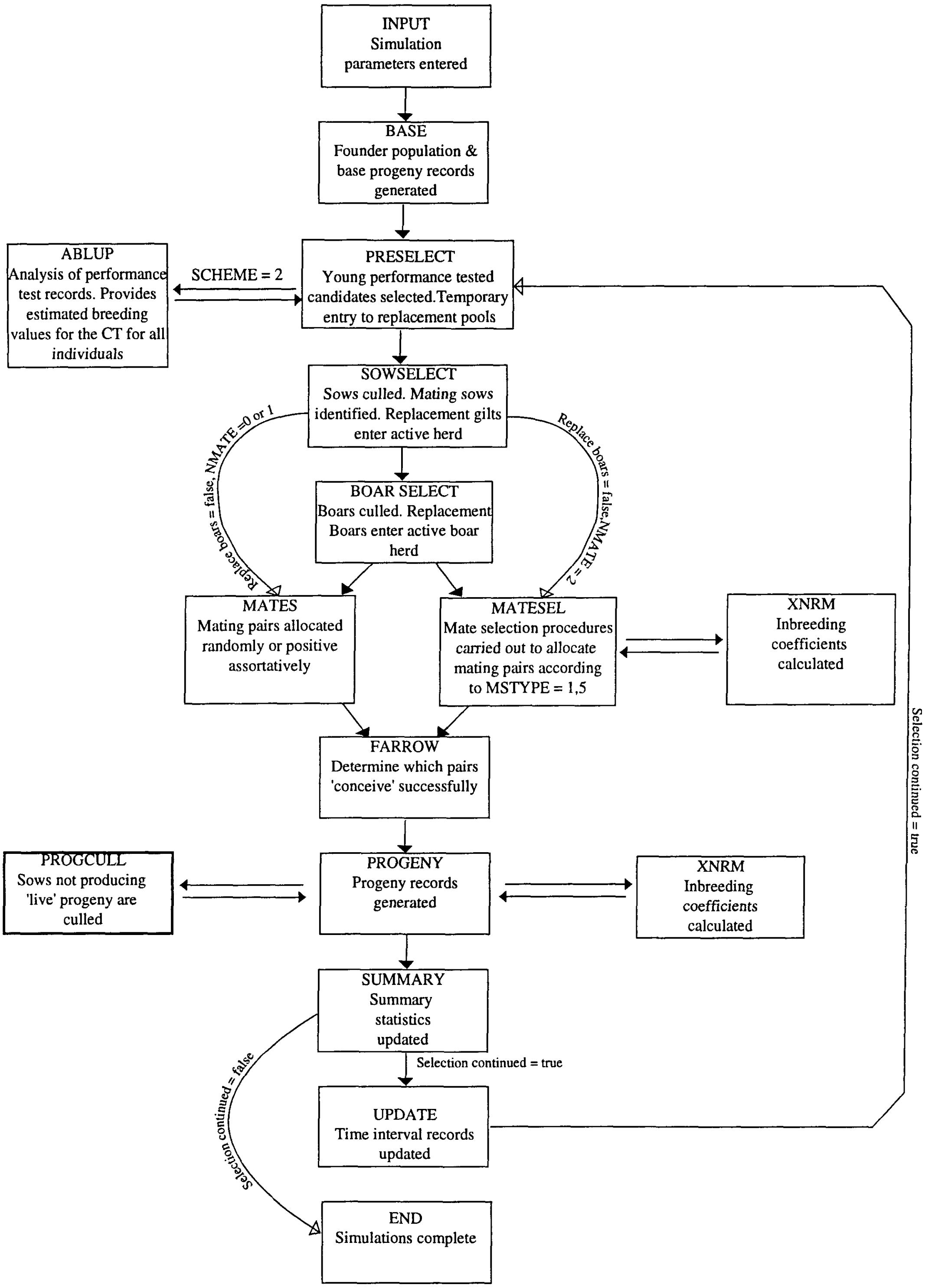

Figure 3.1: Flow diagram of events simulated for a closed herd undergoing selection.

NLIT: number of litters per sow per year. Determines the interval from farrowing to rebreeding. Used to calculate the expected interval between consecutive farrowings, **NWFAR**.

NPAR: maximum number of parities a sow is allowed prior to culling.

PERS: approximate percentage of sows culled per week. Useful for maintaining adequate numbers of gilts in a gilt pool.

MLIT: maximum number of litters all boars may sire. Served as a culling criterion for individual boars. If **MLIT** was large, boars only remained in service until a maximum age of 78 weeks to ensure turnover.

SFAR*: **expected** number of sows farrowing per week, as calculated from **NSOWS** and **NLIT**.

SMATE*: **expected** number of sows mated per week allowing for an average conception rate of 90%. That is, **SFAR/0.9**.

ANBA*: **expected** number of pigs born per litter.

PERC: the percentage of those pigs born and performance tested remaining eligible for selection (eg. due to culling for additional factors). This was allowed for in the simulation by random culling, i.e., unrelated to performance, prior to selection according to **PERC**.

WBREP: weeks between boar replacements. Boars were evaluated at regular time intervals according to **WBREP**. This ensured a relatively constant flow of selected young boars into the active breeding herd. **WBREP** was a function of **NBOARS**.

NWEEKS: total number of weeks. Defined the duration of the breeding program.

NREPS: number of replications required.

Parameters super-scripted with an asterisk were influenced by the stochastic nature of the simulation. As such, **NSOWS**, **SFAR** and **SMATE** were expected values, influenced by post-mating returns to service, which affected the realised total number of sows active in the breeding herd and therefore the number of sows mated and farrowing each week. Variation in **ANBA** resulted from differences in true breeding values for number born alive (NBA), and environmental influences affecting the expression of NBA for parent sows. Additional parameters used to set up specific selection and mating combinations, and characterising the genetic and environmental properties of the trait of interest included:

SCHEME: coded value defining selection scheme alternatives evaluated. For **SCHEME** = 1, 2 or 3, replacement breeding stock were selected to enter the breeding herd at random, based on individual performance or an EBV.

NMATE: coded value defining alternative mating procedures employed. For **NMATE** = 0, 1 or 2, mating pairs are allocated at random, by positive assortative mating (basis for allocation was the selection criterion), or using mate selection (see **MSTYPE**) .

MSTYPE: coded value defining alternative mate selection procedures when **NMATE** = **2**. Values for **MSTYPE** range from 1-5 (see Section 3.2.7).

$\mathbf{h^2}$: heritability of the trait of interest.

σ_p: phenotypic standard deviation of the trait of interest.

Parameters entered into the simulation through subroutine INPUT included: **NSOWS, NSPB, NPAR, PERS, MLIT, NLIT, ANBA, PERC, NWEEKS, NREPS, SCHEME, NMATE, MSTYPE,** $\mathbf{h^2}$ and σ_p. Values for **NBOARS, NWFAR, SFAR, SMATE** and **WBREP** were then derived from this information.

3.2.2 Parameter Values for the Simulated Herd

Parameter values defining the simulated population structure used in this study are presented in Table 3.1. Derived values were: **NBOARS = 13, NWFAR = 23, SFAR* = 11, SMATE* = 12,** and **WBREP = 4**. Features of parameters marked (*) are as mentioned previously. The following subsections are specifically developed assuming these parameter values.

3.2.3 Simulation of Records

Several records, for example age and sex, were required to facilitate each individual's entry into the cycle of activities within the simulation (refer Figure 3.1). Records of

Table 3.1: Input parameter values used for the simulated population.

Parameter		**Value(s)**
NSOWS*	=	260
NSPB	=	20
NPAR	=	4
PERS	=	0.35
MLIT	=	200
NLIT	=	2.25
ANBA*	=	10.5
PERC	=	80%
NWEEKS	=	832
NREPS	=	20
SCHEME	=	0, 1 or 2
NMATE	=	0, 1 or 2
MSTYPE	=	0, 1, 2, 3, 4 or 5
$\mathbf{h}^2$	=	0.1, 0.35 or 0.6
σ_p	=	100.0

this type are operationally useful and commonly recorded in animal breeding programs. In addition, performance test records for the trait of interest (CT) were simulated for all individuals, and inbreeding coefficients (F) were calculated from pedigree information. Details of these records are presented in Table 3.2. Additional records to facilitate mating and culling procedures were required only for selected individuals. For example, phenotypic records for the trait number born alive (NBA) were generated for selected sows which produced progeny. These supplementary records are listed in Table 3.3.

All individuals were permanently identified within the simulation. Although demanding of computer memory, permanent identification allowed rapid entry of individual records into appropriate subroutines when required. Records were arrayed sequentially, allowing access to all records available in the population at a given time.

Table 3.2: Records generated for each individual in the simulated population.

Record	Abbreviation
Identification number (permanent)	**ID**
Sire ID	**P1**
Dam ID	**P2**
Sex	**SEX**
Age (in weeks)	**AGE**
Generation number	**GEN**
Performance test management group	**MGT**
True performance test management group effect	**MGTE**
True breeding value for the trait of interest	$\mathbf{TBV}_{CT}$
True breeding value for number born alive	$\mathbf{TBV}_{NBA}$
Phenotypic value for the trait of interest	$\mathbf{IND}_{CT}$
Calculated inbreeding coefficient (from pedigree)	**F**
†Estimated breeding value (EBV) for the trait of interest	$\mathbf{EBV}_{CT}$

†Only calculated when **SCHEME = 2**

Table 3.3: Additional records generated for selected individuals.

Record	Abbreviation
SOWS	
Dam tag (temporary)	**DAM**
Parity number	**PAR**
† Reproductive status	**STAT**
Value of the permanent environmental effect for NBA	$\mathbf{PE}_{NBA}$
Phenotypic value for NBA	$\mathbf{IND}_{NBA}$
BOARS	
Sire tag (temporary)	**SIRE**
Number of litters sired	**SRED**
Maximum no. of sows mated per week	**MAXS**

† eg. gestating, returning to service or available for breeding.

The Founder Population and Ongoing Records

The founder population consisted of 580 sows and 29 boars systematically sourced to build up a structured population within the production cycle defined by input parameters. All founder individuals were assumed unrelated and unselected. Within this population each boar was randomly assigned to mate 20 sows. Progeny resulting from these matings were defined as generation one, and represented an age distribution between in-utero to 38 weeks of age. This structure allowed immediate access to young performance tested individuals for selection purposes. Of the initial founder population, 13 boars and 260 sows were randomly chosen to remain in the active breeding herd. Sows were distributed equally across parities 1-4, each parity group usually being represented within each week's mating pool. Boars remaining in the active breeding herd were also representative of several age groups. Each replicate within a defined breeding program had independently generated founder populations. The above procedures were carried out in subroutine BASE.

All future progeny records were generated by subroutine PROGENY. Permanent IDs were assigned at 'conception'. This allowed records on all individuals to be included in BLUP mixed model equations and summary statistics when required. Mortality of progeny was not simulated in this study and is unlikely to affect overall conclusions. Davis (1987) noted that increased mortality resulting from inbreeding depression was unlikely to have a large impact on response to selection.

Records for the Criterion Trait

Records for the criterion trait were available on all individuals at the end of performance testing. An infinitesimal model (Bulmer, 1980) was assumed, where the criterion trait was determined by an infinite number of unlinked loci, each contributing a small additive genetic effect. Input parameters used to define the criterion trait included the base population heritability (h^2), phenotypic standard deviation (σ_p), and genetic standard deviation ($\sigma_a = \sqrt{h^2} * \sigma_p$). In all simulations $\sigma_p = 100$. Heritabilities considered were chosen on a linear scale ($h^2 = 0.1$, 0.35 and 0.6).

Phenotypic records (y) for base animals were simulated as the sum of additive genetic (a), environmental (e) and management group effects (mgt) according to:

$$y = mgt + a + e$$

In a mixed model context, the management group effect was considered as a fixed effect common to all animals present in the same performance test group. For base animals, management groups were regarded as unknown, although each individual's record included this effect. Management group effects took several values and were simulated to conform to an arbitrary pseudo-random normal distribution: $mgt \sim N(0, 0.3\sigma_p^2)$, where σ_p^2 is the phenotypic variance of the simulated trait. Random additive genetic and environmental (residual) effects were sampled from a normal distribution with zero mean and appropriate variance: $a \sim N(0, \sigma_a^2)$ and $e \sim N(0, \sigma_e^2)$, where σ_a^2 and σ_e^2 are additive genetic and environmental variation respectively, defined according to the heritability investigated. In practice, performance records of base or founder animals are not likely to be known.

Performance test records (y) of progeny were generated as:

$$y = mgt + \frac{1}{2}(a_s + a_d) + m + e$$

where: a_s and a_d are the true parental breeding values for the trait of interest, mgt and e are sampled from the above distributions (management group is known), and m is a normally distributed random Mendelian sampling effect. In the absence of inbreeding, Mendelian effects are distributed as $m \sim N(0, \frac{1}{2}\sigma_a^2)$. However, in the presence of inbreeding variation due to segregation effects is reduced according to the average inbreeding coefficient of mating partners. In this situation m is modified following Foulley and Chevalet (1981):

$$\sqrt{\frac{1}{2}(1 - \frac{F_s + F_d}{2})} * \sigma_a * N(0, 1)$$

where F_s and F_d are the inbreeding coefficients of the sire and dam respectively. Effects of inbreeding depression on phenotypic performance were not simulated.

Records for Number Born Alive

Although number born alive (NBA) was not the trait of interest, it was simulated to allocate the number of progeny produced from each mating pair. This is more realistic

Table 3.4: Genetic and phenotypic parameters for simulated NBA.

Source of Variation	**Value**
Phenotypic	2.54
Permanent environment	0.61
Temporary environment	2.32
Additive genetic	0.83

than constraining sampling processes to a fixed number of progeny per mating pair, since this may alter variation in the trait observed from expectation. As for the trait of interest, NBA was assumed to comply with the infinitesimal model. Breeding values for NBA were simulated as above using the appropriate genetic variance. Phenotypic records for this trait (y_{NBA}) were only generated for sows producing progeny and were simulated under a simple repeatability model:

$$y_{NBA} = u + a_{NBA} + pe + e_{NBA}$$

where: u is the population mean, and pe and e_{NBA} are the random permanent environmental, and temporary environmental effects specific to each individual and record respectively. This model appropriately allows simulation of repeated records.

Genetic and phenotypic parameters for NBA were obtained from Klassen (1992), and are presented in Table 3.4. The expected genetic correlation between parities was approximately 0.8, with a phenotypic correlation of 0.17 (Klassen, 1992). Heritability of NBA was $h^2_{NBA} = 0.11$. It was assumed that genetic ($r_{A_{CT,NBA}}$) and phenotypic ($r_{P_{CT,NBA}}$) correlations between NBA and the trait of interest were zero. The population mean for NBA was 10.5 piglets per litter. No fixed or parity effects were simulated although it is recognised that these effects exist in reality. As for the trait of interest, inbreeding depression was not simulated.

Inbreeding Coefficients

Two methods were used to calculate inbreeding coefficients for each individual: the traditional path coefficient method, and the tabular method. Choice of method was adapted from Tier (1990). In the simulation, generation of a large number of animals over an extended time period may result in complicated pedigree structures, and potentially high levels of inbreeding. Path coefficient methods are efficient when pedigree structures are uncomplicated and levels of inbreeding are low. As such, this procedure was only used when individuals had four or less generations of ancestors. Conversely, tabular methods are more computationally efficient when pedigree structure is complicated, and were used when the number of generations exceeded four. Calculation of inbreeding coefficients required only one pig per litter to be evaluated, since all pigs within a litter will have the same calculated inbreeding coefficient from pedigree information alone. Inbreeding coefficients were calculated using the subroutine XNRM.

Additional Records

Additional records generated for all individuals included sex, age and generation number. Sex was determined as female when an independent sample from a (0,1) uniform distribution exceeded 0.5, and was obviously required for selection and mating decisions. Age was determined using a counter recording age in weeks from conception (negative values) to birth (zero) and beyond (positive values). This enabled individuals to be included as candidates for selection and mating at the appropriate age. Age was also a criterion for culling of selected boars, as well as gilts and young boars from their respective replacement breeding stock pools. Age was updated weekly using subroutine UPDATE. Generation number was defined as the mean of the parental generation numbers plus one, subsequently rounded up to the nearest integer. This provided a simple basis on which to select the most appropriate algorithm for calculating inbreeding coefficients.

Additional records for selected individuals included parity number and reproductive status for sows, and total number of litters sired for individual boars. These records were also of no direct interest, although essential for logical progression of the simulation. Parity number and total number of litters sired, specific to individual sows or boars respectively, were assigned only for matings producing progeny. These were updated for relevant parents in subroutines SOWSELECT and BOARSELECT. Parity number was used as a culling criterion for sows. Similarly, boars were restricted to siring a maximum number of litters. Reproductive status was determined by **NWFAR** since sows were unavailable for breeding throughout the majority of a simulated year. As such, the appropriate entry of sows into mating routines was maintained.

3.2.4 Calculation of Selection Criteria

The selection criterion was either phenotypic performance or an EBV, derived using BLUP procedures, for the trait of interest. No adjustments were made to performance test records as individuals were initially compared within management group. The BLUP procedures were carried out in subroutine ABLUP (Animal model BLUP) as described below.

BLUP Procedures

EBV's were predicted for all individuals using a reduced animal model (RAM; Quaas and Pollak, 1980) incorporating all information from relatives, accounting for inbreeding, and including fixed management group effects. The RAM facilitated reduced computational demands by fitting breeding values for parent animals only in the mixed-model equations (MME). In pig breeding populations, only a small proportion of individuals will become parents, so the number of equations to be solved is substantially reduced using a RAM compared to a full animal model (AM). EBVs for non-parent animals were calculated by backsolution (Quaas and Pollak, 1980). Although performance records were available for the founder population, these records were not included in the MME since each founder individual represented a separate unknown management group effect. EBVs for the founder population were, therefore, derived from analysis of records on their progeny as founder animals were included in the numerator relationship matrix (NRM).

Following Quaas and Pollak (1980), the mixed model equation for RAM is:

$$y = X\beta + Zu + e$$

where: y is the vector of observations on all animals, parent and non-parent, β is an unknown vector of fixed (management group) effects including the general mean,

X is a known design matrix relating records to fixed effects, u is a random vector of breeding values for parent animals, Z is a known design matrix relating records to breeding values of parent animals, and e is a random vector of environmental (or residual) effects. In a row of Z referring to a parent animal, there is a '1' in the column position corresponding to its BV. In a row referring to a non-parent, there are two '$\frac{1}{2}$'s' in the column positions corresponding to its parent's BVs. Implicit assumptions are that $E(u)$ and $E(e)$ are null and:

$$Var\begin{bmatrix} u \\ e \end{bmatrix} = \begin{bmatrix} A\sigma_a^2 & 0 \\ 0 & R \end{bmatrix}$$

where A is NRM for parent animals, and R is a diagonal matrix, the elements of which are σ_e^2 for parent animals and $\sigma_e^2 + \frac{1}{2}(1 - \frac{F_s+F_d}{2})\sigma_a^2$ for non-parent animals. The mixed model equations are then:

$$\begin{bmatrix} X'R^{-1}X & X'R^{-1}Z \\ Z'R^{-1}X & Z'R^{-1}Z + A^{-1}\sigma_a^2 \end{bmatrix} \begin{bmatrix} \widehat{\beta} \\ \widehat{u} \end{bmatrix} = \begin{bmatrix} X'R^{-1}y \\ Z'R^{-1}y \end{bmatrix}$$

Solutions for $\widehat{\beta}$ and $\widehat{u}$ were obtained using Gauss-Siedel iteration procedures combined with successive over-relaxation techniques. Back-solutions were calculated for EBVs of non-parents (u_i) following Quaas and Pollak (1980):

$$\hat{u_i} = 0.5(\hat{u_s} + \hat{u_d}) + \frac{d_i}{d_i + \alpha}(y_i - mgt_i - 0.5\hat{u_s} - 0.5\hat{u_d})$$

where:

$$d_i = \frac{1}{2} - \frac{1}{4}F_s - \frac{1}{4}F_d$$

and $\alpha = \frac{\sigma_e^2}{\sigma_a^2}$. F is the inbreeding coefficient of individual i's sire (s) and dam (d) respectively, and mgt_i is the fixed effect solution relevant to individual i.

In order to further reduce computing demands, BLUP evaluations were carried out at six month intervals on all individuals generated. This was necessary due to the time consuming nature of repeated BLUP analyses for the large number of records generated. With performance test records assigned at conception, in-utero and pre-performance test animals could be included in the analyses at this time. Preliminary simulations showed that this approach did not greatly influence comparison of alternative BLUP based breeding programs, as each was subject to the same procedure. However, absolute values of genetic gain and levels of inbreeding would be elevated, in comparison to that achieved under individual selection, which must be considered when comparing alternative selection schemes.

3.2.5 Selection and Culling Procedures

Selection of young stock to enter the breeding herd was carried out weekly at random (**SCHEME** = 0), or based on either phenotypic performance (**SCHEME** = 1) or an EBV for the trait of interest (**SCHEME** = 2) in subroutine PRESELECT. Each week comprised a contemporary group available for selection, this group being equivalent to those individuals born and performance tested concurrently. As such, selection of both sexes was practised within contemporary group, although in reality it is usual to have several contemporary groups available for selection simultaneously. The number of individuals available as candidates for selection in a given week was influenced by **PERC** (refer Section 3.2.1). For simulation results presented later **PERC** = 80%, so 20% of performance tested young stock were randomly culled prior to selection. The percentage culled reflects factors which will reduce the number of candidates available for selection post performance testing, examples of which may include soundness, teat number etc.

