Chapter 1

General Introduction

In recent years, Best Linear Unbiased Prediction (BLUP) has become widely accepted as the method of choice for genetic evaluation. Many countries have implemented genetic evaluation procedures based on BLUP. In Australia, these include industry specific systems such as BREEDPLAN (beef cattle) and PIGBLUP (pigs). It is generally accepted that use of BLUP maximises accuracy of selection, although the relative superiority of BLUP in selection response varies according to trait characteristics (Sorensen, 1988), population size (Roehe et al., 1993), data structure (Wood et al., 1991a, 1991b), and attitudes to inbreeding (Quinton et al., 1992). Of concern to breeders is the increased potential for inbreeding with BLUP, which results from greater use of family information in the prediction of genetic merit. These concerns may be very real for pig breeders, who work with a fecund species in which high selection intensities and short generation intervals are achievable. In addition, BLUP is most useful for improving response to selection in lowly heritable traits, but it is this scenario which results in the highest levels of inbreeding.

The potential benefits of BLUP to pig breeding have been examined using simulation of single trait (Belonsky and Kennedy, 1988; Sorensen, 1988; Wray, 1989) and multiple trait (Roehe et al., 1993) selection programs. In addition to illustrating the magnitude of improvement in selection response with BLUP, these researchers also provided evidence of greatly increased rates of inbreeding within closed herds. This result was apparent under random mating and/or where matings between close relatives were avoided. Thus, a concern to pig breeders is that high levels of inbreeding associated with BLUP selection may not be effectively contained with commonly used mating policies. Further, inbreeding depression and reductions in genetic variation resulting from inbreeding may limit the performance of their breeding programs. Quinton et al. (1992) show that at constant levels of inbreeding, selection response is lower for BLUP than other selection methods.

Despite concerns of increased inbreeding, BLUP technology has been implemented in the Australian pig industry (Long et al., 1991). Taken in context, inbreeding is particularly important with selection in closed herds. Herds open to immigration or with a large genetic base will find inbreeding under BLUP presenting fewer problems to an ongoing selection program. For example, Hubbard et al. (1990) observed small increases in inbreeding over ten years for herds involved in the Canadian Swine Improvement program. Free transfer of genetic material between a large number of herds contributed to this result. Within this program, however, some herds were experiencing high levels of inbreeding. Thus, inbreeding may still warrant attention within herds.

Methods to contain rates of inbreeding in closed breeding programs, while using BLUP or index values for selection, have subsequently been examined by Grundy et al. (1994), Klieve et al. (1994), Toro and Nieto (1984), Toro and Pérez-Enciso (1990), Toro and Silio (1992), and Wray and Goddard (1994). Methods include those which help to minimise the impact of selection on inbreeding, as well as those which act to constrain the accumulation of inbreeding within the selected population. However, many of these studies have applied methods to relatively rigid population structures. It is thus not possible to demonstrate methods which may be applicable to the more dynamic nature common to pig breeding enterprises, which operate under a number of constraints. Further, the above studies generally concentrate on single trait selection. Of more interest to breeders is the multiple trait situation, where criteria may be combined into a variety of breeding objectives.

This thesis is primarily concerned with development and evaluation of mate selection procedures which attempt to maximise objectives containing information on inbreeding and genetic merit. The aims were:

- to develop simulation software containing components of 'realistic' constraints for examining breeding program options in a closed pig breeding nucleus.
- to develop and evaluate mate selection procedures which may be used to jointly regulate inbreeding and response to single trait selection.
- to expand the above to simulate traits commonly of interest, and examine the implications of selection and mating alternatives for multiple trait breeding programs.

In Chapter 3, details of simulation procedures and results for single trait studies are presented. The criterion for selection was either individual performance or an estimated breeding value for a single trait ($h^2 = 0.1, 0.35$ or 0.6). Assortative mating and five mate selection algorithms were compared to random mating.

Single trait studies were a precursor to developing multiple trait procedures. Details of these procedures and results are presented in Chapter 4. In this study, the commonly recorded traits average daily gain (ADG), backfat (BF) and number born alive (NBA) were simulated, and information from each trait used to generate an index value for three different breeding objectives. As above, two selection procedures were employed: based on individual performance (or performance of dams for NBA) or an EBV for each trait, combined into the appropriate traditional or BLUP index values respectively. The effects of mating alternatives on response to selection (aggregate response and for individual traits) and inbreeding were evaluated for each selection criterion.