Each week the best six gilts and one young boar were selected from the available candidates as potential replacement breeding stock (RBS). No restrictions were placed on the number of individuals selected from any particular family. Upon selection, gilts and boars entered sex determined RBS pools at 32 weeks of age, and were retained in these pools until a maximum of 38 weeks of age. The RBS pools represented candidates available to enter the breeding herd at sexual maturity, in accordance with the number of replacement stock required. In addition to this primary selection stage, young boars were subjected to an assessment of breeding soundness (eg. sperm count) after entry into their RBS pool. The probability of young boars being culled at this stage was 20%, independent of all other factors. No additional culling criteria existed for gilts, as the occurrence of oestrous is often the main factor which influences the likelihood of a selected gilt entering the breeding sow herd. At this stage, unselected individuals were considered unavailable for future selection decisions.

After entry of RBS into their respective pools, evaluation of the current sow herd was carried out. Sows available for breeding in a given week only included those which had three litters or less, who had returned to service less than twice in previous matings, and were in the appropriate stage of their reproductive cycle. Sows which had already produced four litters or had returned to service twice were automatically culled. In addition, sows were also culled on general failure, commonly associated in practice with reproductive performance, although excluding number born alive for simulation purposes. The independent probabilities of an individual sow being culled for general failure following their 1st, 2nd, or 3rd parity was 10%, 7.5%, and 7.5% respectively. Gilts were then chosen to enter the group available for mating at random, according to the number of additional females required to meet **SMATE**. This procedure resulted in the weekly construction of a sow mating vector, enabling entry of appropriate individuals into mating routines. The above procedures were carried out in subroutine SOWSELECT.

Active boars were evaluated over regular time intervals according to **WBREP**. At this time, any boars who had reached or exceeded **MLIT** and/or 78 weeks of age were replaced. In addition, 10% of mature boars were culled per year as a result of poor performance (eg. infertility, injury). Young boars within the RBS pool were ranked according to their merit for the selection criterion. Entry of young boars into the active breeding herd was then dependent on the number of replacements required, and their estimated merit. In contrast to the gilt pool, failure of young boars to enter the breeding herd at this time led to their disposal, allowing the build up of a new group of young boars for selection in the following weeks. Entry of young boars into the active boar herd was determined in subroutine BOARSELECT.

3.2.6 Mating Procedures - Random and Positive Assortative Mating Systems

Three types of mating system were evaluated with the simulation: random (**R**); positive assortative (**A**), hereafter termed assortative; and several mate selection (**MS**) approaches. Mate selection procedures will be discussed in Section 3.2.7 and were coded in subroutine MATESEL. Both **R** and **A** mating procedures were carried out in subroutine MATES.

For both random and assortative mating systems, the allocation of mating pairs was dependent on both the number of sows available for breeding in each week and the number of services allowed per week per boar. This determined the number of service boars required to complete the necessary matings, given that services per week per boar was age limited. Intrinsic to these mating systems was that all 13 active boars were used as parents, and that each boar was mated to a similar number of sows prior to culling. As such, when the number of sows to be mated was greater or less than 13, some boars had either multiple or zero matings. This implies that the number of matings per individual boar was controlled to ensure each boar produced a similar number of litters per week, as is common in practice. The following steps were used to allocate sows to each boar on a weekly basis.

1. Boars and sows were randomly ordered within their respective mating vectors.

2. The number of sows mated per individual boar was assumed to be one.

3. The difference between the number of sows to be mated (NSM) and **NBOARS** was established.

4. Where this difference was negative (NSM<**NBOARS**), NSM service boars were sequentially chosen to remain in the mating vector. Remaining boars were allocated zero matings. Where NSM≥**NBOARS** all boars were retained as service boars in the mating vector.

5. For assortative mating, service boars and sows were re-ordered within their respective mating vectors according to their relative merit for the selection criterion. For **R** systems no change in order was required.

6. Mating pairs were allocated sequentially from the mating vectors. Where boars were less than 52 weeks old they were restricted to mating one sow per week. Boars ≥ 52 weeks of age were allowed to service up to three sows per week. Additional matings were thus allocated in sequence to individual boars who exceeded 52 weeks of age.

When allocation of mating pairs was complete, subroutine FARROW was used to determine which pairs produced progeny using a 90% conception rate. Failure to conceive resulted in the mating being nullified in subroutine PROGENY, where records for successful matings were generated. Sows which failed to conceive were entered into a new mating group, with a three week interval between the failed mating and their return to service. Any additional failures resulted in their culling in subroutine SOWSELECT. Moreover, sows which conceived but produced no live progeny were culled in subroutine PROGCULL. In order to establish the relative impact of assortative mating on inbreeding, no measures were taken to avoid matings between related individuals for either mating system.

3.2.7 Mate Selection Procedures

In contrast to random and assortative mating systems, selected boars who entered the active group of 13 boars were not necessarily used as sires, and were deliberately allocated to different numbers of sows over their lifetime with mate selection (**MS**) procedures. Allocation of mating pairs was according to paired merit criteria. As such, selected boars were regarded as a group available for breeding, although their suitability for breeding was subject to characteristics of their potential mates. The sequence of events which determined mating pairs for weekly mate selection procedures were as follows.

1. All active boars and sows available to be bred were entered into their respective mating vectors.

2. For all possible mating pairs, the expected additive genetic merit of each mating pair's potential progeny was determined, and entered into a paired merit (PM) array. Additive genetic merit of the progeny was assumed to be equivalent to the mid-parent value for the selection criterion.

3. The variance of values for PM, V_{PM}, for each boar across sows were scaled to achieve $V_{PM} = 1$. Where only additive genetic effects exist, this would not affect the individual ranking of either boars or sows. However, due to the relatively low variation in progeny inbreeding coefficients, this step was necessary if information relating to inbreeding coefficients was to be incorporated into PM values.

4. Inbreeding coefficients were calculated for potential progeny of all possible mating pairs.

5. According to the MS scheme to be evaluated, PM values were then adjusted using information provided by inbreeding coefficients of the potential progeny for each mating pair.

6. Linear programming procedures (H03ABF; NAG Fortran library, 1975) were used to select mating pairs which would maximise total progeny merit (TPM), as characterised by the formulated PM, with the restriction that all sows in the mating vector were to be mated.

7. As with **R** and **A** systems, subroutine FARROW was used to determine which mating pairs produced progeny. Procedures were as noted previously.

The subroutine H03ABF solves the classical transportation problem using the "stepping stone" method, modified to accept degenerate cases. The 1975 version required integer input values and provided integer solutions, as required for animal breeding applications. Solutions contained the optimal choice of mating pairs to maximise TPM each week, given the data. As noted above, all sows were assigned mating partners. However, some boars were not assigned to any sow within a given week. Hence, over time, individual boars were allocated divergent numbers of matings. All selected boars were retained in the male mating vector until culled according to **MLIT** or age. It was possible for boars to be culled with no matings at 78 weeks of age if they were not selected for mating purposes (hence mate selection). No other changes in culling procedures for boars were introduced.

General Formulation of the Mate Selection Problem

Five mate selection schemes were evaluated, although each scheme may be represented by the following generalised linear formulation. For s boars and d sows:
Maximise:

$$TPM = \sum_{i=1}^{s}\sum_{j=1}^{d} x_{ij} INT(f_{ij}(PM))$$

Subject to:

$$\sum_{i=1}^{s} x_{ij} = 1$$

for $x_{ij} = 0$ (mating ignored) or 1 (mating allocated), and where INT$f_{ij}(PM)$ is the expected paired merit value of boar i mated to sow j according to a specified paired merit function, expressed as an integer (INT). This formulation satisfies the requirement that all sows within a mating group must each be mated by only one boar. However, it does not allow flexibility to vary the number of sows mated per individual boar. As mating constraints were explicit for each individual boar i, the problem was reformulated as a transportation problem (adapted from Lee et al. (1981)):
Minimise:

$$Z = \sum_{i=1}^{s}\sum_{j=1}^{d} x_{ij} c_{ij}$$

Subject to:

$$\sum_{i=1}^{s} x_{ij} = m_i$$

$$\sum_{j=1}^{d} x_{ij} = f_j$$

for $x_{ij} = 0$ or 1, and where c_{ij} is the 'cost' associated with mating sow j with boar i, m_i is the sum of available boar services over boars $i = 1,..,s$, and f_j is the sum of demands for service over sows $j = 1,..,d$. The problem was balanced by setting:

$$\sum_{i=1}^{s} m_i = \sum_{j=1}^{d} f_j$$

To satisfy this requirement, a 'dummy sow' was created to receive all remaining services supplied by boars, following Jansen and Wilton (1985).

Transportation problems are designed to minimise the cost (Z) of meeting demand with supply. As such, maximising an objective function defined by $f_{ij}(PM)$ must be converted to minimising the cost objective function defined by c_{ij} in a transportation formulation. PM values for each mating pair were transformed to appropriate integer cost values according to:

$$c_{ij} = a - (PM_{ij} * b)$$

where a is a large positive value, b is a negative multiplier, and both constants are chosen to minimise the cost, rounded to the nearest integer, of superior mating pairs relative to more 'expensive' inferior pairs. In this way, minimising the total cost was analogous to maximising total progeny merit. Moreover, this method ensured that all costs were positive integer values as required for entry into H03ABF. The highest cost value was assigned to the dummy sow, so that the least beneficial matings were by default allocated to this sow.

Mate Selection Schemes Evaluated

Paired merit functions were chosen to represent a range in emphasis placed on additive genetic merit and/or the additive genetic relationship between mates. Table 3.5 shows the objective and formulation of PM for alternative mate selection schemes evaluated, where EBV^*_{ij} refers to the midparent value of boar i and sow j for the selection criterion (i.e., the expected progeny additive genetic merit), F_{ij} is the inbreeding coefficient of their progeny, and h^2 is the heritability of the simulated trait. Values for midparent EBV*s were scaled as described previously to allow information relating to progeny inbreeding coefficients to be included into PM values. Subsequently, the relative emphasis between each source of information was established using three functions, i.e., $h^2, 1.0$ and $\frac{1}{h^2}$ (MS2, MS3, and MS4 respectively) and two independent approaches where full emphasis was on either additive merit (MS1) or additive relationships (MS5). Thus, the change in emphasis placed on inbreeding coefficients between MS2-MS4 schemes was greater at low than high heritabilities. However, the differences between alternative selection criteria (individual performance or EBV selection) on rates of inbreeding were expected to decline with increasing heritability

Table 3.5: The objective, formulation of paired merit for sire i and dam j, and scheme code for five mate selection schemes evaluated by simulation.

Objective (TPM)	**Paired Merit** ($f_{ij}(PM)$)	**Scheme Code**
Maximise	EBV_{ij}^*	MS1
Maximise	$EBV_{ij}^* - h^2 * F_{ij}$	MS2
Maximise	$EBV_{ij}^* - F_{ij}$	MS3
Maximise	$EBV_{ij}^* - \frac{1}{h^2} * F_{ij}$	MS4
Minimise	F_{ij}	MS5

(see Belonsky and Kennedy, 1988; Wray, 1989). As such, a greater range in emphasis was desirable at low heritability from this viewpoint.

The above functions were derived as a consequence of being unable to reliably predict the outcome of using mate selection procedures on rates of inbreeding and genetic gain even for simple population structures (Klieve et al., 1994). Hence, it was difficult to predetermine the relative emphasis which *should* be placed on each source of information to maximise genetic gain, while accounting for inbreeding over time, given the type of approach used. Under this scenario, a simple function relating to trait heritability was potentially appropriate for combining both sources of information given that rates of inbreeding are influenced by heritability. As inbreeding depression was not modelled, it was not considered appropriate to consider the emphasis placed on F as a function of inbreeding depression.

3.2.8 Summary Statistics

Summary statistics were calculated and recorded quarterly (Q) or yearly (Y) for several variables within subroutine SUMMARY. These statistics were derived from N_t contributing observations in each time period. For selection on individual performance (**I**) or BLUP EBVs (**B**) the following statistics were collected.

- **Phenotypic Effects** (**I** and **B** schemes)
  1. Phenotypic mean and variance of the trait of interest (Q).
  2. Phenotypic mean of number born alive (Q).

- **Genetic Effects** (**I** and **B** schemes)
    1. Genetic mean and variance of the trait of interest (Q).
    2. Genetic mean and variance of number born alive (Q).
- **Predicted Genetic Effects** (**B** schemes only)
    1. Mean and variance of EBVs for the trait of interest (Q).
    2. Mean prediction error and prediction error variance of EBVs for the trait of interest (Q).
- **Range Statistics of Selected Individuals**
    1. **I** schemes: maximum and minimum performance test values of selected individuals (Q).
    2. **B** schemes: maximum and minimum EBVs of selected individuals (Q).
- **Inbreeding**
    1. Mean and variance of progeny inbreeding coefficients (Q).
    2. Maximum and minimum recorded progeny coefficients of inbreeding (Q).
- **Culling Statistics**
    1. Maximum, minimum and average number of matings achieved by individual boars prior to culling (Q).
    2. Number of boars replaced (Y).
    3. Number of sows culled for general failure (Y).
    4. Number of sows culled on parity (Y).
    5. Number of sows culled after two returns to service (Y).
- **Herd Statistics**
    1. Number of individuals performance tested (Q).
    2. Number of litters produced (Q).
    3. Mean generation number of progeny (Q).

4. Parity breakdown for sow herd (Y).

Several statistics (eg. culling statistics) were not of direct interest in this study, but were useful for checking the performance of the simulation, given that a particular herd structure and management system was simulated. These will not be discussed in later sections. In addition, some statistics are not sufficiently meaningful to warrant detailed discussion. For example, the calculated variation in inbreeding coefficients does not indicate the degree to which variation in F is skewed. Of primary interest in this study were trends in mean values of genetic effects for the trait of interest, and inbreeding.

Mean values were analysed using SAS General Linear Model procedures (PROC GLM). Details of this procedure are available in the SAS/STAT User's Guide (1988). Although N_t was not identical for each value included in the analyses, this was not explicitly accounted for through use of weighted values in PROC GLM. However, $N_t \rightarrow$ 1000 observations for each mean. Moreover, variation in N_t was also partially accounted for through main effects terms in the model of analysis. Preliminary comparisons of least squares means for main effects obtained from PROC GLM, and averages of weighted means obtained from raw data, showed that identical conclusions would be drawn from results obtained with either analytical approach. PROC GLM, however, enabled a more thorough examination of results to be carried out.

The model of analysis included selection scheme alternative (**SCHEME**), heritability value (h^2), and mating scheme group alternative (**NMATE**) as class effects characterising breeding program alternatives. Mate selection alternatives (**MSTYPE**) were nested within **NMATE**. Levels and values for these effects may be derived from Table 3.1. In addition, year and replicate were also included as class effects in analyses. Year effects included data from each quarter contained within a given year, levels summing to (**NWEEKS**/52)+2. The level of replicates was equivalent to **NREPS**. Valid two, three and four way interactions of main effects were also examined. Random mating control simulations were analysed separately.

3.3 Simulation Results

In this section, results obtained from simulated selection and mating schemes are presented. Values represent least squares means derived from SAS analyses of raw data means from 20 replicated simulations. For assortative mating (h^2=0.35), only 17 replicates under EBV selection were completed. An additional three replications for this scheme were not possible due to decommissioning of the computing system used. To minimise duplication, example herd statistics for multiple trait simulations only are presented in Section 4.2.

3.3.1 The Impact of Selection Criterion

Mean response to selection and percent inbreeding following 16 years (~10 generations) of selection on either individual performance (**I**) or BLUP estimated breeding values (**B**) are presented in Table 3.6 for random mating options. Differences between selection alternatives are only briefly addressed as they have been well illustrated in other studies (Belonsky and Kennedy, 1988; Quinton et al., 1992; Sorensen, 1988; Wray, 1990). Of primary interest in this study are the effects mating scheme has on response to selection and inbreeding, as presented in later Sections.

Table 3.6: Response to selection (Resp.) and percent inbreeding (%F) following sixteen years of selection on either individual performance (**I**) or a BLUP EBV (**B**) for a simulated character with heritability, h^2, under random mating.

Heritability	**I**		**B**	
(h^2)	**Resp.**	**%F**	**Resp.**	**%F**
0.1	194	8.0	318	34.3
0.35	638	10.9	744	25.0
0.6	1066	12.5	1141	18.8

Response to Selection

Selection on BLUP estimated breeding values (EBVs) resulted in superior levels of response relative to that achieved using individual selection for all heritabilities examined. This advantage was observed to decline with increasing heritability (see Table 3.6). **B** schemes resulted in a 64%(17%, 7%) improvement in selection response over individual selection when $h^2 = 0.1(0.35, 0.6)$. Relative gains for BLUP selection were greater than those reported in other studies for characters simulated with corresponding heritabilities (Belonsky and Kennedy, 1988; Sorensen, 1988; Wray, 1986). Herd size and the data structure simulated differed between these studies.

The reduced margin between **I** and **B** in selection response at higher heritabilities was the result of smaller gains in accuracy of selection with EBVs over individual performance measures. This is illustrated in Figure 3.2, which displays trends in the expected correlation ($r_{u,\widehat{u}}$) between true (u) and estimated ($\widehat{u}$) breeding values for **B**, calculated empirically at time t as $r_{u,\widehat{u}_{(t)}} = \sqrt{(1 - [V(u - \widehat{u})_{(t)}]/\sigma^2_{A_{(t)}}}$, compared to the initial accuracy of selection based on individual performance ($r_{u,\widehat{u}} = \sqrt{h^2}$) for traits with heritabilities of either 0.1 or 0.6. Accuracy under individual selection will also decline over time but is not illustrated here.

Genetic trends over time for each selection alternative and heritability are presented in Figure 3.3. For all breeding programs examined, response to selection was essentially linear over time. The greatest increments in response occurred between years two and three, thereafter stabilising to new lower rates of gain. Slowly diminishing rates of response paralleled trends in available genetic variation, which declines over time. Levels of genetic variation between years 1 and 17, expressed relative to initial (base population) levels of variation, are shown in Table 3.7. Within heritability, chance differences between alternative schemes in year one were not significantly different.

Table 3.7 shows that the highest levels of V_A occurred in year two, where all base parents were represented by their offspring (refer Section 3.2.3). Following the commencement of selection in this year, levels of genetic variation rapidly decreased. Within **I**, genetic variation declined under selection more rapidly at high heritability, whereas for EBV selection initial reductions were greatest when h^2=0.1. At high

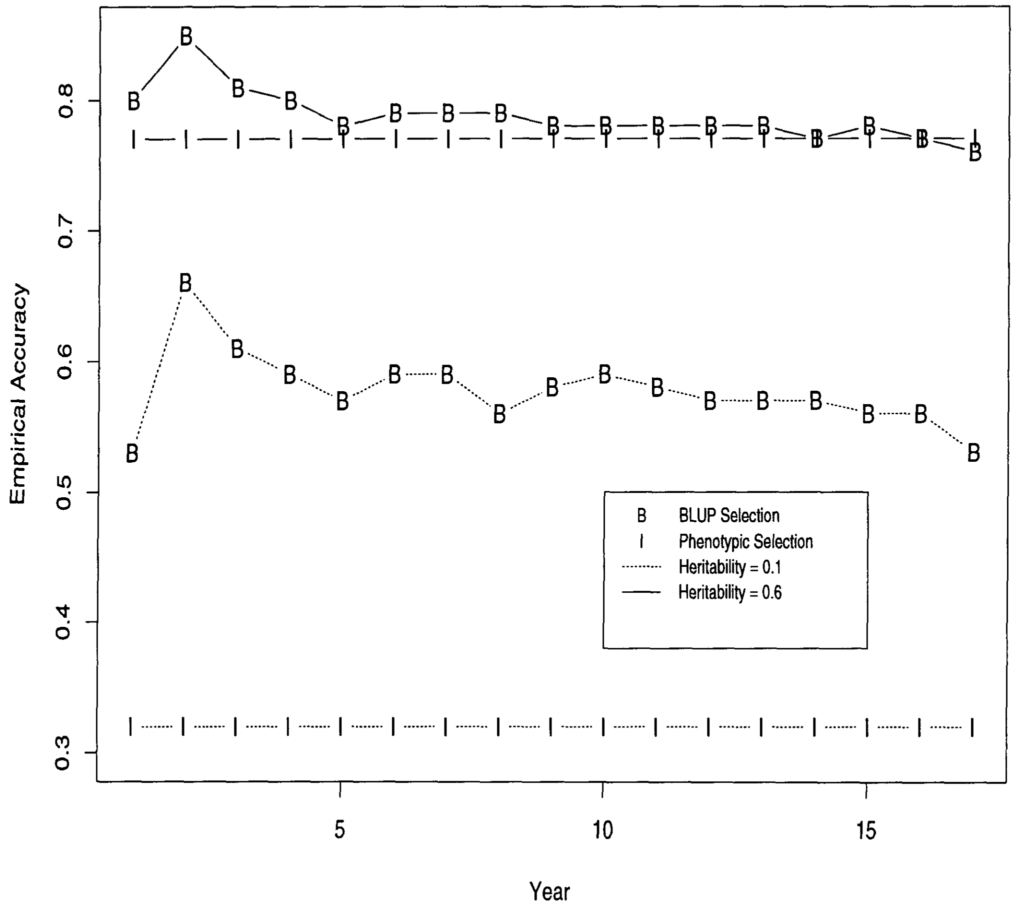

Figure 3.2: The empirical correlation between true and estimated breeding values ($r_{u,\hat{u}}$) when selection is on either phenotypic performance (**I**) or a BLUP EBV (**B**) for a simulated character with h^2=0.1 or 0.6 (random mating).

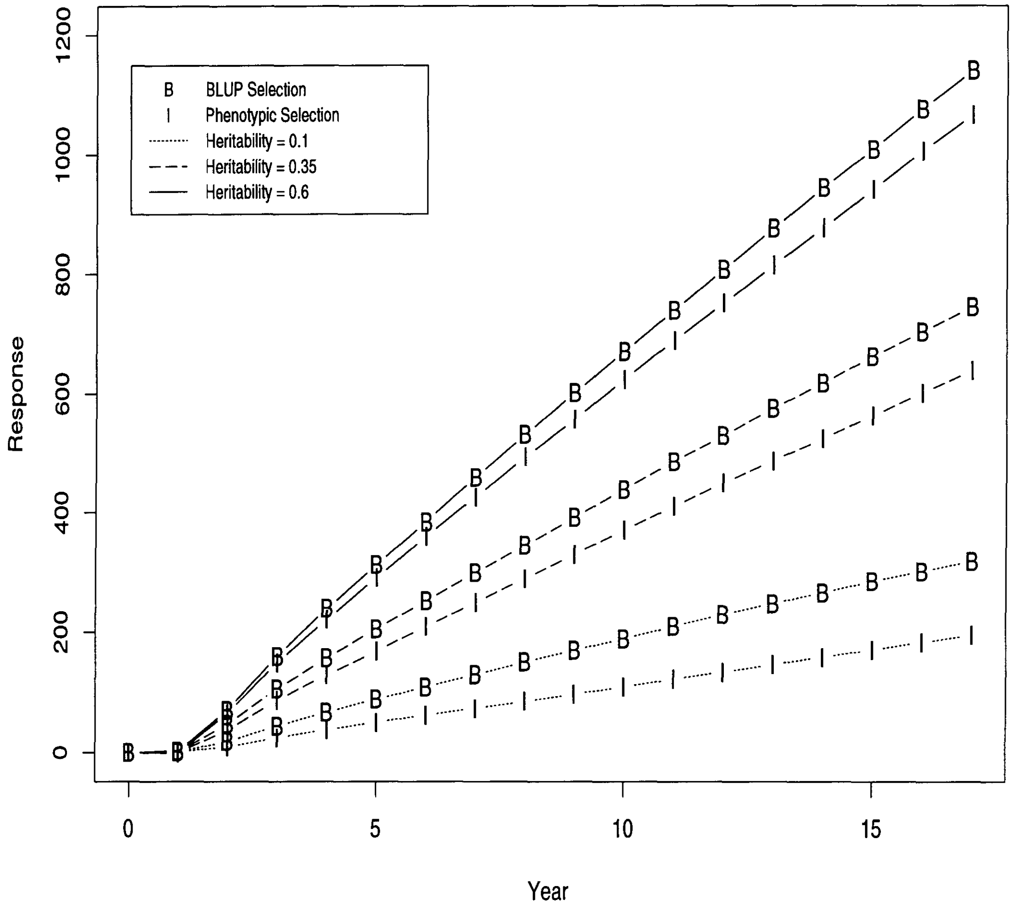

Figure 3.3: Trends in genetic gain over sixteen years of selection on either individual performance (**I**) or an estimated breeding value (**B**) for traits with different heritabilities (random mating).

Table 3.7: Trends in genetic variation, expressed relative to base population levels[†] of genetic variation, where selection is based on either individual performance (**I**) or a BLUP EBV (**B**), for a simulated character with heritability, h^2, under random mating.

	Heritability					
	h^2=**0.1**		h^2=**0.35**		h^2=**0.6**	
Year	**I**	**B**	**I**	**B**	**I**	**B**
1	0.96	1.00	0.98	0.96	0.98	1.00
2	1.01	1.10	1.04	1.07	1.11	1.11
3	0.96	0.92	0.90	0.85	0.85	0.84
4	0.96	0.85	0.84	0.80	0.81	0.79
5	0.95	0.80	0.82	0.77	0.78	0.75
6	0.91	0.81	0.81	0.77	0.77	0.76
7	0.89	0.80	0.82	0.74	0.76	0.75
8	0.88	0.73	0.83	0.74	0.74	0.74
9	0.87	0.74	0.81	0.73	0.76	0.71
10	0.89	0.74	0.80	0.73	0.72	0.70
11	0.89	0.71	0.79	0.70	0.73	0.70
12	0.89	0.68	0.78	0.70	0.71	0.69
13	0.87	0.67	0.77	0.67	0.71	0.69
14	0.86	0.64	0.76	0.66	0.71	0.67
15	0.87	0.62	0.74	0.64	0.71	0.68
16	0.86	0.61	0.76	0.62	0.71	0.65
17	0.86	0.59	0.75	0.62	0.71	0.65

[†] $\sigma_a^2 = h^2 \times 10000$

heritability (h^2=0.6), initial reductions in genetic variation were similar for **I** and **B** alternatives. However, selection on EBVs consistently decreased genetic variation to a greater extent than did selection on individual performance.

Inbreeding

Inbreeding inherent to the population structure and management system simulated, represented by the accumulation of inbreeding under random replacement and mating, averaged 6.5% after 16 years of breeding. From Table 3.6, it can be seen that selection itself increased inbreeding above this base level, as expected from theory (Robertson, 1961).

Within **I**, the level of inbreeding increased with heritability, whereas the reverse was apparent for EBV selection. Relative to **I**, EBV selection resulted in substantially higher levels of inbreeding in year 17 (all heritabilities). Trends in inbreeding are in good agreement with those reported from other studies (Belonsky and Kennedy, 1988; Quinton et al., 1992; Sorensen, 1988; Wray, 1990), although absolute levels under EBV selection are high in comparison. The relationships between heritability and final inbreeding for random and specific non-random mating systems are illustrated in Figure 3.4. Details of non-random mating systems illustrated in this Figure are noted in the following section.

3.3.2 The Impact of Mating System

Selection response and average inbreeding under alternative mating policies, expressed relative to results from random mating options both within and across selection scheme alternatives, are presented in Table 3.8. Details of the mating schemes evaluated were presented in Sections 3.2.6 and 3.2.7. For purposes of abbreviation, mating scheme code is appended to the selection scheme code (**I** or **B**) for given comparisons.

Response to Selection

The influence of non-random mating policies on response to selection was dependent on both the heritability of the simulated trait and the selection alternative used. Relative

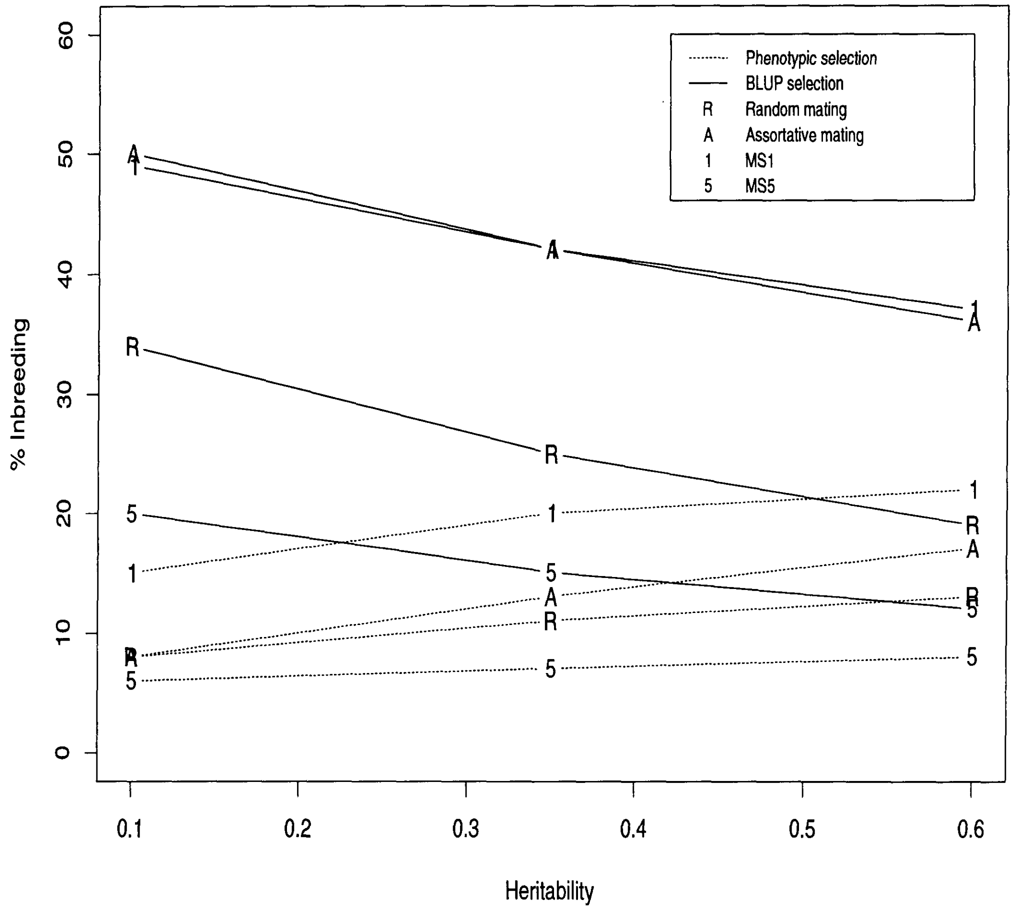

Figure 3.4: The relationship between heritability and final inbreeding following selection on either individual performance (**I**) or a BLUP EBV (**B**) for random (**R**), positive assortative (**A**), and two mate selection (**MS1** and **MS5**) alternatives.

Table 3.8: Response to selection (Resp.) and percent inbreeding (%F) expressed relative to results under random mating[†], following sixteen years of selection on either individual performance (**I vs IR**) or a BLUP EBV (**B vs IR** and **B vs BR**) for a simulated character with heritability, h^2, when mating is at random (**R**), positive assortative (**A**), or one of five (**MS1-MS5**) mate selection alternatives.

Heritability (h^2)	**Mating System**	**I vs IR** Resp.	%F	**B vs BR** Resp.	%F	**B vs IR** Resp.	%F
0.1	R	1.00	1.00	1.00	1.00	1.64	4.28
	A	0.99	1.00	1.08	1.46	1.77	6.26
	MS1	1.02	1.86	1.09	1.44	1.79	6.18
	MS2	1.02	1.58	1.11	1.42	1.81	6.08
	MS3	1.01	1.40	1.12	1.17	1.84	5.03
	MS4	0.95	1.23	1.11	0.88	1.83	3.76
	MS5	0.90	0.70	0.96	0.57	1.57	2.44
0.35	R	1.00	1.00	1.00	1.00	1.17	2.29
	A	1.04	1.17	1.11	1.68	1.29	3.86
	MS1	1.03	1.79	1.14	1.68	1.32	3.85
	MS2	1.05	1.61	1.15	1.47	1.34	3.37
	MS3	1.02	1.39	1.13	1.25	1.32	2.87
	MS4	1.01	1.26	1.15	1.14	1.34	2.62
	MS5	0.95	0.66	0.97	0.58	1.13	1.34
0.6	R	1.00	1.00	1.00	1.00	1.07	1.50
	A	1.05	1.34	1.09	1.91	1.16	2.87
	MS1	1.03	1.79	1.10	1.94	1.18	2.92
	MS2	1.03	1.33	1.11	1.36	1.19	2.04
	MS3	1.04	1.30	1.11	1.24	1.19	1.87
	MS4	1.03	1.25	1.12	1.20	1.19	1.80
	MS5	0.95	0.65	0.97	0.64	1.03	0.97

[†]see Table 3.6

to **IR**, the most efficient non-random mating options increased response by 2%(5%, 5%) within **I** and 84%(34%, 19%) within **B** when h^2=0.1(0.35, 0.6). Within **B**, the highest response was always recorded for a **MS** option, with gains relative to random mating of up to 12%, 15% and 12% for the above heritability values. The mating alternative providing maximum response was inconsistent across selection alternatives and heritability values. Further details are provided below.

Assortative Mating

Positive assortative mating increased response to selection by -1%(4%, 5%) within **I** and by 8%(11%, 9%) within **B** when heritability was 0.1(0.35, 0.6) (Table 3.8). Levels of improvement for **IA** over **IR** alternatives were in good agreement with the 5% maximum gain predicted by Tallis (1989). Gains under **BA** were significantly lower than that reported by Shepherd and Kinghorn (1994), although their study did not consider the effects of inbreeding. Under EBV selection, greater gains in response under **A** were accompanied by increased genetic variation in early years, and overall accuracy of genetic evaluation, relative to random mating. Trends in additive genetic variation for each heritability, expressed relative to initial (base population) levels of variation, following assortative mating are shown in Table 3.9. The increase in overall accuracy of genetic evaluation for **BA** over **BR** was a result of reduced prediction error variances (not presented). Average accuracies, calculated as noted above, are illustrated for each heritability in Table 3.10.

The effects of assortative mating on genetic variation were demonstrated most effectively by results from year two, where selection was minimal (Table 3.9). In early years assortative mating consistently increased levels of additive variation over that occurring under random mating, more so for **B** schemes and with increasing heritability overall. Consequently, the margin between **IA** and **BA** in levels of available genetic variation increased with heritability. By year seventeen this trend was largely reversed, and levels of retained genetic variation were relatively higher for **IA** than **BA** at all heritabilities. This reversal reflected the higher levels of inbreeding which accrued under **BA**. In contrast, improvements in accuracy of evaluation with assortative over random mating were retained over the entire time span of the simulated breeding program for **B** schemes (Table 3.10).

Table 3.9: Trends in genetic variation under positive assortative mating, expressed relative to initial levels of genetic variation†, where selection is based on either individual performance (**I**) or a BLUP EBV (**B**) for a simulated character with heritability, h^2.

	Heritability					
	h^2=**0.1**		h^2=**0.35**		h^2=**0.6**	
Year	**I**	**B**	**I**	**B**	**I**	**B**
1	0.99	1.01	1.00	0.99	0.99	0.99
2	1.04	1.20	1.21	1.43	1.33	1.52
3	0.96	1.07	1.00	1.17	0.98	1.17
4	0.94	0.99	0.94	1.02	0.90	1.03
5	0.95	0.91	0.92	0.94	0.87	0.98
6	0.90	0.87	0.89	0.92	0.84	0.94
7	0.90	0.86	0.90	0.89	0.83	0.89
8	0.90	0.85	0.88	0.84	0.80	0.88
9	0.91	0.79	0.88	0.83	0.79	0.84
10	0.92	0.77	0.86	0.78	0.79	0.84
11	0.92	0.71	0.90	0.74	0.77	0.79
12	0.92	0.66	0.87	0.69	0.76	0.78
13	0.93	0.65	0.85	0.70	0.76	0.76
14	0.90	0.62	0.86	0.67	0.76	0.71
15	0.89	0.58	0.82	0.66	0.77	0.70
16	0.86	0.57	0.84	0.65	0.77	0.70
17	0.86	0.53	0.80	0.64	0.73	0.67

†$\sigma_a^2 = h^2 \times 10000$

Table 3.10: Trends in overall accuracy of genetic evaluation within **B** schemes, for a simulated character with heritability, h^2, under random (**R**) and positive assortative (**A**) mating.

	Heritability					
	h^2=**0.1**		h^2=**0.35**		h^2=**0.6**	
Year	**R**	**A**	**R**	**A**	**R**	**A**
1	0.53	0.52	0.70	0.70	0.80	0.79
2	0.67	0.70	0.77	0.83	0.85	0.89
3	0.61	0.68	0.71	0.79	0.81	0.86
4	0.59	0.66	0.70	0.77	0.80	0.84
5	0.57	0.64	0.69	0.76	0.78	0.84
6	0.59	0.64	0.69	0.77	0.79	0.84
7	0.59	0.64	0.68	0.76	0.79	0.83
8	0.56	0.66	0.69	0.76	0.79	0.83
9	0.58	0.65	0.68	0.76	0.78	0.82
10	0.59	0.66	0.69	0.74	0.78	0.83
11	0.58	0.63	0.69	0.74	0.78	0.82
12	0.57	0.62	0.68	0.73	0.78	0.82
13	0.57	0.63	0.68	0.74	0.78	0.82
14	0.57	0.63	0.68	0.73	0.77	0.81
15	0.56	0.62	0.67	0.74	0.78	0.81
16	0.56	0.63	0.67	0.74	0.77	0.81
17	0.53	0.61	0.66	0.73	0.76	0.80

Mate selection alternatives

The most consistent results for mate selection alternatives occurred under **MS1** and **MS5** schemes, which evaluated mating pairs using information on genetic merit or inbreeding alone. Under EBV selection, **MS1** increased selection response over that achieved with random mating by 9%(14%, 10%) when h^2=0.1(0.35, 0.6)(Table 3.8). These gains exceeded those observed under assortative mating at all heritabilities, although by less than 3% in each case. Within **I**, **MS1** improved selection response by up to 3% over that achieved with random mating, but only exceeded the gains made using assortative mating at low heritability (h^2=0.1). As with assortative mating, the relative efficiency of **MS1** increased with heritability for **I**, but was most efficient at moderate (h^2=0.35) heritability within **B**. In contrast to assortative mating results, genetic variation tended to be reduced under **MS1** options, and average accuracy of prediction was not improved. Relative reductions in genetic variation for each heritability, selection and mating alternative are shown in Table 3.11.

In contrast, **MS5** consistently reduced response to selection below that of random and the remaining non-random mating alternatives. For **MS5**, selection response was reduced relative to random mating by 10%(5%, 5%) within **I** and 4%(3%, 3%) within **B**. However, response under **BMS5** was still 57%(13%, 3%) higher than that achieved under **IR** for the above heritability values. Reductions in response under **MS5** alternatives were despite the relatively higher levels of genetic variation maintained by this option relative to random mating, and compared to other **MS** alternatives (Table 3.11).

The remaining mate selection alternatives (**MS2-MS4**) combined features of **MS1** and **MS5**, details of which were presented in Section 3.2.7. As can be seen from Table 3.8, very similar levels of response were noted for **MS1-MS4** (within heritability). Thus, provided information from the selection criterion was included in the **MS** formulation, response was quite robust to differences in the emphasis placed on progeny inbreeding in the prediction of paired merit. However, within **I**, **MS** schemes overall did not substantially improve response to selection over random or assortative mating alternatives. Within **B**, a significant increase in response to selection was possible using **MS1-MS4** over the remaining mating alternatives.

Table 3.11: Average genetic variation at years nine and seventeen, expressed relative to initial levels of genetic variation[†], where selection is based on either individual performance or a BLUP EBV, for a simulated character with heritability, h^2, when mating is at random (**R**), positive assortative (**A**), or one of five (**MS1-MS5**) mate selection alternatives.

		Selection Criteria					
	Mating	**Individual**			**BLUP EBV**		
Year	**System**	h^2**=0.1**	h^2**=0.35**	h^2**=0.6**	h^2**=0.1**	h^2**=0.35**	h^2**=0.6**
9	R	0.88	0.83	0.77	0.73	0.73	0.71
	A	0.89	0.86	0.80	0.78	0.83	0.83
	MS1	0.88	0.80	0.73	0.65	0.67	0.65
	MS2	0.81	0.80	0.74	0.64	0.68	0.69
	MS3	0.88	0.76	0.72	0.69	0.68	0.68
	MS4	0.86	0.77	0.72	0.69	0.71	0.68
	MS5	0.88	0.82	0.75	0.77	0.76	0.73
17	R	0.87	0.77	0.72	0.58	0.63	0.64
	A	0.84	0.79	0.74	0.53	0.65	0.66
	MS1	0.79	0.68	0.64	0.44	0.49	0.51
	MS2	0.78	0.71	0.66	0.47	0.53	0.58
	MS3	0.76	0.73	0.68	0.51	0.56	0.60
	MS4	0.79	0.74	0.68	0.59	0.58	0.59
	MS5	0.85	0.79	0.73	0.67	0.69	0.67

[†] $\sigma_a^2 = h^2 \times 10000$

Inbreeding

In contrast to the relatively small influence mating scheme had on response to selection, non-random mating policies had a substantial impact on total levels and rates of inbreeding. Overall, positive assortative mating and the **MS1-MS4** options resulted in higher levels of inbreeding than random mating, whereas **MS5** decreased relative inbreeding under both **I** and **B** selection alternatives. The relationships between inbreeding and heritability under different mating alternatives were very similar to that illustrated for random mating in Figure 3.4, indicating that selection policy was more important in defining this relationship than was the mating system employed thereafter.

Assortative Mating

Positive assortative mating increased mean levels of inbreeding over that resulting under random mating by approximately 0%(17%, 34%) within **I** and 46%(68%, 94%) within **B** when h^2=0.1(0.35, 0.6) (Table 3.8). Levels of inbreeding occurring under assortative mating were amongst the highest achieved by any of the mating schemes evaluated. High levels of inbreeding resulting from positive assortative mating were generally not accompanied by large reductions in genetic variation relative to random mating, particularly where assortative mating was efficient in generating additional variation initially (Table 3.11).

Mate Selection Alternatives

Without exception, as the contribution of progeny inbreeding to the evaluation of paired merit increased (**MS1** → **MS5**), the total level of inbreeding accumulated over sixteen years of selection declined (Table 3.8). Thus, **MS1** resulted in the highest levels of inbreeding for each heritability and selection alternative. Relative to assortative mating, total levels of inbreeding which accumulated under this option were similar in magnitude under **B**, but were significantly higher under **I**. At the other extreme, inbreeding under **MS5** was consistently lower than that occurring with random mating. Reductions in inbreeding with **MS5** were greater for **B** than **I** selection alternatives. Moreover, when heritability was high ($h^2 = 0.6$), **BMS5** resulted in levels of inbreeding which were comparable to that resulting under **IR**. Results for **MS2-MS4** were intermediate to these.

MS2-MS5 schemes acted to delay the appearance of inbreeding in progeny generations, with the longest delays generally occurring under **MS5**. Using this mating alternative, inbreeding was delayed by up to two years under **B** or three years under **I** selection alternatives. No delays in the appearance of inbreeding occurred for **R**, **A** and **MS1** alternatives, and the length of delays were inconsistent for **MS2-MS4**. Realised rates of inbreeding, calculated between years four and seventeen as $\Delta F = (\bar{F_{17}} - \bar{F_4})/13$, are presented for each heritability, selection and mating alternative in Table 3.12. By year four all breeding programs exhibited non-zero trends in rates of inbreeding, corresponding to the appearance of inbreeding in the progeny. Therefore, calculated rates allow for differences in delays in inbreeding. With the exception of **MS5**, mate selection alternatives resulted in increased rates of inbreeding and substantial reductions in available genetic variation below that occurring under random mating (Table 3.11).