The study is concluded in Chapter 5 with a general discussion, and a brief summary of implications for breeders. Firstly, however, a detailed review of the literature identifying important factors which influence response to selection is presented in Chapter 2.

Chapter 2

Improving Response to Selection

2.1 Introduction

Breeders continually seek more efficient methods for maximising genetic gain achieved within their breeding herds, since increased productivity, competitive position and profit are perceived as likely outcomes of genetic improvement. Classical quantitative genetics theory has become the foundation on which the principles of genetic improvement in animal breeding populations are based. However, it should be recognised that some assumptions intrinsic to classical theory limit the accuracy of extrapolating predicted theoretical outcomes of selection to that achieved in reality. Applied quantitative genetics theory, as such, must deal with several considerations relevant to practical limitations which affect response to selection within animal breeding enterprises.

There are several areas in which the breeder has input into the running of a breeding program. Quantitative genetics theory enables the breeding strategy to be developed, and theoretical outcomes to be predicted for alternatives. However, realised outcomes of a breeding strategy will be dependent on operational aspects of the breeding program, resources available to the breeder, and genetic factors known to affect response to selection. Operational aspects of a breeding program are depicted in Figure 2.1. Of interest in this review is the impact of genetic evaluation, selection

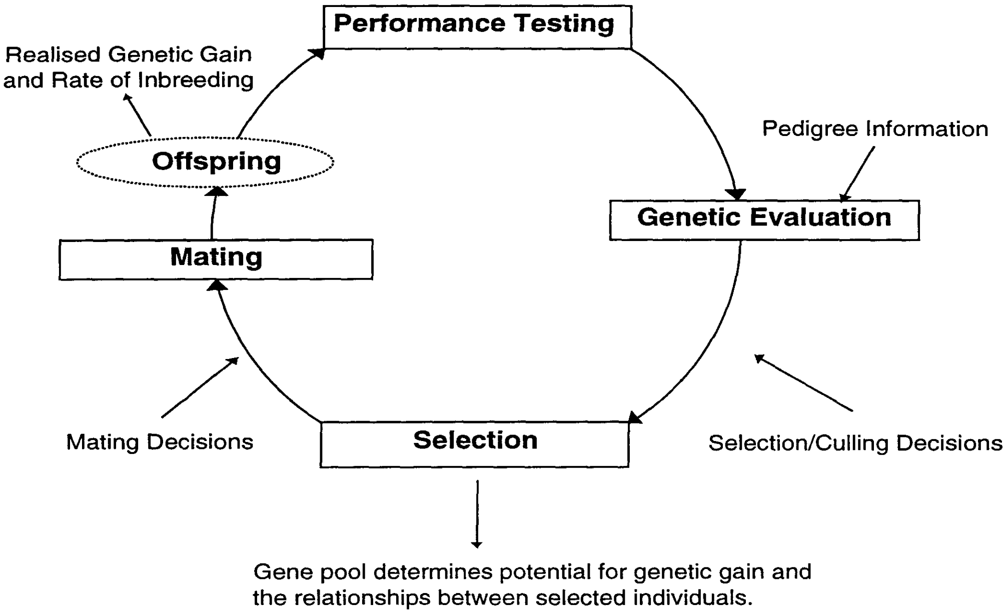

Figure 2.1: Operational aspects of a breeding program.

and mating decisions on selection response and rates of inbreeding. Although performance testing procedures may be important in that they influence accuracy of measurements, traits measured and the individuals tested, it will be assumed in this study that performance testing is not a limiting factor reducing potential response to selection. Hence, performance testing considerations are not reviewed.

Of primary interest in this review are the genetic consequences of applying a breeding program to populations of relatively small size. Classical response theory assumes populations of infinite size, genetic parameters which remain constant, negligible impact of selection itself on genetic parameters, and therefore constant and linear rates of selection response. However, these assumptions are invalid in animal breeding populations for several reasons. Firstly, genetic variation is depleted within finite populations over time due to the effects of genetic drift and inbreeding, even in the absence of selection. Secondly, both population size and family structure influence selection differentials through their effects on the partitioning of variation for quantitative traits. Thirdly, the selection process itself may directly deplete genetic variation. The above considerations, and their relative importance, are discussed in detail in Section 2.2 following a brief introduction to classical response theory.