3.4 Discussion

3.4.1 Simulation Performance

Simulation features noted in Section 3.2 generally contributed to high levels of response to selection and/or high levels of inbreeding for the scenarios examined. Response to selection was favoured by ample genetic variation, high accuracy of performance testing/recording, known true genetic parameters for BLUP analyses, intensive selection in a large tested population, and comparison of many selection candidates within management group. Low levels of inherent inbreeding reflected the relatively large effective population size occurring in the absence of selection and with high sow numbers. However, in the presence of intense selection the above noted features contributed to potentially high levels of inbreeding, as were shown particularly for BLUP breeding programs in the previous section.

3.4.2 The Impact of Selection Criterion

The relative performance of individual and EBV selection alternatives in terms of both response to selection and inbreeding was as expected from previous studies (Belonsky and Kennedy, 1988; Quinton et al., 1990; Roehe et al., 1992, 1993; Satoh and Nishida, 1990; Sorensen, 1988). Improved response under BLUP resulted from increased accuracy of selection. Using information from all known relatives, BLUP simultaneously accounts for genetic trends and changes in trait (co)variances, as well as identifiable environmental (fixed) effects, thereby increasing the accuracy of genetic evaluation. The advantage of EBV selection declined with increasing h^2. In this scenario, the greater emphasis placed on an individuals own record reduces the value of additional pedigree information for the purposes of genetic evaluation, thereby decreasing the advantages of BLUP (Satoh and Nishida, 1990; Wood et al., 1991a).

In comparison to the above-mentioned simulation studies, the relative efficiency of BLUP over individual selection was high (all heritabilities). Herd size and data structure in particular have a significant impact on the relative efficiency of BLUP, especially for traits of low h^2 (Roehe et al., 1993; Satoh and Nishida, 1990). Simulations for this study were characterised by large herd size, high levels of performance testing, and intensive selection. Each of these factors may contribute to the high relative response for **B** over **I**. In addition to a significantly larger herd size, differences between studies also existed in selection intensities, management practices, fixed effects and trait characteristics simulated. Thus, results of these studies are difficult to compare directly.

Elevated rates of response with EBV selection were accompanied by increased levels of inbreeding (random mating). The marked differences between **IR** and **BR** in inbreeding were promoted by high selection intensities (Quinton et al., 1992), use of all data in the BLUP analyses for increased selection accuracy (Satoh and Nishida, 1990), and unrestricted family representation at selection (Toro and Pérez-Enciso, 1990), which act to increase the impact of EBV selection on inbreeding. Higher levels of inbreeding under EBV selection can generally be attributed to increased selection between families, resulting from increased covariances between family members for the selection criterion under BLUP. This increases the probability of unequal family representation in the selected population, thereby increasing variation in family size and resulting in higher levels of inbreeding (Toro and Pérez-Enciso, 1990). Similarly, increases in inbreeding have been reported for selection index procedures, although the relative impact of selection index on inbreeding tends to be less than that of BLUP (Quinton et al., 1992; Roehe et al., 1993). This is a consequence of restricting the amount and type of family information used for predicting genetic merit with selection index procedures, thereby reducing the correlation between family members. Where the emphasis placed on family information is restricted under BLUP, rates of inbreeding are also lowered (Grundy et al., 1994; Toro and Pérez-Enciso, 1990).

Rates of inbreeding increased with heritability for **IR**, but decreased with increasing heritability for **BR** (Figure 3.4). With increasing heritability, covariances between relatives and the level of between family selection increase, subsequently resulting in elevated rates of inbreeding. This trend was demonstrated by results within **IR** alternatives, and has been well established in other studies. Within **BR**, both family information and individual performance contributed to breeding value estimates. However, the relative contributions of each information source to the prediction of EBVs is dependent on trait heritability. At low h^2, much emphasis is placed on family information, thereby increasing rates of inbreeding following selection. This effect is much less pronounced at high heritability where more emphasis is placed on individual records. Relative changes in average accumulated inbreeding across heritability values were greater for **B** than **I**, illustrating the strong relationship between inbreeding and heritability under EBV selection.

Trends in available genetic variation over time reflected both the effects of selection and inbreeding (Table 3.7). A rapid decrease in genetic variation occurred in the initial years of each breeding program due to selection disequilibrium, as would be expected from theory (Bulmer, 1971; Gomez-Raya and Burnside, 1990; Keller et al., 1991). Thereafter, loss in genetic variation was primarily the result of accumulated inbreeding, as disequilibrium in later years eventually becomes balanced by recombination (Bulmer, 1971; Kemp et al., 1986). Overall, the greatest reduction in genetic variation was apparent for **B** when h^2=0.1. This was directly attributable to strong between-family selection initially, and the high levels of inbreeding which subsequently accumulated under this option. Reductions in variation were comparatively less for **I** than **B** alternatives, but were similar for each selection alternative at high heritability.

3.4.3 The Impact of Mating System

Mating alternatives had a relatively small impact on response to selection, but could substantially influence inbreeding accumulated under each selection alternative. In particular, mating schemes were most effective at altering response from that achieved under random mating following accurate selection, but retained their ability to alter inbreeding even at low selection accuracies. Discussion of results from alternative mating schemes follows.

Assortative mating

Results from this study indicated that positive assortative mating was an ineffective tool for manipulating either genetic variation or selection response at low heritabilities ($h^2 = 0.1$), and provided only marginal gains at moderate to high heritabilities, when selection was based on individual performance. In contrast, assortative mating following EBV selection increased response by up to 15%, relative to that achieved under random mating. However, with the exception of **IA** (h^2=0.1), substantial increases in inbreeding were also noted for **A** mating systems, of significantly higher magnitude than relative improvements in response. Increased inbreeding with assortative relative to random mating was a consequence of the impact of assortative pairing on progeny inbreeding coefficients initially, and changes in covariances between relatives and selection outcomes over time. These results were generally in good agreement with findings from previous studies (Hohenboken, 1985; Fernando and Gianola, 1986; Shepherd and Kinghorn, 1994; Smith and Hammond, 1987a; Tallis, 1989). However, assortative mating was less efficient at improving response than shown by Shepherd and Kinghorn (1994), suggesting that the effects of inbreeding can not be ignored in predicting response under assortative mating.

Improved performance of assortative over random mating alternatives with increasing heritability and/or accuracy of selection was expected (Fernando and Gianola, 1986; Smith and Hammond, 1987a; Tallis, 1989). Under these conditions the correlation between true breeding values of mates is higher, and the relative efficiency of assortative mating to manipulate additive genetic variation and selection efficiency is subsequently increased. With more accurate selection criteria (**B** schemes), assortative mating increased genetic variation in early years even for lowly heritable traits (Table 3.9). Shepherd and Kinghorn (1994) also noted increased genetic variation in early generations, and subsequently improved response when positive assortative mating accompanied EBV selection. However, high levels of inbreeding and/or increased efficiency of selection offset the ability of assortative mating to sustain increased levels of genetic variation over time, particularly at low heritability (h^2=0.1) where initial increases in V_A due to assortative mating were relatively small and rates of inbreeding were high. Reductions in the efficiency of **A** due to inbreeding are likely to be greater where high selection intensities are practised.

In addition to influencing variation in progeny generations, assortative mating improved overall accuracy of genetic evaluation relative to **BR**. This improvement was retained over the entire time span of the simulated breeding program for **B** schemes (Table 3.10). In early years this was the result of both increased levels of genetic variation (Table 3.9) and reduced PEV (not presented). In later years, however, lower prediction error variances were the primary source of improved accuracy of evaluation, although it must be noted that within heritability the calculated PEV were not fully independent of the corresponding levels of genetic variation. Lower prediction error variances were reported by Wood et al. (1991a) for BLUP analyses where records represented related individuals compared across fixed effects groups. In this case, block dominance in the mixed model equations contributes to lower PEV, increasing overall accuracy of genetic evaluations. This phenomenon may occur more readily under assortative, compared to random, mating due to increased covariances between relatives and average inbreeding, potentially contributing to the reductions in PEV in this study.

Greater improvements in accuracy, through larger comparative reductions in PEV, were noted with assortative over random mating at low heritability ($h^2 = 0.1$). As such, lower PEV were associated with strong inbreeding in the presence of selection at low h^2, and may aid in maintaining selection response despite potentially large losses in V_A. Compared to random mating, overall accuracy of evaluation was improved under assortative mating by increased distinction between families. However Wood et al. (1991a) also noted that the relative accuracy of comparing related individuals would be decreased. This may further encourage between family selection with BLUP selection criterion at low heritabilities, exacerbating the detrimental effects of EBV selection on inbreeding.

Mate Selection Alternatives

In contrast to random or assortative mating, all **MS** alternatives were characterised by unequal boar use based on merit, optimal allocation of matings under the given constraints using linear programming, and slightly higher selection intensities as a result culling selected boars which were not allocated any matings. These characteristics were consistent with steps which may be taken to improve response to selection in the short term. However, the efficacy of the **MS** algorithms was dependent on accuracy of selection and variation between selected boars in their estimated merit. Accuracy of the selection criterion affected the correct allocation of matings based on differences between boars in genetic merit, whereas variation between boars had implications for additional culling. Allaire and Barr (1990) also noted that accuracy of predicting progeny merit was important to the ranking of mating pairs, and subsequently the efficiency of their mate selection procedures.

Unmated boars were not competitive relative to their selected contemporaries as indicated by their failure to be allocated any sows for mating. However, the degree to which boars were uncompetitive depended on variation between boars in the selection criterion. This variation was large and constant for **I** across heritabilities (constant σ_p^2), but smaller and increasing with heritability under **B**. Consequently, compared to **R** or **A**, the total number of boars used as sires was consistently lower under all **MS** schemes. Under EBV selection, decreases in the number of sires used with **MS** alternatives was negligible. In comparison, up to 2.5 fewer boars were used, on average, as sires per year under **IMS** schemes. Hence, the degree to which selection intensities were increased as a result of culling unmated boars was greater for **I** than **B**. However, at the prevailing high selection intensities simulated, a reduction in the number of sires used would only have a small impact on overall intensity of selection. Differences between mating schemes in the number of sires used is illustrated for multiple trait studies in Section 4.3.1.

Slightly higher selection intensities and unequal use of parents under **MS** schemes acted to increase rates of inbreeding and decrease genetic variation relative to **R** or **A**, as would be expected (Keller et al., 1990). The exception was **MS5**, which showed lower rates of inbreeding and comparable genetic variation to that achieved under random mating (see Tables 3.11 and 3.12) as a result of avoiding matings between relatives. The accuracy with which use of individual boars reflected their genetic merit was important in determining response for **MS** schemes relative to **R** or **A**, given that available variation for selection purposes was lower for **MS** alternatives. Overall, mating schemes which used information on genetic merit to determine partners and/or overall use as parents (i.e. **A** and **MS1-MS4**) were more effective at improving response under EBV selection.

MS1 schemes were expected to convey some advantage over random mating by allowing differential use of boars to increase selection differentials. In addition, linear programming techniques (LP) are superior to ranking methods of mate allocation, which may further advantage **MS1** over **A** (Kinghorn, 1987). Results from this study illustrated that **MS1** increased response to selection over that achieved under random mating in all cases. Gains were no more than 3% within **I**, but were up to 15% under **B**. In contrast, response relative to assortative mating was decreased under **I** but increased under **B**. Under **IMS1**, lower response reflected higher inbreeding and reduced genetic variation relative to that occurring under **IA**, as a result of unequal boar use and differences in selection intensity. The reverse trend was apparent under EBV selection, where selection accuracy (Table 3.10) and subsequently inbreeding was higher under assortative mating (Table 3.12). Thus, where the effects of selection on inbreeding were already strong, unequal boar use or additional culling of boars had marginally less impact on inbreeding.

In contrast to other **MS** alternatives, **MS5** reduced response to selection. However, rates of inbreeding were substantially lower than achieved under all other mating systems evaluated, which may advantage this type of scheme in the presence of inbreeding depression. These results were in good agreement with those of other simulation studies examining the effects of avoidance mating systems (De Roo, 1988; Toro and Pérez-Enciso, 1990) and are supported in theory (Wright, 1921; Kimura and Crow, 1963). Reductions in response for **MS5** alternatives were despite the relatively high levels of genetic variation maintained by this option relative to **R**, and compared to other **MS** alternatives (Table 3.11). Thus, in the absence of inbreeding depression, avoiding inbreeding is an ineffective tool for improving response to selection in the short term. However, unequal boar use under **MS5** was potentially less of a constraint to decreasing rates of inbreeding than would be expected from theory (Robertson, 1961). This may not be the case at lower selection intensities where the opportunity for increased variation in family size following selection with unequal boar use is greater, thereby increasing its impact on results.

A mechanism by which the mating of less related pairs reduces response was proposed by De Roo (1988a). He suggested that avoiding matings between relatives increased the frequency of matings for genetically inferior boars, as fewer relatives are selected and mated from families of lower merit. Therefore, where genetically superior individuals are expected to be more inbred themselves (Morley, 1954), and related to other members of the breeding herd, the best selected boars may tend to be mated less frequently using **MS5** mating schemes. Greater reductions in response under **MS5** within **I** may have reflected the greater variation in true breeding values of selected boars for this selection criterion. In comparison, within **B**, boars may be more similar in both true breeding value and their degree of relatedness to available breeding sows (through increased family selection). This would encourage more equal use of genetically similar boars, reducing the negative impact of avoiding matings between relatives on response to selection.

The remaining mate selection alternatives (**MS2-MS4**) combined features of **MS1** and **MS5**. As can be seen from Table 3.8, similar levels of total response to selection were noted for **MS1-MS4** mate selection alternatives despite marked differences in levels of inbreeding. LP solutions for the paired merit formulations evaluated were dominated by information relating to genetic merit, facilitating similar levels of response across a range of penalties against inbreeding in the prediction of paired merit.

No obvious trends in the most appropriate emphasis to place on avoiding inbreeding for improving response to selection were shown in this study, particularly within **I**. Within **B**, however, there was a slight tendency for response to improve where information on inbreeding was included in the formulation of paired merit (eg. **BMS1** vs **BMS2-BMS4**). This was likely a consequence of selecting matings which resulted in fewer inbred progeny, increasing levels of genetic variation for selection purposes in **BMS2-BMS4** compared to **BMS1** (Table 3.11).

As noted previously, with the exception of **MS5** (all heritabilities) and **IMS4** (h^2=0.1) all other **MS** schemes exhibited increased rates of inbreeding relative to random mating (see Tables 3.6 and 3.12) due to increased selection intensities, reduced effective population size, and an increased probability of pairing related individuals where additive relationships were not considered. As such, the relative emphasis placed on progeny inbreeding coefficients for these schemes was insufficient to counteract the effects of differential boar use and higher selection intensities on inbreeding. However, with increasing use of information on progeny inbreeding (**MS1** → **MS5**), the total level of inbreeding accumulated over sixteen years of selection declined (Table 3.6). The consistency of this result can be attributed to fact that progeny inbreeding coefficients were known with certainty (unlike estimates of genetic merit). Thus, differences in contributions to progeny inbreeding could be compared with 100% accuracy *within* each boar's array, allowing correct selection between mating pairs to reduce average progeny inbreeding. In comparison, selection *between* boar arrays was influenced more by differences in predicted genetic merit (except **MS5**). Hence, selection of the best combination of matings to reduce inbreeding was more probable as the emphasis placed on inbreeding in predicting paired merit increased, making differences between boars in average relatedness more significant. Where the effects of selection on inbreeding were relatively low, and the penalty placed against inbreeding was sufficiently high, it was also possible to reduce relative rates of inbreeding (eg. **IMS4**: h^2=0.1).

For **MS2-MS5**, reducing inbreeding levels below that achieved under **MS1** was the result of both delaying the appearance of, and rates of, inbreeding. Initially, the selection process determines family structure, average degree of relationship between contemporaries in the breeding population, and thus the potential for avoiding matings between relatives within a given mating period. Thus, where fewer families are represented in the selected population at time t, more limited opportunities exist to differentiate between mating pairs on the basis of genetic relationships, or influence future selection outcomes. This is illustrated by the similarity of trends for all mating schemes shown in Figure 3.4. However, with recurrent selection the persistence of relatives in future breeding populations is affected by both selection and mating outcomes (Figure 2.1). Hence, greater opportunity may exist to reduce rates of inbreeding where the mating scheme acts to reduce not only progeny inbreeding coefficients at time t, but also the impact of selection on inbreeding.

Following on, it may be speculated that where the combination of matings between relatives was chosen to reduce progeny inbreeding coefficients (**MS2**-**MS5**) families (overall) of more diverse genetic merit were paired at mating. Subsequently, over time family means become more similar, within family variation is maintained, and variation between families is less likely to be exploited for selection purposes. In addition, the selective advantage of any particular family may be reduced by dispersing genetic merit across different families, thereby decreasing variation in family size at selection. The net effect would be to reduce the impact of selection on inbreeding, the extent to which would then depend on the degree of avoidance mating practised and choice of selection criterion. The greatest relative reductions in rates of inbreeding with **MS5** occurred where the impact of selection on inbreeding was largest, that is at high heritability within **I** and low heritability within **B**. Thus, choice of mating pairs was an important tool for reducing the effects of selection on inbreeding, particularly for **B** where differences between families in merit are highlighted.

3.4.4 Limitations of Mate Selection Algorithms

The ability of **MS** algorithms evaluated to reduce rates of inbreeding and/or increase response to selection was limited by their formulation and nature of application. An intrinsic limitation was that information for decision making was confined to that provided by a single generation. That is, the optimum LP solution at time t did not consider future implications of the current solution. Hence, where differential use of boars was made on the basis of their progeny's inbreeding coefficients, a generalised rather than strategic solution was used to minimise progeny inbreeding coefficients at time t rather than *rates* of inbreeding over time. Only for **MS5** was the generalised LP approach sufficient to reduce rates of inbreeding below that resulting from random mating. However, allowing for implications to future generations is difficult in practice.

Additional culling of uncompetitive boars was affected by formulation of the **MS** algorithms, and could have been avoided by suitably scaling variation in paired merit between boars (within sows). Choice of scale would then relate to the acceptable relative merit of selected individuals. Alternatively, sequential culling may remove the need for this approach if variation between selected boars in genetic merit is reduced. A further alternative is to allow more boars than the minimum required to be included in the mating lists for evaluation, reducing the likelihood of unduly increased selection intensities. The average relationship of sires with the current breeding herd could also be considered prior to selection to aid in the control of inbreeding, as was suggested by Goddard and Smith (1990). This may also act to reduce excessive additional culling of selected boars when additive relationships are considered in the above mate selection options.

Of final consideration, opportunities to exploit the mate selection approach were limited due to the necessity of solution constraints related to biological limitations. For example, although the total number of mating combinations was potentially large, restrictions on boar and sow usage could reduce the relative advantage of LP techniques over ranking for selecting mating pairs, as noted by Kinghorn (1989). In addition, initial selection on individual merit may have removed individuals which could have contributed to mating pairs of higher paired merit, thereby reducing the efficiency of mate selection procedures relative to the unified approach discussed in Section 2.5.2, and as addressed by Jansen and Wilton (1985). However, these constraints are likely to exist in practical applications, and results were encouraging from this viewpoint.

3.5 Conclusions

In this study, three main components contributing to the performance of breeding programs were examined. These included: choice of selection criterion, the mating scheme employed thereafter, and underlying trait heritability. As with other studies (Belonsky and Kennedy, 1988; De Vries, 1988; Quinton et al., 1992; Sorensen, 1988; Wray, 1990), results overall illustrated that with increasing trait heritability and/or accuracy of genetic evaluation, both genetic gain and rates of inbreeding were increased (random mating). Differences between selection alternatives were minimised at high heritability values, where little advantage was gained in accuracy of selection through use of family information. In comparison to selection decisions, choice of mating system had relatively little impact on response to selection, but could substantially influence levels and rates of inbreeding.

Mating systems which used information on genetic merit to allocate mates were most effective at improving response to selection when accuracy of selection was high. Positive assortative mating increased response to selection by up to 3% under individual performance, but by up to 15% under EBV selection. However, rates of inbreeding were also elevated relative to random mating. Compared to assortative mating, it was possible to achieve further improvements in response while reducing inbreeding through use of the mate selection algorithms evaluated. A significant interaction between mating system and selection effects was apparent, making it difficult to identify the most appropriate breeding program which balanced high rates of genetic gain with acceptable levels of inbreeding.

Increased genetic gain with **MS** schemes could be attributed to the greater use of genetically superior boars, and in part slightly higher selection intensities. These practices generally contributed to increased equilibrium rates of inbreeding compared to random mating, although partially offset over a fixed time interval by delays in the appearance of inbreeding. For **MS5**, where use of boars was based on average additive relationships, both a delay in the appearance of and reduced rates of inbreeding relative to random mating were apparent. These results suggest that **MS5** schemes acted to reduce the effects of selection on inbreeding through manipulating family structure.

Simultaneously, however, **MS5** schemes consistently reduced rates of genetic gain below that of random mating despite higher selection intensities, similar levels of genetic variation and lower rates of inbreeding. Hill (1985a) noted that selection differentials could be reduced as a consequence of altering family structure to decrease rates of inbreeding, thereby reducing rates of response to selection. De Roo's (1988a) simulation results also support this.

In contrast, **MS** schemes which used information on inbreeding and genetic merit to predict paired merit (**MS2-MS4**) generally resulted in improved rates of genetic gain, particularly within **B** alternatives where inbreeding is elevated by the effect of more accurate selection between families. In this situation, the effect of differential boar use on inbreeding was tempered by ensuring that matings were made between less related individuals. In comparison, **MS1** resulted in high rates of inbreeding and loss in genetic variation, whereas **MS5** did not allow for differences in genetic merit, both factors acting to reduce response to selection. Results to date suggest that similar levels of response may be achieved using a range of penalties against progeny inbreeding coefficients with the **MS2-MS4** alternatives evaluated. Choice of the most appropriate **MS** approach, however, would depend on the predicted detrimental effects of inbreeding on herd performance and the breeders attitude to risk. Results indicated that the type of approach evaluated, i.e., adjusting merit for additive relationships, would be useful for manipulating response and inbreeding in practical applications.

Chapter 4

Multiple Trait Selection within a Closed Pig Breeding Herd

4.1 Introduction

In the previous chapter, the influence of alternative selection criteria and mating schemes on genetic gain and rates of inbreeding were examined in a single trait scenario. Results comparing alternative selection criteria under random mating were similar to those of earlier studies (Belonsky and Kennedy, 1988; Quinton et al., 1992; Sorensen, 1988; Wray, 1989). That is, in comparison to individual selection, use of BLUP selection criteria resulted in significant increases in *both* genetic gain and rates of inbreeding, the relative magnitude of which depended on trait heritability. However, results presented in Section 3.3 also illustrated that both selection response and levels of inbreeding could be substantially altered from that shown under random mating using non-random mating schemes. Moreover, at low heritabilities, where the highest increases in inbreeding may be expected from BLUP based selection criteria, strong opportunity existed to favourably influence both response to selection and level of inbreeding relative to random mating with specific mate selection schemes. Of interest in this chapter is the influence of selection for an aggregate genotype on genetic gain and rates of inbreeding under both random and non-random mating systems.

Where selection is for an aggregate genotype, few studies have examined the impact of alternative selection criteria on both genetic gain and the accumulation of inbreeding. For selection indices, expected genetic gains in component traits may be calculated without knowledge of population structure using selection index theory. However, for BLUP based indices, predictions require simplifying assumptions on population size and structure, and therefore data structure (Schneeberger et al., 1992). Moreover, current literature does not contain approaches for predicting the influence of using multiple trait selection criteria on inbreeding. Wray et al. (1990) noted that current methods for predicting inbreeding were useful where the selection criterion (single trait) was derived using family indices. However, this may not be the case where substantially different amounts of information contribute to the predicted genetic merit of separate individuals, as is commonly the case with BLUP selection criteria. Further, where several traits are included in the selection criterion, varying accuracy of evaluation for different traits may influence the results of selection on inbreeding.

It may be speculated that including several traits in the breeding objective, reducing the absolute selection emphasis placed on any one trait, would lower rates of inbreeding when compared to single trait selection. As noted by De Vries et al. (1990), including information from several traits in selection indices may decrease the correlation between indices of sibs, thereby reducing the likelihood of selecting sibs and potentially lowering rates of inbreeding. Moreover, opportunity may exist to decrease selection between families and rates of inbreeding where:

- traits are genetically uncorrelated or unfavourably correlated,
- traits included are of high heritability, and
- the sample of genes contributing favourably to all traits are represented initially in several families.

For example, where two traits are uncorrelated or unfavourably correlated, selecting for both traits is likely to lead to more families being represented in the selected population than when traits are favourably correlated. Similarly, where traits are of high heritability, less use of family information is required to obtain optimal rates of response. In these situations, rates of inbreeding may be expected to be lower. Conversely, where sufficiently favourable genetic correlations between component traits exist, increased rates of inbreeding may be expected. Hence, including more traits in the selection criterion may not necessarily reduce rates of inbreeding when genetic correlations are accounted for.

Selection emphasis may also be important in determining the impact of including additional traits in the selection criteria. De Vries (1989) found that indices including both reproduction and production traits increased rates of inbreeding over that achieved when selection was based on production traits alone. This result was attributed to the increased use of family information required for accurate evaluation of reproductive traits, and occurred despite zero genetic correlations assumed between production and reproduction traits investigated. Further, Roehe et al. (1992) noted increased rates of inbreeding for EBV selection over a selection index alternative, also for an aggregate genotype. No literature has been found to date which directly investigates the influence of genetic correlations between traits, or their economic weights, on rates of inbreeding under multiple trait selection.

Of further interest is the effect of inbreeding on gain in aggregate merit. De Roo (1988a) found that component traits of a selection index did not contribute to aggregate merit according to their expected gains, and that component traits deviated from expectation by different amounts. No explanation of this result was presented by the author. This phenomenon was also noted by Roehe et al. (1992) for both selection and BLUP based indices. Roehe et al. (1992) attributed changes in gain of component traits with BLUP indices to differing relative levels of improvement in the accuracy of evaluating component traits with BLUP, compared to selection index measures. Thus, for BLUP indices, relative gain in component traits was dependent on trait heritability and population size and structure, as well as the usual influence of economic values and correlations.

The work of Roehe et al. (1992) also illustrated that higher genetic gain with larger herd size was primarily a consequence of reduced rates of inbreeding (inbreeding depression absent) rather than increased accuracy resulting from the better use of more data. Moreover, relative increases in accuracy differed for individual traits at the same level of inbreeding. Hence, although increases in the total data available will increase the accuracy of evaluation to varying degrees for traits of different heritabilities (Satoh and Nishida, 1990), it may also be speculated that the effects of inbreeding are likely to influence the accuracy of evaluation by varying amounts for different traits over time. This is likely given that the genetic relationships between individuals influence accuracy of evaluation with BLUP (Wood et al., 1991a) and selection index (De Vries, 1989). Further, trait heritability and the correlations between traits will influence the relative impact that genetic relationships have on accuracy of evaluation. As such, differences in accuracy of evaluation with BLUP over alternative indices need to be addressed, and relationships with inbreeding established. In addition, the impact of non-random mating systems on genetic gain in an aggregate genotype and rates of inbreeding should also be addressed.

Thus, the aim of this study was to examine the effects of alternative selection criteria and mating schemes on gain in both aggregate breeding value and component traits, as well as on the accumulation of inbreeding within a closed pig breeding nucleus. The traits used as selection criteria included average daily gain, P2 backfat and number born alive. These criteria were used in three types of indices: a general purpose index, a specialised terminal sire line index, or a maternal dam line index. In addition, three types of mating system were examined: random, positive assortative and mate selection approaches. In Section 4.2 multiple trait simulation procedures are presented. In Section 4.3 simulation results obtained are presented, and discussed in Section 4.4. The studies conducted in this and the previous Chapter are concluded with a general discussion in Section 5.

4.2 Simulation Procedures

Many characteristics of multiple trait simulations are identical to the procedures presented in Section 3.2. As such, only changes to the original methods will be outlined, and additional features noted, to briefly review procedures carried out. For multiple trait simulations, the simulation program's ability to model a variety of population structures was maintained, although only one population size and structure was examined in this study. The simulation modelled a management/production system which was characterised by continuous cycles of performance testing, genetic evaluation, selection, mating, and the creation of progeny under a framework of overlapping generations. The cycle of events for multiple trait simulation procedures are adequately depicted by Figure 3.1. Changes in subroutines used are noted in the appropriate sections.

Three traits were simulated for the current study. These were number born alive (NBA), lifetime average daily gain (ADG) and P2 backfat (BF), traits commonly measured and recorded in pig breeding enterprises. Individual records for NBA were available on all parent sows. The remaining traits, ADG and BF, were generated as performance test records. Mortality from birth to weaning, and potential restrictions on performance testing facilities were simulated as random constraints. These were accommodated on a percentage basis, and were not expected to change over time. All performance tested pigs were placed in batches with their birth management group contemporaries.

Selection was based on the criterion of predicted aggregate genetic merit. This criterion was either a conventional selection index (**SI**) or an economic index for use with BLUP breeding values (**BI**). Three types of **SI** and equivalent **BI** indices were examined. These were loosely defined as general purpose (**GP**), maternal (**MAT**) and terminal sire (**TS**) indices, the derivation of which is discussed in Section 4.2.3. For comparison, single trait selection for NBA, ADG and BF using either phenotypic criteria or EBVs, along with a random selection and mating option, were also carried out for the same population. After entry to the breeding herd no additional culling based on performance occurred. Some random factors removing individuals from the breeding herd were simulated (eg. failure to conceive), which are noted later. Matings between selected individuals were of three types: **R**, **A** and **MS** procedures, as defined in Section 3.2. As with single trait simulations, selection and mating decisions were made weekly.

4.2.1 Parameters for the Simulated Herd

Several parameters outlined in Section 3.2.1 were common to both single and multiple trait simulations, and were used in multiple trait simulations to define the size of the breeding operation and the sequence of events for each individual. These parameters are presented in Table 4.1 with their input values. For multiple trait simulations, values of some parameter variables were altered to more realistic levels than those used in single trait studies. Parameters which are not exactly as defined in Section 3.2.1, and additional parameters required for multiple trait simulations, are also listed in Table 4.1 and described below.

ANBA: the average NBA for first parity litters. In single trait studies no parity effect existed for NBA, and ANBA was chosen to represent a common 2nd - 3rd parity mean. Parity effects were present in this simulation.

SURV: the percentage of those pigs born which survived from birth until weaning. This reduced at random the sample of pigs available for performance testing through mortality.

PERC: the percentage of those pigs surviving until weaning which were performance tested. Not all pigs are likely to be performance tested due to additional considerations (eg. poor conformation, limited testing facilities). NB. SURV+PERC in multiple traits studies is equivalent to the variable PERC defined for single trait studies.

SCHEME: coded value for selection schemes evaluated. For **SCHEME** = 1, replacement breeding stock were selected at random. For **SCHEME** = 2 or 3, selection was for an aggregate genotype based on one of three (see **TYPE** below) **SI** or **BI** indices respectively. For **SCHEME** = 4, 5 or 6, selection was for a single trait using average NBA of the parental sow, or a performance test record for ADG or BF, respectively. For **SCHEME** = 7, 8 or 9, selection was also for a single trait, where the selection criterion were individual BLUP EBVs for NBA, ADG and BF respectively. Selection schemes 1 and 4-9 were primarily generated for comparative purposes.

TYPE: coded value for index type alternative. For **TYPE** = 0, no index was used. This implied that **SCHEME** = 1 or 4-9 where random replacement or single trait selection was practiced. When **TYPE** = 1, 2 or 3, selection indices were defined for general purpose, terminal sire and maternal selection lines respectively.

Table 4.1: Parameter values used for the simulated population.

Parameter		Value(s)
NSOWS*	=	260
NSPB	=	20
NPAR	=	4
PERS	=	0.35
MLIT	=	50
NLIT	=	2.1
ANBA*	=	9.0
SURV	=	80%
PERC	=	90%
NWEEKS	=	832
NREPS	=	20
SCHEME	=	1 - 9
TYPE	=	0 - 3
NMATE	=	0, 1 or 2
MSTYPE	=	1 - 5

MSTYPE: coded value for alternative mate selection procedures, only executable where NMATE = 2. Values for **MSTYPE** range from 1 - 5. Mate selection scheme details are presented in Table 4.4.

Values calculated using parameters were: **NBOARS = 13, NWFAR = 25, SFAR* = 11** and **SMATE* = 12**. In order to ensure rapid replacement of boars exceeding **MLIT**, **WBREP** was reduced to two weeks. **ANBA***, **NSOWS***, **SFAR*** and **SMATE*** were expected average values only and influenced by the stochastic nature of the simulation, as described in Section 3.2.1. The above parameters were entered and/or calculated using subroutine INPUT.

4.2.2 Simulation of Records

Records generated for all individuals which were common to both single and multiple trait simulations included **ID, P1, P2, SEX, AGE, MGT, MGTE,** $\mathbf{TBV}_{NBA}$, **F** and **GEN**. In addition, **DAM, PAR, STAT,** $\mathbf{PE}_{NBA}$, $\mathbf{IND}_{NBA}$, **SIRE, SRED** and **MAXS** records for selected individuals were also used. Generation of these

Table 4.2: Heritabilities ($h^2 = \sigma_a^2/\sigma_p^2$), temporary environmental values ($c^2 = \sigma_{cl}^2/\sigma_p^2$), and variances for genetic (σ_a^2), environmental (σ_e^2), common litter (σ_{cl}^2) and permanent environmental (σ_{pe}^2) effects, as well as the phenotypic variance (σ_p^2) of traits simulated.

			Variance Component				
Trait	h^2	c^2	σ_a^2	σ_{cl}^2	σ_{pe}^2	σ_e^2	σ_p^2
NBA	0.11	-	0.69	-	0.37	5.38	6.44
ADG	0.24	0.10	672.00	291.00	-	1852.00	2815.00
BF	0.45	0.09	2.06	0.43	-	2.10	4.59

$r_{g_{NBA,ADG}} = 0, r_{g_{NBA,BF}} = 0, r_{g_{ADG,BF}} = 0.12$
$r_{e_{NBA,ADG}} = 0, r_{e_{NBA,BF}} = 0, r_{e_{ADG,BF}} = 0.33$
$r_{cl_{ADG,BF}} = 0$

records was described in Section 3.2.3. Any changes in methodology are noted in the following sections. For multiple trait simulations, additional records were generated for the traits simulated. These included true breeding values for ADG ($\mathbf{TBV}_{ADG}$) and BF ($\mathbf{TBV}_{BF}$) for all individuals, in addition to $\mathbf{TBV}_{NBA}$. Phenotypic records, **PADG** and **PBF** for ADG and BF respectively, were generated for individuals which completed performance testing. Correspondingly, EBVs were predicted and recorded only for those individuals which were performance tested, and founder population individuals. All individuals were permanently identified and records were stored for sequential access.

Genetic and phenotypic parameters for the traits simulated are presented in Table 4.2. These parameters were obtained by Klassen (1992) from Australian data. Units of measurement for NBA, ADG and BF were pigs per litter (*pigs/litter*), grams per day (*g/day*) and millimetres (*mm*) respectively. The repeatability of NBA was 0.17.

The Founder Population and Ongoing Records

The founder population consisted of 540 sows and 27 boars, assumed to be unrelated. Each boar of this population was randomly assigned to mate 20 sows. Their resulting progeny were designated as generation one. Of the initial founder population, 13 boars and 260 females were randomly chosen to remain in the breeding herd. These individuals included sows distributed equally across parities 1 - 4, each parity group being represented in each week's mating pool. Boars were also spread across several age groups. The structure of the breeding population at generation zero, as such, was of an unselected population in production cycle equilibrium. Selections were first carried out on generation one progeny. Founder populations were generated independently for each simulation replicate. The above procedures were carried out in subroutine BASE.

Progeny were assigned permanent ID's at conception. Although demanding of computer memory, this allowed records of relevant individuals to be sequentially included in BLUP mixed model equations and summary statistics when required. Progeny represented all age categories from conception to sexual maturity. This ensured that performance tested individuals were always available for selection. Ongoing records were generated in subroutine PROGENY.

Trait Records

Phenotypic records for ADG and BF were generated for all individuals completing performance testing. Records for NBA were only produced for parental sows. All traits were assumed to be controlled at the gene level according to the infinitesimal model (Bulmer, 1980). As NBA was uncorrelated with either ADG or BF, separate loci were presumed to control this trait. However, genetic and environmental correlations between ADG and BF suggest some common loci and environmental effects. These effects were accounted for in the simulation by generating trait effects simultaneously, allowing for zero and non-zero covariances between traits where appropriate, as described below.

Parameters for the simulated traits were presented in Table 4.2. Genetic (G), environmental (E) and common environmental (CL) effect (co)variance matrices were constructed describing the relationships between NBA, ADG and BF. For any given matrix, Q, an alternate expression is $Q = LL'$, where L is a lower triangular matrix. The elements of L are computed using a Cholesky decomposition such that L is given by:

$$L = \begin{bmatrix} L_{1,1} & & & \\ L_{2,1} & L_{2,2} & & \\ \vdots & \vdots & \ddots & \\ L_{n,1} & L_{n,2} & \dots & L_{n,n} \end{bmatrix}$$

where n is the number of traits included in Q and subscripts refer to a given trait. For a vector of independent random normal deviates, x, where $x \sim N(0,1)$ and $E(x) = 0$, the expression $Q = Q(Lx) = LL'$ holds and $E(Lx) = 0$. Values for a given effect (eg. breeding values, a) were thus generated as:

$$\begin{array}{lclclcl} a_1 & = & L_{1,1}x_1 & & & & \\ a_2 & = & L_{2,1}x_1 & + & L_{2,2}x_2 & & \\ \vdots & & \vdots & & \vdots & & \\ a_n & = & L_{n,1}x_1 & + & L_{n,2}x_2 & + \cdots + & L_{n,n}x_n \end{array}$$

where subscripts are as defined previously.

Records for founder population animals were generated using two separate models. The repeatability model used for NBA, presented in Section 3.2.3, was expanded to include parity effects according to:

$$y_{NBA} = u_{NBA} + par + a_{NBA} + pe + e_{NBA}$$

where: u_{NBA} was the founder population mean; par was the prevailing parity effect; and a_{NBA}, pe and e_{NBA} were random additive genetic, permanent environmental and residual environmental effects respectively. y_{NBA} was rounded to the nearest integer. In contrast to single trait simulations, u_{NBA} was dependent on the distribution of sows across parity and was subsequently greater than **ANBA** at generation zero. Parity effects took the values +0.0, +0.32 and +1.37 for parities 1, 2-3 and 4+ respectively (adapted from Klassen, 1992). However, sows are unlikely to show the effect of parity to the same extent, for example due to age differences and nutritional considerations. Consequently, values for parity i (par_i) were sampled from a pseudo-random normal distribution with mean par_i and variance 0.11. This variance was chosen to give a maximum deviation due to parity of one piglet from par_i for individual sows within a given parity effect. Random effects specific to each individual (a_{NBA}, pe and e_{NBA}) were sampled from independent normal distributions with zero mean and appropriate variances. No management group effects were simulated for NBA.

Records (y) for ADG and BF were generated using the following model:

$$y = u + mgt + sex + a + cl + e$$

where: u, mgt, sex, a, cl and e were the mean, contemporary group effect, sex effect, true breeding value, common litter and temporary environmental effects respectively. Base means chosen for ADG and BF were $500g/day$ and $13mm$ respectively. These values were chosen to depict a relatively lean fast growing population of animals. Variances between management group effects for ADG and BF were adapted from PIGBLUP analyses of real data providing solutions for fixed effects. Between management group variation was sex specific for both traits. Variances for mgt_{ADG} were $850(g/day)^2$ and $900(g/day)^2$ for males and females respectively. Corresponding variances for mgt_{BF} were $0.75mm^2$ and $0.88mm^2$. Zero covariance between mgt effects for the different traits was assumed. Management group effects were thus sampled from sex dependent pseudo-random normal distributions with mean zero and appropriate variance. Estimates of sex effects were also obtained from data analyses. The average differences between sexes in performance for ADG and BF were taken as $20g/day$ and $1.15mm$ respectively.

Base population values for a, e and cl were derived as described above. For example, where: $G = L_G L'_G, E = L_E L'_E$ and $CL = L_{CL} L'_{CL}$; and $x \sim N(0,1), y \sim N(0,1)$ and $z \sim N(0,1)$, for the independent random normal variables x, y and z; then $L_G x, L_E y$ and $L_{CL} z$ represent breeding values (a), residual values (e) and common litter values (cl) respectively. No covariance between litters was assumed in this study. Values for e and cl were derived using these procedures over the time span of the simulation. True breeding values of progeny for each trait were derived as described in Section 3.2.

Scale Effects

Preliminary studies showed that the high heritability and relatively large variation of BF allowed rapid rates of response for BF with the intensive selection simulated. When selection was for reduced BF, over time phenotypic means could approach very low levels, and some individuals achieved negative BF phenotypes. This was not realistic from either a practical or biological viewpoint. As such, the method of simulating BF records was modified to accommodate a scale effect, where it was assumed that rates of response in BF would decrease with the mean.

Simulation of a scale effect for BF was carried out through modification of the (co)variance structure between traits as mean BF declined. Management group and sex effects were assumed to remain constant under selection. Effects contributing to BF records which altered with the mean, as such, were confined to common litter (cl), additive genetic (a) and environmental (e) effects. In addition, covariances between BF and ADG were adjusted to maintain constant genetic and environmental correlations between these traits. As simulated data were used for BLUP genetic evaluations, it was desirable that data remained comparatively normally distributed with the introduction of a scale effect. This proved possible due to the relatively low phenotypic coefficient of variation for the simulated BF ($CV = 16.5\%$: Klassen, 1992).

A CV below 20% reduces the impact scale effects may have on departure from normality (Falconer, 1981). Consequently, from a statistical viewpoint non-normality of the adjusted distribution for BF was minimal and could be ignored. All adjustments to variances were made under the restriction of a constant CV. Both h^2 and c^2 were maintained as constants when variances were adjusted. Steps required for calculating appropriate effect (co)variances (i.e., cl, a and e) were as follows:

1. The phenotypic standard deviation (σ_p) associated with a particular mean BF (MBF) was given by $\sigma_p = MBF \times CV$. The phenotypic variation, σ_p^2, at MBF was then derived, where σ_p^2 was assumed to be a summation of variance components for cl, a and e effects only.

2. Assuming a constant heritability, $h_{BF}^2 = 0.45$, additive genetic variation (σ_a^2) was given by $\sigma_a^2 = h_{BF}^2 \times \sigma_p^2$.

3. Assuming constant $c^2_{BF} = 0.09$, variation due to common litter effects was calculated as $\sigma^2_{cl} = c^2_{BF} \times \sigma^2_p$.
4. Given the above, environmental variation was thus calculated as $\sigma^2_e = \sigma^2_p - \sigma^2_a - \sigma^2_{cl}$.
5. Genetic and environmental covariances between ADG and BF were accommodated by assuming $r_a = 0.12$ and $r_e = 0.33$ remained constant. Covariances adjusted for changes in MBF were calculated as $CoV_{ADG,BF_i} = \sigma_{ADG_i} \times \sigma_{BF_i} \times r_{ADG,BF_i}$, where i was either a genetic or environmental component of (co)variance.
6. Adjusted (co)variances were recalculated when the population mean reached a threshold value, which reduced in $1mm$ intervals. When $MBF = 13$ original input (co)variance matrices were used.