Further to the direct effects of inbreeding on genetic variation, the joint effects of selection and inbreeding on genetic variation are discussed in Section 2.3. In this section, inbreeding depression is also examined, given that considerable evidence exists for depressed performance of inbred individuals over non-inbred individuals within both selected (Bereskin et al., 1968; Bereskin et al., 1970; Takahashi et al., 1991) and unselected (von Krosigk and Lush, 1958) populations. Inbreeding depression may reduce the accuracy of selection by masking additive merit for inbred individuals. In addition, the mean performance of an inbred population for traits sensitive to inbreeding depression is expected to decline, although the magnitude of this effect will depend on prior selection history (Pirchner, 1983). Further, inbreeding depression may detrimentally affect selection intensities by reducing reproductive fitness. Although the effects of inbreeding depression may be a reality, in later sections it is usually assumed that the effect of inbreeding on genetic variation is of greater relative importance, since it is difficult to precisely quantify inbreeding depression for different populations.

Following discussion of genetic effects known to influence response to selection, areas in which the breeder may act to manipulate the genetic composition of the breeding population are examined. From Figure 2.1, these include decisions made at selection or mating, as well as choice of the genetic evaluation system. Classical theory most accurately deals with a simple scenario, where selection is on individual performance and mating is at random. However, in practice breeders may choose to maintain only approximate random mating systems by allowing the avoidance of particular undesired matings (eg. between related individuals or for corrective mating purposes). Further, it is possible to create specific regular mating systems which are designed to use differences or similarities between selected individuals. For example, deliberate inbreeding, inbreeding avoidance and assortative mating systems have been evaluated by several authors as methods for manipulating the level of genetic variation or it's partitioning, and as tools for improving genetic gain. Section 2.4 reviews random and non-random mating systems, with the aim of examining the impact of non-random mating systems on additive genetic gain. Of particular interest is the impact of alternative mating systems on the efficiency of selection, since non-random mating systems alone do not provide increased genetic gain (Goddard, 1983).

In Section 2.5, the concepts of non-random mating systems are expanded to include mate allocation and mate selection procedures. Regular mating systems evaluated in Section 2.4 usually imply a structured approach to define mating systems, following *a priori* truncation selection of superior individuals. However, mate allocation and mate selection procedures accommodate unstructured techniques for defining the most appropriate matings, by reducing mating decisions to the level of paired merit of selected individuals through mate selection rules. In addition, it is possible to use paired merit for unifying selection and mating decisions into one process. This approach is commonly known as mate selection, and may also be associated with relaxing truncation selection procedures assumed in classical theory. Kinghorn (1987) noted that selection and mating of specific pairs is only appropriate when this approach changes the mean merit of the progeny or variance among progeny. This aspect is examined in terms of selection response for several scenarios where mate selection rules would appear appropriate.

In addition to altering mating systems, the breeder may choose to use genetic evaluation systems which provide alternative selection criteria to individual performance measures. In Section 2.6, alternative genetic evaluation systems are discussed, since these influence accuracy of selection, the impact of different mating systems, and subsequently selection response. Breeders have traditionally relied on the development of more efficient genetic evaluation procedures to aid in selection decisions. It may be argued that increasing response to selection is more easily achieved by maximising the correlation between estimated and true breeding value ($r_{\hat{A},A}$) since selection intensity and genetic variation may be hard to manipulate in practical animal breeding applications. Moreover, maximising additive genetic merit is mostly obtained from selection, since contributions of individuals to progeny merit are independent of their mate under a purely additive mode of inheritance (Allaire, 1980). For these reasons, research emphasis for practical animal breeding applications has been focused on improving genetic evaluation procedures. However, accuracy of selection may impact on other factors which affect selection response; for example, rates of inbreeding and the efficiency of different mating systems applied post selection. These factors must also be considered for long term selection response.

In the Section 2.7, brief conclusions are drawn as to the relative contributions of various factors to genetic improvement, and the breeders ability to direct the genetic properties of a population towards a favourable outcome. Given the cyclical nature of events in a breeding program, as shown in Figure 2.1, it should be obvious that the decisions breeders make to improve selection response will not be entirely independent of each other. As such, the aim of this review is to highlight methods which may be employed to alter the genetic properties of a population, and factors which may affect their efficiency, while keeping in mind that interactions between breeding program operations may be important.

2.2 Factors Affecting Selection Response and its Prediction

In animal breeding enterprises the breeder may act to influence the genetic properties of the breeding population in two main ways (Falconer, 1981): through selection of particular individuals for breeding and; through choice of which individuals to mate together. Predicted response to selection is the benchmark by which breeders can compare alternative breeding programs, which may differ in population structure, intensity of selection and selection criteria. With the introduction of new technology to animal breeding (eg. multiple ovulation and embryo transfer (MOET), sex determination, Best Linear Unbiased Prediction (BLUP)), more options for breeding program design become available. If these are to be evaluated precisely it is necessary that predictions are accurate over the appropriate time span. An understanding of the factors which influence response to selection will aid in this process. The implications of alternative mating systems will be discussed in Sections 2.4 and 2.5.

2.2.1 Classical Response Theory

For a single generation of selection, classical quantitative genetics theory predicts response to selection for a trait under purely additive genetic control as:

$$R = ir_{\hat{A},A}\sigma_A \tag{2.1}$$

where i is the overall selection intensity (standardised), $r_{\hat{A},A}$ is the correlation between the estimated and true breeding value (accuracy of selection), and σ_A is the genetic standard deviation of the selected trait. In populations with overlapping generations and a stable age structure, equation 2.1 may be expanded to give the approximation:

$$R_{yr} = \frac{ir_{\hat{A},A}\sigma_A}{L} \tag{2.2}$$

where R_{yr} is the selection response per year, i, $r_{\hat{A},A}$ and σ_A are defined as previously, and L is the average generation interval. Cumulative response to recurrent selection in both cases is then simply the summation of response for each round of selection.

These predictive formulae clearly indicate potential methods available to the breeder for improving selection response. From a classical viewpoint, response to selection would be enhanced at high selection intensities and low generation intervals (limited by reproductive capabilities of the species), where additive genetic variation is large, and where selection criteria are accurate indicators of true genetic merit. Breeding program design could be optimised for the relationship between i and L by maximising the ratio i/L. The breeder may also increase accuracy of selection by using improved genetic evaluation techniques. However, manipulation of genetic variation for the selection criteria and objectives within the structure of a breeding program is less easy to achieve (Hohenboken, 1985).

Equations 2.1 and 2.2, however, are precise only under several very simplifying assumptions. These include: trait expression controlled by an infinite number of genes of small effect and no linkage (the infinitesimal model) and normally distributed; an additive mode of inheritance allowing for dominance but not epistasis; infinite population size; strict truncation selection and discrete generations; random mating; no mutation or migration; and constant genetic parameters and (co)variances over time. These assumptions are rarely relevant for animal breeding applications. Several researchers have shown, through both simulation and experimental results, that classical response equations may considerably overestimate selection response, particularly over long time horizons, due to declining genetic variation and rates of response. Finite population size is in obvious breach of the classical assumptions which must be addressed, even if other assumptions hold. Mutation and migration will not be discussed in this review.

2.2.2 The Effects of Finite Population Size

Finite population size introduces the concepts of inbreeding and sampling effects associated with genetic drift, which influence genetic variation and the calculation of selection differentials. These considerations are not accounted for in simple classical theory.

Genetic Drift

The phenomenon of genetic drift is associated with finite population size due to the sampling of a restricted number of parents in each generation. This has two immediate ramifications intrinsic to genetic drift; only a finite number of gametes will be sampled from the parental generation and; the number of matings will be limited. Sampling a finite number of gametes is associated with random changes in gene frequencies in the parental generation. Additionally, the limited number of matings between these parents will result in some realised correlations of gametic effects and accumulated inbreeding even if selection is not carried out (Gill, 1965). Through random changes in gene frequencies and the chance loss or fixation of particular alleles within the population, resulting in increased homozygosity, the net effect of genetic drift is to decrease genetic variance over time.