The adjusted variances calculated for BF, and the new covariances between BF and ADG, replaced the original corresponding elements of the G, E and C matrices, hereafter denoted G_2, E_2 and C_2. Elements of L for each effect were then calculated using a Cholesky decomposition. Where uniform random deviates sampled for either a, cl or e effects for BF were positive, values were obtained for each effect as described previously. Where these deviates were negative, values were derived using the appropriate elements of L_{G_2}, L_{E_2} and L_{C_2}. Loss in σ^2_a due to inbreeding was accounted for as discussed previously in Chapter 3.2.

4.2.3 Calculation of Selection Criterion

Breeding objectives evaluated were for general purpose (GP), terminal sire (TS) and maternal (MAT) selection lines. The objectives were:

$$\begin{aligned} H_{GP} &= \$23.25NBA + \$2.27ADG - \$29.75BF - \$150.00FCE \\ H_{TS} &= \$2.27ADG - \$29.75BF - \$150.00FCE \\ H_{MAT} &= \$23.25NBA + \$1.14ADG - \$14.88BF - \$75.00FCE \end{aligned}$$

where FCE represents the breeding value of feed conversion efficiency. Economic values for a GP objective were obtained from Long et al. (1990b). All economic values were expressed in units per litter and were assumed to be strictly linear in

Table 4.3: Index weightings, standard deviations of the index (SD_I) and objective (SD_H), and the correlation between the index and breeding objective (r_{IH}) for traditional selection (**SI**) and EBV based (**BI**) indices.

Index	**NBA**	**ADG**	**BF**	**SD**$_I$	**SD**$_H$	r_{IH}
SI$_{GP}$	+1.43	+0.77	-17.09	48.62	85.63	0.57
SI$_{TS}$	-	+0.77	-17.09	48.48	84.20	0.58
SI$_{MAT}$	+1.34	+0.39	-8.55	24.53	44.67	0.55
BI$_{GP}$	+26.73	+2.82	-34.78	-	85.63	-
BI$_{TS}$	-	+2.82	-34.78	-	84.20	-
BI$_{MAT}$	+24.99	+1.41	-17.39	-	44.67	-

nature. In reality, this only holds for small amounts of genetic change. Economic values for production traits were assumed to be identical for GP and TS selection lines, although increased economic values for ADG and BF may occur for TS lines. Economic values for ADG and BF were halved for MAT lines according to Smith (1964). This was under the assumption that expression of NBA at the commercial level doubled the value of reproductive traits compared to production traits.

For each breeding objective, traditional selection indices (SI) and indices for use with BLUP EBVs (BI) were calculated for comparison, including NBA, ADG and BF as criterion traits. Response in FCE was assumed to be realised indirectly through genetic correlations with the selection criteria. ADG and BF performance test records were available for all individuals, and these records alone contributed to SI for production traits. However, NBA was not directly measurable on selection candidates. Thus, the contribution of NBA to an individual's SI value was estimated from the mean NBA of their dam. In contrast, EBVs for all traits simulated were available for all selection candidates, contributing to BI values. Selection index weights for SI were calculated using 'SELIND' (Cunningham, 1970). BI for each breeding objective were derived following Schneeberger et al. (1992). Covariance matrices relating the objective traits to the traits used as selection criteria are derived from Table 4.2 for NBA, ADG and BF. Genetic covariances between these traits and FCE were $CoV_{NBA,FCE} = -0.02, CoV_{ADG,FCE} = -2.30$ and $CoV_{BF,FCE} = 0.05$. Characteristics of SI and BI for each breeding objective are presented in Table 4.3.

For the relevant breeding objective, SI values were computed for founder population females using appropriate indices, derived for use with their own records for NBA. For base population males, no information was available on NBA (dams unknown). All founder individuals were assumed to be from the same management group for SI indices, although this was not required for BI indices.

From Table 4.3, it can be seen that the standard deviation of predicted aggregate breeding values, SD_H, was equivalent for SI and BI indices calculated for the same breeding objective, as expected. However, the predicted standard deviation of the index, SD_I, can only be calculated for BI alternatives with knowledge of the covariance of EBVs for traits included in the index. This is in turn dependent on population structure, which influences the type and structure of recorded information available for both individuals and their relatives. Retrospectively, knowledge of prediction error variances and covariances may be useful for deriving the (co)variance of EBVs (Schneeberger et al., 1992). As a specific population structure was not defined for the simulations, SD_I was not calculated, and the correlation between the indices and objectives were not predicted for BI schemes.

For calculation of SI, an additional consideration was that candidates available for selection had dams with differing numbers of records for NBA. The SI criteria used in the simulations assumed that one record per dam was the standard measure for NBA. However, the mean of several records is a more accurate predictor of merit. As such, mean NBA ($MNBA$), expressed as a deviation from environmental contemporaries, was the measure of interest when dams had more than one record. Values for $MNBA$ were adjusted for use with the standard indices (i.e., one record per dam) according to:

$$MNBA'_n = MNBA \times \frac{1}{r + \frac{1-r}{n}}$$

where $MNBA'_n$ is the new mean adjusted for n contributing records, and r is repeatability of NBA. Consequently, the index weightings for NBA presented in Table 4.3 were appropriate for use with $MNBA'$ criteria. The number of records for NBA contributing to predicted EBVs for NBA was already accounted for with economic indices. This was because index weights for BI indices are not dependent on the number of records contributing to each individuals EBVs (Schneeberger et al., 1992).

BLUP Procedures

Two separate BLUP procedures were required in the simulation: EBVs for NBA were predicted using a single trait reduced animal model for repeated records (AMR); and a multiple trait reduced animal model (RAM) was used for deriving EBVs for ADG and BF. Both procedures properly accounted for inbreeding.

The mixed model for the AMR was:

$$y = X\beta + Zu + Wpe + e$$

where: y is the vector of observations for parent females only, β is an unknown vector of fixed (parity) effects including the general mean, X is a known design matrix relating records to fixed effects, u is a random vector of breeding values for all parents, Z is a known design matrix relating records to breeding values of all parents, pe is a random vector of permanent environmental effects for female parents, W is a known design matrix relating records to permanent environmental effects of female parents, and e is a random vector of environmental (or residual) effects.

Implicit assumptions are that $E(u), E(pe)$ and $E(e)$ are null and:

$$Var\begin{bmatrix} u \\ pe \\ e \end{bmatrix} = \begin{bmatrix} A\sigma_a^2 & 0 & 0 \\ 0 & I\sigma_{pe}^2 & 0 \\ 0 & 0 & I\sigma_e^2 \end{bmatrix}$$

where A is the numerator relationship matrix (NRM) for all animals, I is an identity matrix, and $\sigma_a^2, \sigma_{pe}^2$ and σ_e^2 are additive genetic, permanent environmental, and residual variances for NBA respectively. Permanent environment equations were implicitly absorbed according to Quaas (1984). The mixed model equations are then:

$$\begin{bmatrix} X'R^{-1}X & X'R^{-1}Z \\ Z'R^{-1}X & Z'R^{-1}Z + \alpha_1 A^{-1} \end{bmatrix} \begin{bmatrix} \hat{\beta} \\ \hat{u} \end{bmatrix} = \begin{bmatrix} X'R^{-1}y \\ Z'R^{-1}y \end{bmatrix}$$

where A^{-1} is the inverse of the NRM, $\alpha_1 = (1 - r)/h^2$ where r and h^2 are the repeatability and heritability of NBA respectively, and $R^{-1} = (\alpha_2^{-1}WW' + I)^{-1}$ where $\alpha_2 = (1 - r)/(r - h^2)$.

Solutions for $\widehat{\beta}$ and $\widehat{u}$ were obtained using Gauss-Siedel iteration procedures combined with successive over-relaxation techniques. EBVs of non-parents were mid-parent EBVs. Records of founder population females were included in the MME as this was the primary source of information for NBA in early years of the simulated breeding programs.

The mixed model for RAM was:

$$y = X\beta + Zu + Wcl + e$$

where: y is the vector of observations for BF and ADG on all animals ordered animal within trait, β is an unknown vector of fixed (management group) effects including the general mean, X is a known design matrix relating records to fixed effects, u is a random vector of breeding values for parent animals, ordered animal within trait, Z is a known design matrix relating records to breeding values of parent animals, cl is a random vector of common environmental (litter) effects, one for each litter, W is a known design matrix relating records to litter effects, and e is a random vector of environmental (or residual) effects. In a row of Z pertaining to a parent animal there is a '1' in the column position corresponding to it's BV. In a row pertaining to a non-parent, there are two '$\frac{1}{2}$'s in the column positions corresponding to it's parents' equations.

Implicit assumptions are that $E(u), E(cl)$ and $E(e)$ are null and:

$$Var\begin{bmatrix} u \\ cl \\ e \end{bmatrix} = \begin{bmatrix} G\otimes A & 0 & 0 \\ 0 & C\otimes I_l & 0 \\ 0 & 0 & R \end{bmatrix}$$

where G is the genetic (co)variance matrix for t traits, A is the numerator relationship matrix (NRM) for parent animals, C is the (co)variance matrix of common litter effects, I_l is an identity matrix of order l litters, $R = R_i * I_a$ where R_i is the residual (co)variance matrix for the ith animal, I_a is an identity matrix of order n, where n is the number of animals with records, and $\otimes$ denotes the Kronecker product. The mixed model equations are:

$$\begin{bmatrix} X'R^{-1}X & X'R^{-1}Z & X'R^{-1}W \\ Z'R^{-1}X & Z'R^{-1}Z+G^{-1}\otimes A^{-1} & Z'R^{-1}W \\ W'R^{-1}X & W'R^{-1}Z & W'R^{-1}W+C^{-1}\otimes I_l \end{bmatrix} \begin{bmatrix} \widehat{\beta} \\ \widehat{u} \\ \widehat{cl} \end{bmatrix} = \begin{bmatrix} X'R^{-1}y \\ Z'R^{-1}y \\ W'R^{-1}y \end{bmatrix}$$

and were transformed following Tier and Graser (1992):

$$\begin{bmatrix} X'R^{-1}X & X'R^{-1}Z(L\otimes I) & X'R^{-1}W \\ (L'\otimes I)Z'R^{-1}X & (L'\otimes I)Z'R^{-1}Z(L\otimes I)+I\otimes A^{-1} & (L'\otimes I)Z'R^{-1}W \\ W'R^{-1}X & W'R^{-1}Z(L\otimes I) & W'R^{-1}W+C^{-1}\otimes I_l \end{bmatrix} \begin{bmatrix} \widehat{\beta} \\ \widehat{u^*} \\ \widehat{cl} \end{bmatrix}$$

$$= \begin{bmatrix} X'R^{-1}y \\ (L'\otimes I)Z'R^{-1}y \\ W'R^{-1}y \end{bmatrix}$$

where L is the Cholesky decomposition of G, I_t is an identity matrix of order t traits, I is an identity matrix with order equivalent to the number of breeding values for one trait, and $\widehat{u^*}$ is a linear function of breeding values.

Solutions for $\widehat{\beta}, \widehat{u^*}$ and $\widehat{cl}$ were obtained using Gauss-Siedel iteration procedures combined with successive over-relaxation techniques. EBVs for parent animals were obtained using the $\widehat{u^*}$ solutions: $\widehat{u^*} = (L^{-1}\otimes I)\widehat{u}$. Backsolutions were calculated for EBVs of non-parents ($\widehat{u}_i$) following Pollak and Quaas (1981):

$$\widehat{u}_i = 0.5(\widehat{u}_s + \widehat{u}_d) + [R^{-1} + d_i^{-1}G^{-1}]^{-1}R^{-1}(y_o - 0.5\widehat{u}_s - 0.5\widehat{u}_d)$$

where:

$$d_i = \frac{1}{2} - \frac{1}{4}F_s - \frac{1}{4}F_d$$

and F_s and F_d are the inbreeding coefficients of individual i's sire and dam respectively; y_o are vectors of records adjusted for mgt effects such that $y_o = y - \widehat{mgt}$; and $\widehat{u}_s$ and $\widehat{u}_d$ are EBVs of i's sire and dam respectively.

Performance records for founder population individuals were not included in the RAM MME as management groups of these individuals were unknown, a situation common in reality. However, their inclusion in the NRM ensured that EBVs were estimated for founder animals from progeny records. As with simulation procedures presented in Chapter 3, BLUP evaluations were carried out at six month intervals to reduce computing demands.

4.2.4 Selection and Culling Procedures

Weekly selections were made based on the relevant selection criterion with no restrictions placed on the number of sibs selected per family or sibship. Selections were made within contemporary group, the number of selection candidates within these groups being determined by **SURV** and **PERC** (refer Section 4.2.1). For simulation results presented later, **SURV**=80% and **PERC**=90%. As such, approximately 72% of individuals generated were selection candidates. Unlike single trait simulation procedures, separate sex contemporary groups were simulated. The best six gilts and two boars were selected as replacement breeding stock (RBS) from their respective groups. Unselected young stock were then unavailable for any future selection decisions.

Selected gilts and boars entered separate sex RBS pools at 32 weeks of age and remained in these pools until 38 weeks of age. Individuals from the RBS pools were able to enter the breeding herd over this time period when replacements were required. Gilts entered the sow herd at random, since the appearance of oestrous rather than estimated genetic merit usually determines whether a selected gilt enters the sow herd or not. Boars were re-evaluated for breeding soundness prior to entering the boar herd. The probability of an individual boar failing this examination was 20%. The remaining boars were available for entry into the boar breeding herd, and were then selected to enter the breeding herd according to their estimated merit.

Sows were replaced at weekly intervals for three reasons: having produced their fourth litter; returning to service twice; and for general failure (eg. leg problems). The probability of an individual sow being culled for general failure following her 1st, 2nd or 3rd parity was 10%, 7.5% and 7.5% respectively. The number of gilts required each week, as such, was determined by the difference between the number of sows culled and **SMATE**. This procedure resulted in the weekly construction of a sow mating vector. The boar herd was evaluated at regular intervals according to **WBREP**. Boars which had produced litters in excess of **MLIT** or which had reached 65 weeks of age were replaced at this stage. In addition, 10% of boars in service were culled per year through poor performance (eg. injury, breeding difficulties). The number of replacement boars required was determined by the difference between boars culled and **NBOARS**.

4.2.5 Mating Procedures

R, **A** and **MS** mating schemes follow procedures which are, in principle, equivalent to those outlined in Sections 3.2.6 and 3.2.7. Changes in methodology from single trait procedures, and a brief review of the mating schemes used are presented in this section.

R and **A** schemes were characterised by the use of 13 boars consecutively as sires. Matings were manipulated so that each boar produced a similar number of litters prior to culling, and there was no direct avoidance of matings between relatives. Procedures are as outlined in Section 3.2.6. The maximum number of litters sired per boar per week was reduced from three to two for boars exceeding 52 weeks of age. If additional matings were required, young boars ($\leq$ 52 weeks old) were chosen at random to complete the required number of matings.

In contrast, **MS** schemes were characterised by unequal use of boars as sires. Boars were considered as a group of individuals available for breeding. However, the extent to which they were used as sires was dependent on their paired merit, as determined by their individual merit and the attributes of available sows. For **MS** schemes, matings were selected according to paired merit criteria using linear programming routines (H03ABF, Nag Fortran Library, 1975). Procedures and their general formulation are as presented in Section 3.2.7. The specific formulation of paired merit for alternative mate selection schemes evaluated in multiple trait studies is presented in Table 4.4. The weightings in the LP objective for each scheme code are related in pattern to their equivalents in Table 3.5.

From Table 4.4, ABV_{ij} is the mid-parent value of boar i and sow j for the prevailing selection criterion. That is, the predicted aggregate breeding value under SI or BI alternatives. This was the expected additive progeny merit for the aggregate genotype, although giving no indication of the expected relative contribution of each trait to merit. As with single trait simulations, variation within boars across sows in ABV_{ij} was scaled to unity prior to calculating progeny merit (PM_{ij}) in order to give the desired balance to emphasis on each of breeding value and inbreeding coefficient. Weightings chosen to reduce overall PM_{ij} according to progeny inbreeding coefficients, F_{ij}, were somewhat arbitrary. From single trait results, these weights were expected

Table 4.4: Formulation of paired merit for sire i and dam j, based on a measure of aggregate breeding value (ABV_{ij}) and progeny inbreeding (F_{ij}), for five mate selection schemes evaluated by simulation (see text for details).

Objective	**Paired Merit** ($f_{ij}(PM)$)	**Scheme Code**
Maximise	ABV_{ij}	**MS1**
Maximise	ABV_{ij} - 0.1 * F_{ij}	**MS2**
Maximise	ABV_{ij} - 1.0 * F_{ij}	**MS3**
Maximise	ABV_{ij} - 10.0 * F_{ij}	**MS4**
Minimise	F_{ij}	**MS5**

to be divergent enough to result in different rates of inbreeding. Of primary interest in this study was the relative behaviour of traits under different mating schemes rather than the identification of the most appropriate weight against inbreeding. As with **R** and **A** schemes, the maximum number of litters sired per mature boar (52^+ weeks of age) per week was reduced from three to two, and young boars were chosen to make any additional matings required.

4.2.6 Summary Statistics

As with single trait simulations, summary statistics for several variables were calculated and recorded quarterly (Q) or yearly (Y). Categories of variables common to both single and multiple trait simulations are recorded in Section 3.2.8, which provides a guide-line for the following information on equivalent statistics recorded for multiple trait simulations, noted below.

- **Phenotypic Effects**
  1. Phenotypic mean of NBA, both overall and within each parity group (Q).
  2. Phenotypic means and variances of ADG and BF (Q).
- **Genetic Effects**
  1. Genetic means and variances of NBA, ADG and BF (Q).

2. Genetic correlations between NBA and ADG, NBA and BF, and ADG and BF (Q).

- **Predicted Genetic Effects**

  1. Means and variances of EBV_{NBA}, EBV_{ADG} and EBV_{BF}, as well as prediction error variances for NBA, ADG and BF (Q).

- **Aggregate Merit**

  1. Means and variances of SI and BI indices for GP, TS and MAT objectives where appropriate (Q).
  2. Correlations between SI and BI values within GP, TS or MAT objectives where appropriate (Q).

Aggregate merit statistics (measured in $ terms) replaced the simple range statistics presented in Section 3.2.8, although maxima and minima for alternative selection criteria were available. Statistics relating to inbreeding and culling are as noted for single trait simulations. In addition to the herd statistics reported in Section 3.2.8, average generation intervals for sows and boars, as well as the actual number of individuals selected, were also recorded. Of prime interest in this study were genetic trends for NBA, ADG and BF, and inbreeding.

Mean values for these variables were analysed using SAS General Linear Model procedures (PROC GLM). Details of procedures and the model of analysis are as described in Section 3.2.8. For multiple trait studies, levels and values for effects included in the model of analysis may be derived from Table 4.1.

4.3 Simulation Results

In this section, results from multiple trait simulations are presented. Values are least squares means derived from SAS analyses of raw data means from 20 replicates. Herd statistics representative for the population simulated in this study are presented below.

4.3.1 Population Statistics

The following statistics describe a simulated population undergoing random selection of breeding replacements and random mating (Scheme 1). The population was characterised by 22.0 boars and 162.3 sows entering the breeding herd each year, representing a total of 378.4 sires and 3137.0 dams (including 27 males and 540 females in the founder population) over the time span of the simulation. Thirteen boars were available for use as sires concurrently, individual boars remaining in service until they had either sired 50 litters or reached 78 weeks in age. Boars averaged 25.5 litters prior to being culled, with litters sired ranging from 21.8 to 28.4 (averaged over years). Total sow herd size was 271.3 sows, and sows were kept in the breeding herd for up to four parities. The percentage of sows in parities 0, 1, 2, 3 or 4 were 1.9, 29.4, 25.9, 23.3 and 19.6 respectively, including sows waiting for remating. The average farrowing interval was 23.3 weeks.

Average generation intervals for boars and sows were 62.0 and 80.6 weeks respectively. Litter size averaged over years was 9.9 pigs per litter, and 540.1 litters were produced per year. Of the progeny generated, 80% survived until weaning, and 90% of those remaining were performance tested. The mean generation number of progeny born in year seventeen was 9.6. Sow herd size and structure, number of litters produced per sow per year, total number of litters, farrowing interval, and average sow generation interval were unaffected by choice of selection criterion or mating scheme. In contrast, boar herd statistics were affected by these variables.

For comparison, the total number of sires used and the average generation number of progeny is illustrated in Table 4.5 for index selection (Schemes 2 and 3) and each mating system. Selection itself reduced the total number of sires represented over the time span of the breeding program relative to that occurring under random replacement, but was consistent across selection alternatives (random mating). Mate selection alternatives (excluding **MS5**) further reduced the total number of boars used as sires relative to **R** by up to 10% under SI and up to 1% under BI (Table 4.5). Generation number was higher under BI than SI, indicating shorter generation intervals under BI. Similar generation intervals were apparent across mating alternatives.

Table 4.5: Least squares means for total number of sires represented (Sires) and average generation number of progeny (Gen. No.) under random (**R**), positive assortative (**A**), and five mate selection (**MS1-MS5**) alternatives, where selection is based on selection (**SI**) or BLUP (**BI**) indices.

Mating Scheme	Sires		Gen. No.	
	SI	**BI**	**SI**	**BI**
R	373.0	372.0	10.2	11.2
A	373.0	372.1	10.2	11.9
MS1	332.3	368.7	10.1	11.6
MS2	332.2	368.4	10.1	11.6
MS3	333.2	368.9	10.1	11.4
MS4	341.9	369.9	10.0	11.1
MS5	372.0	370.2	9.9	10.7

For each mating system, maximum, minimum, and the average number of litters sired per boar prior to culling, averaged across Schemes 2 and 3, are shown in Table 4.6. **R** and **A** mating alternatives exhibited considerably less variation in the number of litters sired per boar relative to mate selection approaches. However, the mean number of litters sired per boar was similar for all mating alternatives (Table 4.6).