Genetic drift resulting from finite population size has several implications for animal breeders. In small populations undergoing artificial selection, drift is an important source of variation in selection response around the predicted value due to creating changes in additive genetic variance available for selection over time (Avery and Hill, 1977; Hill, 1985a). In particular, the effects of drift and associated loss of genetic variance become important factors influencing long term response. For discrete, random mating populations, loss of genetic variation due to drift accumulates in proportion to the average inbreeding coefficient, F. For an idealised population, drift variance would be proportional to t/N_e, where t is the generation number and N_e is the effective population size (Hill, 1985a). Further, the inbreeding component of drift may be associated with phenotypic depression of performance traits and reduced selection response.

Genetic drift may be minimised if population size and the number of loci controlling the trait are large. In this situation the likelihood of chance gene fixation or loss and changes in gene frequencies is much lower, particularly if selection intensity is low. Similarly, large population size may reduce the frequency of chance matings between related individuals, reducing the rate of inbreeding due to finite population size. Hence, the variability of selection response and additive genetic variance may be reduced. For populations subject to artificial selection, Nicholas (1980) presented methods for calculating the population size required to reduce the effects of drift to more acceptable (lower) levels. Large populations were found to be required if observed and expected response were to be comparable over short time periods.

Selection Differentials

The second effect of finite population size is statistical in origin and related to the processes of selection. With infinite population size, selection differentials may be calculated with minimal error from normal distribution theory as parameters are constant and samples are uncorrelated. The *genetic* selection differential is then derived using knowledge of trait heritability. Selection differentials for finite populations, however, are reduced due to the indirect consequences of sampling and selection, which deplete genetic variation through drift, changes in family structure and the accumulation of inbreeding (Robertson, 1961). Finite population size may be allowed for using order statistics or appropriate approximations (Burrows, 1972) but, as discussed by Hill (1976, 1985a), under selection it is also necessary to take into account family structure within a breeding population when calculating selection differentials.

Following Hill (1985a), for a population of size M individuals and n families of equal size, there are n sets of correlated variables and M/n samples of family effects. The correlation of performance traits between family members further increases over time due to inbreeding, so samples will become increasingly correlated, thereby reducing selection differentials over time. The *genetic* selection differential may be further reduced from that expected due to a restricted number of families. Further, family structure may be manipulated by the breeder, usually in an effort to control inbreeding, which will also impact on the calculation of selection differentials. This may be seen as an effect on V_A as noted by Till (1986).

Hill (1976, 1985a) determined that the selection differential is most affected by family structure when the intraclass correlation (r) of family members is high. This may result in more intensive selection between families, resulting in increased variation of family contributions to future generations. For selection on criteria using family information, higher r values will almost certainly reduce selection differentials from those expected, particularly when selection decisions are made within small contemporary groups of a large population (eg. pig breeding). In many situations, however, high intraclass correlations are unlikely and the effect of finite population size on selection differentials will be small.

High intraclass correlations are also closely associated with increased rates of inbreeding and subsequent loss of genetic variation (Keller et al., 1990). Increased inbreeding may act indirectly to reduce selection intensity through decreasing fertility, and subsequently the number of animals available for selection. Davis (1987) predicted that this would have a relatively small effect on response to selection. Conversely, Hill (1985a) noted that manipulating family structure to control inbreeding may significantly influence selection differentials. As such, the relationship between inbreeding and selection differentials may be important, particularly in the presence of inbreeding depression. This is discussed in more detail in Section 2.3.

Overall, Keller et al. (1990) found that adjusting calculated selection differentials for population size and structure had a small but constant effect on improving predicted selection response. With increasing r associated with inbreeding this modification became more important. Hence, correcting for family structure is more important at higher selection intensities in very small populations (Till, 1986). The correct calculation of selection differentials, however, appears considerably less important for predicting selection response than the effects of gametic phase disequilibrium, inbreeding, inbreeding depression, and sampling losses due to drift (Keller et al., 1990).