4.3.2 Control Simulations

Response in NBA, ADG and BF, and average percent inbreeding, following sixteen years of random replacement (Scheme=1) or single trait selection for these traits (control simulations) under random mating are shown in Table 4.7. Details of each scheme were presented in Section 4.2.1.

Response to Selection

For each control scheme, average genetic merit for NBA significantly increased from zero even where directional selection for NBA was not carried out (Schemes 1,5,6,8 and 9). However, genetic merit for ADG and BF did not deviate significantly from zero where random replacement or selection for NBA alone was practised (Schemes 1,

Table 4.6: Least squares means for the maximum (MAX), minimum (MIN*) and average (AV*) number of litters sired per boar prior to culling under random (**R**), positive assortative (**A**), and five mate selection (**MS1-MS5**) alternatives.

Mating Scheme	MAX	MIN*	AV*
R	28.8	22.4	25.9
A	28.8	22.4	25.9
MS1	40.2	9.4	26.4
MS2	40.3	9.4	26.5
MS3	40.2	9.6	26.6
MS4	40.0	9.9	26.5
MS5	36.3	14.5	26.2

*for boars which were mated

Table 4.7: Response in **NBA** ($s.e. = 0.04 pigs/litter$), **ADG** ($s.e. = 1.1 gm/day$) and **BF** ($s.e. = 0.05 mm$), and percent inbreeding (%**F**: s.e.=0.2%), following sixteen years of single trait selection for each trait (control simulations: see **Scheme**) under random mating.

Selection criterion	**Trait selected**	**Scheme code**	**NBA**	**ADG**	**BF**	**%F**
Random	none	**1**	0.40	0	0.07	4.8
Index	NBA	**4**	3.49	-7	-0.08	12.1
Mass	ADG	**5**	0.47	233	1.52	7.4
Mass	BF	**6**	0.53	-48	-9.38	8.5
BLUP	NBA	**7**	4.76	1	-0.38	33.1
BLUP	ADG	**8**	0.32	282	1.38	22.3
BLUP	BF	**9**	0.38	-19	-10.10	17.4

4 and 7). Total response in NBA using selection index was 3.49 pigs/litter (Scheme 4). Response in NBA was improved by 36% to 4.76 pigs/litter using NBA EBVs as the selection criterion (Scheme 7). For comparison, total response in ADG and BF were improved by only 21% (Scheme 5 vs 8) and 8% (Scheme 6 vs 9) respectively using EBVs as the selection criterion. Correlated responses in ADG or BF were proportionally larger under individual selection for each of these two traits (Schemes 5 and 6) than where selection was based on EBVs (Schemes 8 and 9).

Inbreeding

Inbreeding inherent to the population structure and management system simulated, represented by the accumulation of inbreeding under random replacement and mating following sixteen years of selection, was approximately 4.8% (Table 4.7: Scheme 1). Under directional selection (Schemes 4 to 9), levels of inbreeding increased above this value in all cases. However, final levels of inbreeding depended on characteristics of the selection criterion. Single trait selection for NBA (Schemes 4 and 7) resulted in the highest levels of inbreeding overall. Rates of inbreeding under selection for ADG and BF, which were not evaluated using family information, were lower. Further, EBV selection increased inbreeding relative to that occurring under individual and/or index selection for the same trait. For NBA, EBV selection increased mean levels of inbreeding by 174% relative to index selection. However, where selection was for ADG or BF, EBV selection increased levels of inbreeding by 201% (Scheme 5 vs 8) and 105% (Scheme 6 vs 9) respectively.

4.3.3 The Impact of Selection Criterion

Total levels of response in component traits (NBA, ADG, and BF), overall $ merit for the aggregate genotype, and percent inbreeding following sixteen years of selection on either a traditional selection or BLUP index (Schemes 2 and 3), and for three different breeding objectives, are presented in Table 4.8.

Table 4.8: Response in **NBA**, **ADG**, **BF**, **$** response for the aggregate genotype (**AGG**), and percent inbreeding (%F) following sixteen years of selection on either a selection or BLUP index, where the index defines a general purpose (**GP**), maternal (**MAT**), or terminal sire (**TS**) line, under random mating.

	Selection Alternative									
	Selection Index					**BLUP Index**				
Index	**NBA**	**ADG**	**BF**	**AGG**	**%F**	**NBA**	**ADG**	**BF**	**AGG**	**%F**
GP	0.81	186	-6.4	631	8.4	1.25	237	- 5.9	743	21.0
TS	0.31	185	-6.6	616	8.6	0.27	238	- 5.8	714	20.1
MAT	1.16	181	-6.4	328	8.7	1.65	232	- 5.8	388	20.8

Response to Selection

The type of selection index used (GP, TS or MAT) had a significant impact on response to selection in NBA, but only marginal effects on response in ADG and BF. Total response for each of the production traits did not significantly differ between GP and TS indices, but were slightly lower under maternal indices (Table 4.8). In comparison, response in NBA was higher under maternal indices where its relative selection emphasis was higher. High levels of response in ADG and BF contributed to large $ gains in aggregate merit for GP and TS indices, where the economic value for these traits is high. Aggregate merit is not directly comparable across different breeding objectives. The lower $ response for MAT indices reflected lower economic values for production traits under this breeding objective, and the relatively small response made in NBA.

Averaged over index types, selection on BLUP indices increased response to selection in ADG by 28%, but decreased response in BF by approximately 9% relative to SI. Total response in NBA was improved by 54% under the GP index and by 42% under the maternal index, using BLUP over traditional selection indices. Relative to SI, drift in NBA under TS was lower where selection was based on BLUP indices, suggesting that individuals from larger families were favoured less under BI selection. Overall, improvements in aggregate merit under BI ranged from 16% to 19%, and were limited by the unfavourable result under BI for backfat. The result for BF

Table 4.9: Mean levels of genetic variation for **NBA**, **ADG** and **BF**, expressed relative to initial levels of genetic variation[†], following sixteen years of selection on either a selection or BLUP index, where the index defines a general purpose (**GP**), maternal (**MAT**), or terminal sire (**TS**) line, under random mating.

	Selection Alternative					
	Selection Index			**BLUP Index**		
Index	**NBA**	**ADG**	**BF**	**NBA**	**ADG**	**BF**
GP	0.93	0.82	0.43	0.78	0.68	0.39
TS	0.90	0.82	0.42	0.77	0.71	0.41
MAT	0.88	0.83	0.42	0.81	0.69	0.40

[†] see Table 4.2

was inconsistent with the superior ranking of EBV selection for BF under single trait selection (Table 4.7: Scheme 6 vs 9).

Final levels of genetic variation remaining, relative to initial levels, for each trait under SI and BI selection alternatives and for each index type are presented in Table 4.9. Similar levels of genetic variation were apparent across different indices for each trait. This result was consistent with the comparable levels of inbreeding achieved under each index (Table 4.8). With the exception of BF, EBV selection decreased variation in component traits to a greater extent than that occurring under SI. Similar levels of genetic variation remained for BF under either SI or BI alternatives. Overall, substantial reductions in genetic variation were apparent for BF relative to NBA and ADG following selection.

For each mating scheme under **BI**, empirical prediction error variances, calculated from the difference between true and estimated breeding values, and the direction and magnitude of bias in estimates for each trait are presented in Table 4.10. Under random mating no significant bias in EBVs was identified for NBA and ADG, although merit for ADG was slightly over-estimated. In contrast, a substantial bias in EBVs was identified for BF, which was simulated with a scale effect. EBVs for BF were consistently under-estimated relative to true breeding values.

Selection was accompanied by changes in genetic covariances between ADG and BF, which were consistent under both SI and BI alternatives. The correlation between

Table 4.10: Empirical prediction error variances (**PEV**$_{subscript}$) for **NBA**, **ADG** and **BF**, and the magnitude and direction of bias, expressed in base population genetic standard deviation units (**PE**$_{NBA}$, **PE**$_{ADG}$, and **PE**$_{BF}$ respectively), following sixteen years of selection on a BLUP index, where the index defines a general purpose (**GP**), maternal (**MAT**), or terminal sire (**TS**) line, and where mating is at random (**R**), positive assortative (**A**) or one of five (**MS1-MS5**) mate selection alternatives.

Index	**Mating Scheme**	**PEV**$_{NBA}$	**PE**$_{NBA}$	**PEV**$_{ADG}$	**PE**$_{ADG}$	**PEV**$_{BF}$	**PE**$_{BF}$
GP	R	0.47	0.02	298	-2.65	0.42	-1.35
	A	0.37	-0.01	254	-0.89	0.35	-1.64
	MS1	0.39	0.00	267	-0.37	0.38	-1.74
	MS2	0.42	0.00	283	-0.41	0.39	-1.64
	MS3	0.44	0.00	302	-0.36	0.40	-1.69
	MS4	0.46	0.01	310	-0.51	0.43	-1.47
	MS5	0.51	0.01	328	-0.81	0.46	-1.03
TS	R	0.46	-0.02	305	-2.66	0.43	-1.13
	A	0.36	-0.01	248	-1.08	0.35	-1.60
	MS1	0.38	-0.02	269	-0.44	0.37	-1.63
	MS2	0.42	-0.04	279	-0.51	0.38	-1.64
	MS3	0.43	-0.07	302	-0.52	0.41	-1.49
	MS4	0.47	0.00	313	-0.57	0.44	-1.41
	MS5	0.50	-0.12	328	-0.72	0.47	-0.98
MAT	R	0.47	0.05	299	-2.48	0.43	-1.34
	A	0.39	0.06	255	-1.08	0.36	-1.74
	MS1	0.39	0.02	265	-0.25	0.37	-1.78
	MS2	0.41	0.00	276	-0.33	0.39	-1.82
	MS3	0.44	0.01	298	-0.34	0.41	-1.72
	MS4	0.48	0.05	313	-0.42	0.43	-1.58
	MS5	0.49	0.04	321	-0.67	0.45	-1.26

true breeding values of these traits was 0.12 in the base population, and increased to 0.13 under single trait selection for either of these traits. In comparison, a final value of 0.18 resulted under index selection where information from both traits was used in the selection criterion.

Inbreeding

Control simulations showed that inbreeding inherent to the unselected population simulated was approximately 4.8% (Scheme 1: Table 4.7). Under traditional index selection average inbreeding increased to approximately 8.6%, and was further increased by 150% using a BLUP index to 20.6%, averaged over indices. Index type had minimal impact on the inbreeding accumulated. However, within SI, there was a tendency for slightly higher levels of inbreeding under TS and MAT indices compared to GP. Within BI, levels of inbreeding were slightly higher under GP and MAT, relative to TS. These trends were marginal in significance. Therefore, the impact of selection criterion on inbreeding may be summarised across index alternatives.

Total inbreeding under selection for an aggregate genotype was similar to that resulting from single trait selection for BF under SI, and intermediate to that resulting from single trait selection for either ADG and BF under BI, in the same population (Table 4.8 vs Table 4.7). Initial index heritabilities ranged from approximately 0.30 (MAT) to 0.34 (TS) under SI, and were intermediate in value to the heritabilities of ADG ($h^2 = 0.24$) and BF ($h^2 = 0.45$). Index heritabilities were not computed under BI, but would be expected to be higher than the corresponding SI due to greater accuracy of genetic evaluation.

4.3.4 The Impact of Mating System

Response to selection in the aggregate genotype and percent inbreeding under alternative mating policies, expressed relative to results from random mating options both within and across selection alternatives, are presented in Table 4.11. Details of the mating schemes evaluated were presented in Section 4.2.5. Response in component traits contributing to aggregate merit, expressed relative to their response under random mating, for each index and mating alternative are shown in Table 4.12. Response in NBA under the TS index is of little direct interest in this study as improved NBA did not contribute to economic merit under this index, and was not directionally selected for. Thus, relative merit for NBA under TS are not presented for alternative mating schemes.

Response to Selection

For both SI and BI alternatives, response in aggregate merit was higher under assortative mating and **MS1-MS4** alternatives relative to response under random mating. Improvements in aggregate merit ranged from 4%-6% under SI and 8%-9% under BI, using the best non-random mating system (Table 4.11). Under EBV selection the highest response consistently occurred under **MS3**, but the mating alternative resulting in the highest response was inconsistent under SI. Response in aggregate merit was consistently decreased under **MS5** relative to all other mating options (Table 4.11), with overall reductions ranging from 2%-3% relative to random mating.

Improved aggregate merit under **A** and **MS1-MS4** mating options relative to random mating was not reflected by improved gains in all traits included in the index. For GP and MAT indices under SI, and GP under BI, relative response in NBA was increased under assortative mating but decreased under all **MS** alternatives (Table 4.12). For the maternal index under BI, **A** and **MS1-MS2** mating alternatives increased response in NBA, whereas the remaining **MS** options decreased response in this trait. Improved response in NBA under assortative mating was associated with slight increases in genetic variation of this trait in early years (not presented), and increased accuracy of evaluation for NBA relative to that occurring under random mating (Table 4.10). Assortative mating increased relative response in NBA moreso under GP than MAT indices for SI, although the reverse trend was apparent under BI. In comparison, mate selection procedures consistently reduced genetic variation for NBA in early years (not presented). In addition, prediction error variances were greater for NBA under **MS** relative to **A**, but tended to be lower relative to **R** (Table 4.10).

Table 4.11: Response to selection in the aggregate genotype (Resp.) and percent inbreeding (%F), expressed relative to results under random mating[†], following sixteen years of selection on either a traditional selection (**SI vs SI(R)**) or BLUP index (**BI vs SI(R)** and **BI vs BI(R)**), where the index defines a general purpose (**GP**), maternal (**MAT**) or terminal sire line (**TS**), and mating is at random (**R**), positive assortative (**A**), or one of five (**MS1-MS5**) mate selection alternatives.

Index	**Mating**	**SI vs SI(R)**		**BI vs BI(R)**		**BI vs SI(R)**	
(Type)	**System**	**Resp.**	**%F**	**Resp.**	**%F**	**Resp.**	**%F**
GP	R	1.00	1.00	1.00	1.00	1.18	2.50
	A	1.04	1.20	1.04	1.76	1.23	4.39
	MS1	1.02	1.43	1.07	1.51	1.26	3.79
	MS2	1.02	1.31	1.06	1.33	1.25	3.33
	MS3	1.02	1.02	1.08	1.07	1.27	2.67
	MS4	1.01	0.88	1.05	0.81	1.24	2.04
	MS5	0.96	0.62	0.95	0.59	1.12	1.46
TS	R	1.00	1.00	1.00	1.00	1.16	2.34
	A	1.01	1.14	1.06	1.87	1.23	4.37
	MS1	1.05	1.33	1.06	1.59	1.24	3.71
	MS2	1.03	1.27	1.07	1.38	1.24	3.23
	MS3	1.04	1.02	1.09	1.07	1.26	2.50
	MS4	1.02	0.86	1.06	0.84	1.23	1.97
	MS5	0.95	0.60	0.98	0.61	1.14	1.42
MAT	R	1.00	1.00	1.00	1.00	1.19	2.39
	A	1.06	1.26	1.08	1.71	1.28	4.09
	MS1	1.02	1.25	1.09	1.53	1.29	3.66
	MS2	1.03	1.28	1.08	1.43	1.28	3.41
	MS3	1.04	1.02	1.09	1.10	1.29	2.63
	MS4	1.02	0.86	1.07	0.83	1.27	1.98
	MS5	0.97	0.61	0.98	0.63	1.17	1.51

[†] see Table 4.8

Table 4.12: Response in **NBA**, **ADG** and **BF**, expressed relative to response under random mating[†], following sixteen years of selection on either a selection or BLUP index, where the index defines a general purpose (**GP**), maternal (**MAT**), or terminal sire (**TS**) line, under positive assortative mating (**A**) or one of five (**MS1-MS5**) mate selection alternatives.

		Selection Alternative					
	Mating	**Selection Index**			**BLUP Index**		
Index	**Scheme**	**NBA**	**ADG**	**BF**	**NBA**	**ADG**	**BF**
GP	A	1.09	1.04	1.03	1.05	1.04	1.06
	MS1	0.99	1.02	1.04	0.86	1.09	1.03
	MS2	0.89	1.02	1.04	0.86	1.07	1.06
	MS3	0.72	1.03	1.02	0.94	1.10	1.06
	MS4	0.91	1.01	1.02	0.82	1.07	1.04
	MS5	0.99	0.95	0.98	0.63	0.96	0.98
TS	A	-	1.02	1.00	-	1.07	1.05
	MS1	-	1.06	1.01	-	1.06	1.08
	MS2	-	1.04	1.01	-	1.07	1.09
	MS3	-	1.05	1.02	-	1.09	1.09
	MS4	-	1.04	0.99	-	1.06	1.05
	MS5	-	0.95	0.96	-	0.98	0.99
MAT	A	1.04	1.08	1.03	1.13	1.09	1.03
	MS1	0.91	1.03	1.01	1.12	1.10	1.03
	MS2	0.88	1.06	1.00	1.16	1.08	1.07
	MS3	0.94	1.05	1.04	0.98	1.12	1.06
	MS4	0.88	1.04	1.01	0.99	1.08	1.06
	MS5	0.92	0.97	0.97	0.87	0.99	1.02

[†]see Table 4.8

Table 4.13: Mean levels of genetic variation for **NBA**, **ADG** and **BF** averaged over indices, expressed relative to initial levels of genetic variation[†], following sixteen years of selection on either a selection or BLUP index, where the index defines a general purpose (**GP**), maternal (**MAT**), or terminal sire (**TS**) line, under random **R**, positive assortative **A** mating, or one of five **MS1-MS5** mate selection alternatives.

Mating	**Selection Alternative**					
	Selection Index			**BLUP Index**		
System	**NBA**	**ADG**	**BF**	**NBA**	**ADG**	**BF**
R	0.90	0.82	0.42	0.78	0.69	0.40
A	0.88	0.84	0.40	0.62	0.64	0.31
MS1	0.88	0.80	0.40	0.65	0.60	0.33
MS2	0.86	0.82	0.40	0.70	0.63	0.34
MS3	0.86	0.81	0.40	0.71	0.68	0.36
MS4	0.87	0.82	0.41	0.77	0.70	0.38
MS5	0.88	0.84	0.43	0.83	0.75	0.42

[†] see Table 4.2

Final levels of genetic variation under each mating option, averaged over indices and expressed relative to initial levels of variation, are presented in Table 4.13. With the exception of results for **MS5**, inbreeding resulting under non-random mating options tended to be higher than that resulting under random mating. Initial increases in genetic variation under assortative mating were thus depleted under selection. Moreover, levels of genetic variation remaining under **MS1-MS4** tended to be lower than that resulting under **A** for SI. In comparison, variation under **MS1-MS4** was greater under BI, relative to **A**.

In contrast to results for NBA, response in ADG was consistently increased relative to random mating under **A** and **MS1-MS4** mating alternatives. Relative gains in ADG ranged from 1%-8% under SI and 4%-12% under BI, according to index. Relative gains in BF under **A** or **MS1-MS4** mating systems were generally lower and marginal for TS and MAT SI indices, but were consistently higher (up to 9%) under BI for all indices. Overall, it was not possible to identify which mating scheme consistently resulted in the highest response for a given trait. In contrast, **MS5** consistently decreased response to selection in all traits. Reductions in response for component traits under **MS5** tended to be relatively greater for NBA than for ADG or BF. For GP and MAT indices, response for NBA was reduced by 1-8% under SI and 37-13% under BI respectively. In comparison, response in ADG or BF was decreased by no more than 5% over all indices.

Inbreeding

As noted previously, the effects of selection criterion on inbreeding may be averaged across indices under random mating. Moreover, average inbreeding resulting under each mating alternative did not differ across index types, although there was a tendency for slightly higher levels of inbreeding for all **MS** options under MAT (relative to GP or TS indices).

For both SI and BI indices, **A** and **MS1-MS3** mating alternatives increased, and **MS4-MS5** alternatives decreased, total levels of inbreeding from that achieved under random mating (Table 4.11). Total levels of inbreeding declined as the cost attributed to progeny inbreeding in parental paired merit increased (**MS1** → **MS5**). Within SI, the highest levels of inbreeding resulted under **MS1-MS2** alternatives, in which progeny inbreeding contributed little to paired merit. Within BI, assortative mating consistently resulted in the highest levels of inbreeding. Overall, average inbreeding increased by 28%-43% under SI, and 71%-87% under BI, using the worst mating option (relative to random mating), across indices. **MS4** and **MS5** consistently reduced inbreeding below that achieved under random mating. Average inbreeding under **MS4** was 87% and 83% of that resulting under **R** for SI and BI, and 61% for both selection options under **MS5**. No **MS** alternative reduced levels of inbreeding under BI to below that of the corresponding SI alternative.

4.4 Discussion

A detailed discussion of factors affecting the relative performance of selection and mating alternatives under single trait selection was presented in Section 3.3. Much of this discussion is relevant to the current study, but for conciseness is not repeated here. In the following section, results are discussed for multiple trait simulations, with particular emphasis on response in component traits contributing to merit in the aggregate genotype. In Chapter 5, a general discussion will draw results from the two studies together.

4.4.1 Simulation Performance

Herd Statistics

The simulation performed as expected regarding sow herd size and population structure. Sow parity distribution indicated that more sows were in later parities than is usual in practice. Higher rates of replacement in early parities would alleviate this problem. Sow herd statistics (eg. total number of sows, total number of litters, number of litters per sow per year, sow parity distribution, sow generation and farrowing intervals) were unaffected by choice of selection criterion or mating policy. However, selection decreased both the total number of boars used as sires and overall generation intervals relative to random replacement (Table 4.5). Superior candidates for selection generally have a longer selection history, younger parents and subsequently a higher generation number. Thus, replacement boars and gilts tended to be younger under selection, and boars needed replacing less frequently under a fixed age at replacement policy.