2.2.3 Additional Effects of Selection on Genetic Variation

In addition to the effects of drift (inbreeding and sampling effects) on genetic variation, selection itself may also influence genetic parameters in several ways. Selection may directly affect genetic variation through changing gene frequencies at selected loci. If the number of loci is large and the magnitude of gene effects is small, as is implied by the infinitesimal model, then this effect will be negligible and can be ignored (Crow and Kimura, 1970). Selection also results in gametic phase disequilibrium, known as linkage (Bulmer, 1971) or selection disequilibrium, which acts to reduce between family genetic variation. Indirectly, selection may result in increased rates of inbreeding above that of an unselected population of equivalent size, introducing the potential for phenotypic depression. The effects of inbreeding on genetic variance and selection response will be discussed in more detail in Section 2.3.

Disequilibrium

Gametic phase disequilibrium generated as a consequence of selection is an important factor resulting in a direct reduction of genetic variance for selected traits (Bulmer, 1971; Bulmer, 1976; Gomez-Raya and Burnside, 1990). Assuming an infinitesimal model, selection will reduce additive genetic variation through the generation of negative covariances between genotypic values at different loci. As such, the probability of all pairs or groups of loci having equal joint representation in selected animals is lowered since selection favours particular genotypes. This directly reduces genetic variation in the selected parental population, and hence in their progeny, although offset to some extent by recombination during meiosis. Within a few cycles of recurrent selection, loss of genetic variation due to disequilibrium becomes balanced by regeneration of variation through recombination. The net effect is a temporary reduction in genetic variation which will be maintained under ongoing selection.

If selection was relaxed, and disequilibrium was the only factor influencing genetic variation, recombination would reduce the covariance between loci and genetic variation would return to its original level (Bulmer, 1971). However, in animal breeding populations subject to recurrent selection, disequilibrium, along with inbreeding, is an important contributor to loss of genetic variation available for selection. Permanent reduction in genetic variation due to selection is dependent on the number of loci involved, with increasing effect as locus number decreases. If the number of loci is large then the effects of selection disequilibrium will be of greater importance than the potential for permanent reductions in genetic variation (Bulmer, 1971). Disequilibrium may also be expected to reduce genetic variation in traits genetically correlated with the selected trait.

Diminished genetic variation due to disequilibrium may reduce heritability and accuracy of selection, and subsequently response to selection. The proportional decrease in selection response due to disequilibrium is mediated through it's influence on genetic variation, which is dependent on the original heritability in the unselected population, accuracy of selection, and selection intensity. With increasing heritability, both the absolute and proportional loss of genetic variation due to disequilibrium is amplified. With increased accuracy of selection (eg. through BLUP genetic evaluation) loss of between family genetic variation may also increase (Gomez-Raya and Burnside, 1990). The effect of increasing selection intensity is marginally less (Keller et al., 1990).

Using a deterministic approach, Keller et al. (1990) compared, separately and jointly, the relative importance of the effects of drift, inbreeding, calculation of selection differentials and disequilibrium on selection response. In this study, disequilibrium was found to be the dominant factor reducing selection response in early generations of selection until loss in genetic variation due to this cause stabilised. Interestingly, population size had little effect on loss of genetic variation due to disequilibrium when selection intensity was constant. This may not be the case when larger population size facilitates more intensive selection. However, when all factors were considered jointly, the magnitude of effect of any one factor is reduced due to interactions between factors in their effects (Keller et al., 1990).

2.2.4 Predicting Selection Response in Finite Populations

Classical equations overpredict achievable genetic gain by assuming uncorrelated sampling, constant genetic parameters and therefore constant rates of response. As such, they are only strictly appropriate for predicting response to one generation of selection. In finite populations, the relative merit of different selection schemes will be altered by prior selection (Wray and Hill, 1989). Rates of response in this scenario thus reflect diminishing returns to selection until an asymptote is reached, where approximately constant rates of genetic gain are expected. Unlike classical theory, maximum response then does not equate with maximising the ratio of i/L. Alternative approaches to classical theory attempt to account for the joint effects of finite population size, selection and inbreeding simultaneously for each generation of selection. Methods to predict selection response may be recursive, considering the effects of the previous generation of selection only (Verrier et al., 1991), or asymptotic, where the impact of all prior generations of selection may be accounted for (Wray and Hill, 1989).

Verrier et al. (1991) presented a recursive method for predicting selection response which addressed the joint effects of selection and drift on genetic variation. The authors found that accounting for selection disequilibrium, inbreeding and sampling effects simultaneously greatly improved accuracy of predicting selection response over alternative methods which consider these effects independently. Loss of genetic variation due to the effects of selection was maximal in the first generations, with sampling considerations prevalent in later generations (Verrier et al., 1991). In contrast, Keller et al. (1990) found that although disequilibrium had a major impact on selection response in early generations, reductions in genetic variation due to inbreeding accumulated linearly over time, and sampling effects equilibrated to a constant level.

Verrier et al. (1991) attributed this phenomenon to loss in selection accuracy as genetic variation declined, reducing the future impact of selection on genetic parameters. Additionally, the relative impact of sampling losses at later time periods will be increased as covariances between family members increase, while accuracy of selection may further decline due to this effect. Dekkers (1990) showed how accuracy of selection declined under selection due to loss of between family variation and subsequently the increasing value of selection within families. This effect was amplified with increased use of pedigree information. As such, improving the accuracy of selection would be partially offset by the detrimental effects of selection on genetic variation. This would result in lower rates of selection response than expected. This theory is indirectly supported by the results of Keller et al. (1990) who found that the joint inclusion of all factors known to influence selection response reduced the cumulative magnitude of effects from that summed over each factor considered separately.

Recursive methodology illustrates changing response rates over time, which may be valuable for economic comparisons of alternative selection schemes where discounting is considered. An alternative view held by Wray and Hill (1989) is that predicting asymptotic rates of response, and hence the equilibrium rate of genetic gain, provides a more valid comparison between alternative breeding programs. The same authors, however, also found that the ranking of alternative schemes was not greatly affected by differences in approach, and it is likely that both viewpoints are useful in practice. Of more interest to animal breeders may be the relative rates of response in the short and long term, and the relative importance of factors which affect selection response over the time frame of a breeding program.

The effects of selection and genetic drift have been shown to contribute to reduced selection response, particularly for small populations subject to selection over long time horizons. The factors discussed highlight the weaknesses of the assumptions on which classical formulae are based. If predictive formulae are to accurately assess the impact of more complex situations of practical importance, such as selection from overlapping generations, non-random mating systems and selection with information from relatives, then these factors must be adequately accounted for.

2.3 Inbreeding

Inbreeding is most simply defined as the mating of individuals which are related by common ancestry. In populations of restricted size the sampling of a finite number of parents, and therefore a limited number of possible matings and independent ancestors, will result in inbreeding even in the absence of selection. In addition, parents do not have equal probabilities of contributing to the next generation due to differences in inherent fertility, fecundity and progeny survival (Robertson, 1961). Rates of inbreeding may be further increased under selection due to the superiority of certain individuals for the trait(s) of interest, influencing the probability of their offspring and other descendants being selected in future generations (Wray et al., 1990). Even if selected parents contributed equal numbers of progeny to the group of individuals measured, variation in the progeny between families would result in unequal representation of families in the following generation (Robertson, 1961). Hence, inbreeding coefficients would be greater than those of an unselected random mating population of equivalent size due to a lower effective population size (N_e) than expected from the actual number of parents selected (N).

Inbreeding has two distinct consequences: 1) increased homozygosity of loci due to the accumulation of genes which are identical by descent, and 2) random changes in gene frequencies associated with genetic drift. This has several implications for animal breeders if the accumulation of inbreeding is appreciable. For example: within selection lines additive genetic variation is reduced; performance of related animals for quantitative traits will become increasingly correlated (assuming no changes in non-genetic components of variance) and; for traits subject to dominance, inbreeding depression may occur. In addition, increased homozygosity may be reflected by increased frequencies of lethal or deleterious genes (Biémont, 1991; Pirchner, 1983). For a given population, however, the realised effects of inbreeding will be dependent on the sample of individuals in the founder population and potentially the mechanisms by which inbreeding accumulated (Ehiobu et al., 1989; Hohenboken et al., 1991).