Mating scheme had a significant impact on the number of litters sired per boar, total number of sires represented, boar generation intervals and the average generation number of progeny (Table 4.6). Under **MS** options, some boars were required to sire a large number of litters in order to compensate for those boars producing few or no litters. Averaged over boars, the mean number of litters per boar was similar across mating options reflecting constant sow herd size. Boars producing no litters under **MS** schemes were uncompetitive relative to their contemporaries in either genetic merit and/or average relationship with the sow herd, and were subsequently culled. Thus, the total number of sires was reduced under **MS** alternatives relative to **R** or **A**. Greater variation in aggregate merit between selected boars under SI increased the chance of boars being culled without progeny relative to BI. Overall, there was a tendency for less variation in the number of litters sired per boar as more emphasis was placed on the avoidance of matings between relatives. These results illustrate how choice of mating scheme may affect selection outcomes through influencing population and data structures.

Control Simulations

Relative response to selection for each trait was consistent with their genetic characteristics. The exception to this was a positive drift in NBA in the absence of directional selection for this trait as a result of sampling considerations (Table 4.7: Schemes 1,5,6,8 and 9). Drift in NBA resulted from increased selection of replacement breeding stock from larger families, which were advantaged by the availability of more selection candidates. Positive drift in NBA was more apparent where phenotypic measures were the criterion for selection. However, other studies have indicated little impact of small improvements in reproductive performance on selection differentials (Davis, 1987). Thus, drift in NBA was not considered a problem in this study. In reality, increases in NBA may not be apparent due to restricted performance testing which reduces sampling differences between families. In addition, increased sampling may be offset where piglet mortality or performance for other selected traits is mediated via litter size, as was suggested by Haley (1989).

Control simulations illustrated the relative magnitude of response possible for each trait under single trait selection, and for each selection criterion in the simulation environment. These are likely to be higher than that achieved in reality, but are consistent in magnitude with results of other researchers for traits with similar genetic characteristics (Avalos and Smith, 1987; Belonsky and Kennedy, 1988; Wray, 1989). Relatively large improvements in response for NBA using EBV selection (+36%) illustrated the significant impact BLUP has on response in lowly heritable and/or sex limited traits compared to index selection. In comparison, EBV selection improved response in ADG and BF by 21% and 8% respectively. These traits were more highly heritable than NBA, reducing the relative impact of BLUP on response.

Production traits were simulated with a genetic correlation of 0.12 in the base population. Thus, single trait selection on either of ADG or BF resulted in a correlated response. Response resulting from indirect selection was higher where selection was based on individual performance measures. This phenomenon was implicitly suggested by formulae presented by Strandén et al. (1993), who indicated that unfavourable changes in the genetic correlation are less under phenotypic than EBV selection, thereby facilitating a greater correlated response in the unselected trait using phenotypic measures. However, this cause was unsubstantiated in this study, as changes in the genetic correlation were similar across selection alternatives.

Inbreeding inherent to the population simulated was almost 2% lower than that reported for single trait studies in Section 3.3. Fewer litters per boar and more boars used per year in the population simulated for this study contributed to lower inbreeding overall. Selection increased inbreeding above inherent levels defined by population size and breeding strategies. The highest levels of inbreeding occurred under selection for NBA. Records from female relatives were the only source of information available to predict genetic merit for this trait, increasing covariances between sibs (Scheme 4) and other family members (Scheme 7), and therefore the probability of selecting related individuals for breeding. Where selection was for ADG or BF, individual performance was the criterion for selection, reducing the effect of selection on inbreeding relative to index selection for NBA. Moreover, the higher heritability of production traits reduced the emphasis placed on family information in the mixed model equations, thereby contributing to relatively lower rates of inbreeding under EBV selection for these traits.

Relative increases in inbreeding under EBV selection were greatest for single trait selection on ADG (201%), followed by NBA (174%) and BF (104%). Data accumulation was slow for NBA which limited additional information which could be used in BLUP procedures, thereby reducing the potential difference in inbreeding between index and EBV selection for this trait. In comparison, a much greater volume of data accumulated for both ADG and BF, and both traits contributed to EBVs for each trait in the multi-trait BLUP. In combination with moderate trait heritability, these factors contributed to an increased accuracy of evaluation for ADG relative to NBA, thereby increasing the effects of EBV selection for ADG on inbreeding. The high heritability of BF, however, minimised differences in inbreeding between individual and EBV selection. In addition, the simulated scale effect for BF had unfavourable implications for the accuracy of genetic evaluation (discussed below).

4.4.2 The Impact of Selection Criterion

Selection on BLUP indices resulted in a 16%-19% higher response in aggregate merit relative to traditional selection index procedures. However, relative gains in each trait under EBV selection differed according to trait characteristics (noted above) and index type. Within selection alternative, predicted gains in ADG and BF under index selection were equivalent for GP, TS and MAT indices. Thus, the similar levels of response obtained in each of these traits under each index were as expected. Averaged over indices, EBV selection increased response in ADG by 28%, but decreased response in BF by approximately 9% relative to SI. Results for BF were inconsistent with results from control simulations, which showed improved response in BF under EBV selection (Table 4.7: Scheme 6 vs 9). Relative improvements in response in NBA ranged from 42%-54% according to index type. Overall, improvements in aggregate merit under BI were limited by the unfavourable result under this selection alternative for backfat.

Response in NBA was the result of both directional selection and drift. Drift in NBA was present under all indices, as noted above, and was illustrated by increased merit for NBA in the absence of direct selection for this trait (Table 4.8: TS index). Relative to SI, drift in NBA was lower where selection was based on BLUP indices, suggesting that individuals from larger families were favoured less under BI selection. This would appear logical, as higher accuracy of evaluation may alleviate sampling differences overall. Under directional selection, response in NBA was highest under MAT (relative to GP) due to its high economic value and subsequently stronger selection emphasis under a maternal breeding objective. Relative gains in NBA under BI were higher than those occurring under single trait EBV selection for this trait (Table 4.7: Scheme 7) as a result of lower inbreeding.

Relative improvements in response of ADG under BLUP index selection were lower than those for NBA, as expected. However, lower response in BF under BI relative to SI was not as expected, and conflicted with control results. Reductions in response in BF under BI relative to SI could not be attributed solely to scale effects or BLUP procedures, which were common across control and index selection schemes. The poorer performance of BI alternatives for BF may have resulted from inadequately accounting for unfavourable changes in the genetic correlation under multiple trait selection. Unfavourable changes in r_g between traits are expected to be greater where traits are divergently selected upon, relative to single trait selection on either trait (Itoh, 1991; Strandén et al., 1993). In this study, the genetic correlation changed from 0.12 to 0.18 under index selection, but only increased to 0.13 under control simulations.

As a result of scale effects and changes in the genetic correlation, predictions of breeding values for production traits were biased. Changes in the genetic correlation under selection and scale effects are problematical for BLUP genetic evaluation systems, which do not account for these effects. Breeding values were slightly overestimated for ADG but greatly underestimated for BF (Table 4.10), suggesting much of the bias was due to the simulated scale effect. Bias due to scale effects would not affect ranking under index procedures using performance measures, although changing trait covariances would impact on the accuracy of selection index values. Further studies may clarify and quantify under what conditions changes in the genetic correlation adversely affect gain in component traits of an index under multiple trait selection, particularly where advanced genetic evaluation systems are used to estimate breeding values. In addition, the implications of scale effects for BLUP genetic evaluation may be of some importance in the comparison of selection outcomes, and should be examined further.

As noted above, relative improvements in response for each trait under EBV selection differed according to trait characteristics. This contributed to the differences between SI and BI in relative response for component traits under the same index, as has also been noted in other studies (De Roo, 1988a). This result has implications for breeders, as predicted gains in each trait may differ under the same breeding objective according to the method of genetic evaluation. Roehe et al. (1992) also noted that increased response to selection for aggregate breeding values depended on economic weights, trait additive variances, accuracy of selection and the selection strategy chosen. Thus, more frequent re-evaluation of breeding objectives may be required under BLUP based breeding programs, particularly if significant departures from desired trait gains occurs.

Averaged over indices, inbreeding under BI was up to 150% higher than that resulting under SI. Elevated levels of inbreeding for BI were expected given the more extensive use of family information in the prediction of trait EBVs. However, inclusion of several traits in the selection criterion may have acted to reduce the relative impact of BLUP on inbreeding compared to that expected under single trait selection for a trait of similar heritability. This is more likely where traits are uncorrelated or unfavourably correlated, allowing members of different families to rank highly on index value from superior merit in different traits. For example, inbreeding under single trait selection (h^2=0.35) was approximately 11% under individual selection and 25% under EBV selection (see Section 3.3), whereas inbreeding under TS ($\sqrt{r_{IH}} = 0.34$) was 8.6% under SI and 20.1% under BI. Even allowing for the 1.7% difference in inbreeding inherent to each population, the accumulation of inbreeding was less where more than one trait was included in the breeding objective.

In this study, final levels of inbreeding were similar for each index type (within selection alternative), and indices evaluated had similar accuracies. Insofar as an index value may be thought of as a single measure, it may be speculated that index heritability was a good predictor of the magnitude of inbreeding which resulted under selection. However, there was a tendency for slightly higher levels of inbreeding under both TS and MAT indices compared to GP under SI. This was due to the use of fewer traits as criteria under TS indices, and slightly lower index heritability combined with greater use of family information under MAT. Within BI, levels of inbreeding were higher under GP and MAT relative to TS, under which NBA was not included. These trends were marginal in significance, suggesting that the indices compared were too similar to affect relative levels of inbreeding overall. Examination of trends in inbreeding for more diverse breeding objectives may aid in clarifying the importance of index heritability and composition on the accumulation of inbreeding.

4.4.3 The Impact of Mating System

With the exception of results for BF, choice of selection criterion had a much greater impact on improving response in aggregate merit and/or component traits than did choice of mating system used thereafter. Further, relative response in component traits under non-random mating alternatives differed according to trait and accuracy of evaluation. Maximum improvements in aggregate merit through choice of the best mating system ranged from 4%-6% under SI to 8%-9% under BI, according to index. However, response in NBA tended to be adversely affected under **MS** options, with the exception of results for **MS1-MS2** under a maternal BLUP index. In contrast, response in NBA was improved under positive assortative mating, and relative response in ADG and BF were consistently improved under **A** and **MS1-MS4** mating systems. Response in all component traits and subsequently aggregate merit were reduced under **MS5**.

Assortative pairing of mates based on index values increased initial levels of genetic variation in component traits (not presented) and the aggregate genotype. In addition, **A** increased the accuracy of evaluation under BI for each trait relative to **R**, as illustrated by lower prediction error variances in Table 4.10. Improved accuracy of evaluation was maintained over the time span of the breeding program, and acted to offset the detrimental effects of enhanced selection efficiency and higher inbreeding under **A** on overall variance loss under selection and inbreeding (Table 4.13). Relative gains under **A** differed according to trait heritability, accuracy of evaluation, genetic variation and selection emphasis, as defined by trait characteristics and index type. Results for individual traits under **A** were consistent with that predicted from theory (Hohenboken, 1985; Smith and Hammond, 1987a; Fernando and Gianola, 1986)

In comparison to **A**, mate selection procedures reduced genetic variation for each trait in early years as a result of unequal sire use and slightly higher selection intensities. In addition, overall accuracy of genetic evaluation under BI was reduced relative to **A** for **MS** alternatives, probably as a result of reduced covariances between relatives and poorer data structure under **MS** (see Wood et al., 1991a). Thus, improvements in trait response under **MS** alternatives were largely the result of making more use of genetically superior boars to increase selection differentials, and slight increases in selection intensity (negligible under BI). Under more accurate selection (BI schemes), correct ranking and allocation of matings to superior individuals was more likely, thereby increasing the relative efficiency of these mating schemes for improving response to selection. In addition, genetic variation under **MS** alternatives was preserved relative to **A** in later years as a result of lower selection accuracy (**MS1-MS5**), reducing the effect of selection on inbreeding, and through avoiding inbreeding in the progeny (**MS2-MS5**).

Under non-random mating, response in component traits was a function of each traits contribution to differences between index values of selected boars. Relative contributions were determined by trait variation, heritability and economic values, and changes in genetic parameters for each trait under selection and inbreeding. Index values were generally dominated by merit for ADG over time and BF in early years, particularly under SI where information contributing to merit in NBA was restricted. Therefore, differential use of boars based on index values generally reflected differences between boars in merit for production traits, and subsequently generated additional response in these. Differences in merit for NBA were masked by information from production traits and, as a result of reduced selection efficiency, relative response in this trait declined under **MS** alternatives. In contrast, under the maternal BLUP index, the high economic value of NBA combined with more accurate evaluation increased the relative contribution of this trait to variation between boars in their index values. Thus, mating schemes using BLUP index information to allocate mates (**A** and **MS1-MS4**) were more successful at improving response in NBA relative to response under a traditional selection index.

Improvements in response of BF under **A** or **MS1-MS4** mating systems were generally low under SI (1%-4%) relative to BI (3%-9%), and lower than would be expected for a highly heritable trait. However, over time the ability to differentiate between BF measures of boars was reduced due to the simulated scale effect, and relative superiority of boars was less efficiently identified. Thus, real genetic differences between boars in BF were largely not used at mating under SI. In contrast, differences between boars in their EBVs for BF were apparent even where phenotypic differences were not, making it possible to identify and allocate more matings to genetically superior boars under BI, thereby increasing response in BF more effectively. Improved response in BF under BI for **A** or **MS1-MS4** was sufficient to re-rank the relative superiority of BI with SI for this trait. Results suggested that the accuracy of BLUP EBVs was improved for traits affected by scale considerations by mating like to like. By increasing the efficiency of selection between families, differences between family means are reduced and scale effects become more uniform across families, thereby increasing accuracy of evaluation (Table 4.10: eg **A** vs **MS5**).

As noted above, **MS5** consistently decreased response in component traits and aggregate merit overall. However, relative reductions in component traits varied according to trait characteristics and the method of genetic evaluation. Under **MS5**, response in NBA was reduced by 1%-8% under SI and 37%-13% under BI, according to index. In comparison, response in ADG or BF was reduced by no more than 5% across all indices, and overall reductions in aggregate merit were no more than 2%-3% under **MS5**. Small reductions in aggregate merit under **MS5** were the result of a limited impact of NBA on total merit. Substantial reductions in response for NBA under **MS5** were the result of decreasing the mating frequency of boars superior in genetic merit for this trait. Individuals more related to other members of the breeding herd were likely to be so because of common family information contributing to estimated merit for NBA. Thus, larger relative reductions in NBA under BI reflected greater use of family information in predicting merit for this trait. The detrimental effects of **MS5** on response were in part offset by reductions in inbreeding, particularly under BI where the effects of selection on inbreeding were greater relative to SI.

In contrast to the relatively small effects mating scheme had on response in overall merit, inbreeding in the short term was markedly affected by mating policy. However, regardless of mating scheme, inbreeding under BI was consistently higher than inbreeding under SI for all selection indices. This result suggested that, for the indices examined, it was not possible to fully negate the effects of more accurate selection on inbreeding through choice of mating system. However, this may not be the case where traits used as criteria for selection are more highly heritable and/or are evaluated with less emphasis placed on family information. Results presented in Section 3.3 showed that for a more highly heritable trait ($h^2 = 0.6$) re-ranking of selection alternatives for inbreeding (individual performance vs EBV) was possible with the appropriate mating scheme.

Mating schemes influenced the accumulation of inbreeding in three main ways. Firstly, the direct effect of increasing or decreasing the frequency of matings between related individuals, relative to **R**, correspondingly altered progeny inbreeding in the immediate future. As noted in Section 3.3, alternative mating pairs could be evaluated with 100% accuracy for their direct contribution to progeny inbreeding. Secondly, unequal use of boars as parents and slightly higher selection intensities increased the likelihood of higher inbreeding under **MS** alternatives, relative to **R** or **A**. Thirdly, the indirect effect of mating scheme on the future efficiency of selection was also important, as long term changes in inbreeding are ultimately dependent on each mating options ability to influence outcomes at selection (see Figure 2.1). For **MS** alternatives, the resultant inbreeding outcome was a balance of all three factors. For **R** and **A**, however, the frequency of matings between related individuals and selection accuracy were the principal causes of differences in inbreeding.

Overall, **A** and **MS1-MS3** mating alternatives increased, and **MS4-MS5** alternatives decreased, total levels of inbreeding from that achieved under random mating. However, it was not obvious from this study which non-random mating scheme would consistently result in the highest response in aggregate merit and acceptable (low) levels of inbreeding. At least for BI, it appeared beneficial in terms of selection response to assign some merit to less inbred litters (Table 4.11: **MS1** vs **MS3**). The reduced inbreeding under **MS4** relative to **R** indicated that the penalty placed against progeny inbreeding was sufficient to offset unequal boar use and higher selection intensities under the indices examined. In contrast to results for **MS5**, this outcome was achieved without significantly reducing response relative to random mating.

4.5 Conclusions

In this study, several variables contributing to response and inbreeding under multi-trait breeding programs were examined. These included: underlying breeding objective and index formulation, method of genetic evaluation, and mating scheme employed thereafter. Overall, results showed that improved accuracy of genetic evaluation under BLUP increased both response in aggregate merit (16%-19%) and inbreeding (42%-150%) relative to that achieved using a traditional selection index (random mating). Relative gains in individual traits contributing to aggregate merit differed according to index, as expected. In addition, relative gains in individual traits under the same breeding objective differed according to the method of genetic evaluation. These results were consistent with those of other multi-trait selection studies (De Roo, 1988; De Vries, 1989; Roehe et al., 1992). In comparison to the effects of selection criterion, choice of mating scheme thereafter had relatively less impact on aggregate response. However, mating scheme could significantly alter response in individual traits contributing to aggregate merit, as well as levels of inbreeding accumulated at comparable levels of response.

Traits simulated in this study were number born alive (NBA), average daily gain (ADG) and P2 backfat (BF), where BF was simulated with an underlying scale effect. These traits are commonly directionally selected in pig breeding programs. Information from each was combined under breeding objectives representing general purpose (GP), terminal sire (TS) and maternal (MAT) selection lines. Overall, characteristics of indices formulated were too similar to result in marked differences in inbreeding under a given selection criterion and mating option. However, breeding objectives were characterised by differing levels of selection emphasis placed on NBA. Thus, the emphasis placed on family information for at least one trait in the breeding objective differed across indices. This appeared to have a slight, but not significant, impact on results for inbreeding. Results for all index types were presented in order to illustrate general implications of index type on selection and mating outcomes.

Averaged over indices, relative improvements in response of individual traits under BLUP were greatest for NBA (36%) and ADG (28%). BLUP has a larger impact on response in lowly heritable and/or sex-limited traits relative to more highly heritable performance tested traits (Sorensen, 1988). In contrast, response for BF was reduced by 9% under index selection (random mating), although this conflicted with the 8% improvement in response for BF noted under single-trait EBV selection for BF (Table 4.7: Schemes 6 vs 9). In the absence of conflicting evidence, reduced response in BF under BLUP index selection was thought to result from biased evaluations and unfavourable changes in covariances between ADG and BF in the presence of a scale effect. Thus, the influence of the simulated scale effect made it more difficult to predict selection outcomes for this trait. Overall, differing results for individual traits under index selection may decrease the predictability of overall response in aggregate merit for selection alternatives.

Mating systems using information on genetic merit to allocate mates (**A** and **MS1-MS4**) increased response in aggregate merit relative to random mating. Maximum differences in aggregate response between random and non-random mating options were no more than 6% under traditional index selection and up to 9% under a BLUP index, where accuracy of selection was higher. Compared to assortative mating, it was possible to achieve further improvements in response while reducing inbreeding using mate selection. However, relative response for individual traits differed according to mating scheme. For example, assortative and **MS1-MS4** mating schemes increased response in ADG and BF (1%-12%) but decreased response in NBA by 1%-37%. Gains in production traits under non-random mating reflected their larger contributions to index variation in selected individuals. Where NBA contributed more to index variation (maternal BLUP index), **A** and **MS1-MS2** also increased relative response for this trait. Placing an artificially higher economic weight on NBA may counteract undesirable negative gains in this trait.

In comparison, **MS5** decreased response to selection in all traits included in the objective. Reduced accuracy of selection under BLUP in this study (Table 4.10) and lower selection differentials (De Roo, 1988a; Hill, 1985) acted to lower relative response. Reductions in NBA under **MS5** were greater than losses in ADG or BF. Selected individuals more related to each other were likely to be so because of family information contributing to index values or EBVs for NBA. Hence, avoiding matings between related individuals decreased the frequency of matings made by boars superior in merit for NBA. Avoiding matings between relatives is a common method for controlling inbreeding in pig breeding. Thus, it may be speculated that where family information is used to evaluate genetic merit for this trait, gains in NBA are hindered in reality by this practice. Alternative reasons for reduced response in NBA were suggested by Haley (1989).

The most appropriate weight to place on avoiding progeny inbreeding was not identified in this study. Similar levels of response in aggregate merit were obtained over a range of penalties (**MS1-MS5**), suggesting that response under index selection was quite robust to different mating practices. However, overall response in aggregate merit masked differences in response of individual traits under non-random mating. Thus, individual trait characteristics were important determinants of relative response under the same breeding objective for different selection and mating options. Overall, results indicated that adjusting index merit for additive relationships would be useful for jointly manipulating response and inbreeding in practical applications. However, outcomes may be less predictable as a result of variable individual trait contributions to merit.

Two problems not directly examined in this study were highlighted in the above paragraphs. Firstly, relative gains in component traits differed under the same breeding objective according to method of genetic evaluation (ignoring results for BF). This implies that where particular trait gains are desired, more frequent re-evaluation of breeding objectives may be required under BLUP based programs. Further, scale effects were poorly dealt with using multi-trait BLUP under divergent selection for ADG and BF. Thus, it may be expected that traits influenced by real scale effects will also result in biased EBVs. These areas were not further dealt with in this study, although it is recognised that they have practical implications for breeders.