In contrast to selection, which results in depletion of between family genetic variation, inbreeding is associated with loss of within family genetic variation due to increasing covariances between mates. As such, inbreeding may act as an antagonist to maximising genetic gain through its direct effects on genetic variation, by influencing the accuracy of selection, and potentially phenotypic expression of traits. Additionally, increasing homozygosity through inbreeding under selection is not only confined to loci controlling the selected trait(s), but to all loci (Robertson, 1961). This has important implications for traits related to fitness. As mentioned in Section 2.2.2, reduced reproductive performance due to inbreeding may reduce selection differentials. This effect may be exacerbated if survival of offspring is further reduced. The effects of inbreeding in the absence of selection were noted in Section 2.2. In Section 2.3.1, the effects of inbreeding in the presence of selection are addressed.

2.3.1 Loss of Genetic Variation Due to Inbreeding

In a population of infinite size, and in the absence of other factors which affect total genetic variation, additive genetic variation (V_A) is defined by the total genetic variation such that $V_A = V_G$. In this scenario, V_A is equally distributed both between (b) and within (w) families in progeny generations as $V_{A_b} = V_{A_w} = \frac{1}{2}V_A$. For random mating populations of finite size, however, loss of additive genetic variance declines linearly with the average inbreeding coefficient according to:

$$V_{A_t} = V_{A_0}(1 - F_t)$$

where V_{A_0} is the additive genetic variation in the base population, and V_{A_t} and F_t are the additive genetic variation and the average inbreeding coefficient at generation t. With slow inbreeding, solely as the result of finite population size under random mating, the equal partitioning of V_A within and between families is undisturbed (Falconer, 1981). As noted previously, loss of homozygosity due to the inbreeding component of genetic drift for t generations is then proportional to t/N_e, where N_e is the effective population size (Hill, 1985a).

However, with selection the relationship between V_{A_w} and V_{A_b} is modified due to repartitioning of V_A both within and between families through increasing covariances between family members, and gametic phase disequilibrium respectively. Truncation selection of parents reduces parental additive variance by a factor of $1 - h^2k$ (Bulmer, 1971; Falconer, 1981; Keightley and Hill, 1987), where h^2 is the heritability, and $k = i(i - x)$. Here i is the selection intensity and x is the standardised deviation of the truncation point from the population mean. In the progeny generation, V_{A_b} is thus reduced to $(1 - h^2k)V_A/2$ whereas V_{A_w} remains at $V_A/2$ due to recombination (in the absence of inbreeding). In the presence of additional inbreeding generated by selection, V_{A_w} will be reduced from that expected as a result of changing covariances between relatives. The relative magnitude of these opposing effects is difficult to generalise over repeated cycles of selection.

Covariances Between Relatives

Harris (1964) argued that it is not possible to establish in general terms how genetic variation in a population or covariances between relatives will alter with changing levels of inbreeding unless true genetic parameters (eg. mechanism of effects at the gene level) are known. Under a purely additive model and in the absence of selection, increasing homozygosity due to inbreeding would be expected to increase the covariances between relatives for quantitative characters. This is the assumed effect of inbreeding on covariances, as evidenced by use of the numerator relationship matrix in BLUP procedures. Thus, when inbreeding within a line is complete ($F = 1$), all animals would be genetically identical, covariances between relatives are zero, and no further additive genetic variation would be available for selection. This expectation is not always supported by experimental evidence.

With selection, the true dispersion of gene frequencies and subsequent loss of genetic variation may further differ from that indicated by the average inbreeding coefficient due to delayed fixation and therefore a reduced proportion of homozygotes (Falconer, 1981). Should selection favour heterozygotes, loss of additive genetic variation and changes in covariances between relatives may substantially differ from expectation. Moreover, selection combined with deliberate inbreeding will alter the partitioning of genetic variation within and between families. Lush (1947) indicated that deliberate inbreeding would increase the intraclass correlation (r) between breeding values of members within the same family, the extent to which depended on the type of family structure generated. This enabled more efficient selection between inbred but unrelated families due to higher covariances between relatives, reducing V_A below that indicated by covariances alone. This effect is ultimately balanced within breeding populations as inbred families will eventually become related to one another so selection between families is less effective. Loss of additive genetic variance due to inbreeding and selection would then result in reduced heritability and accuracy of selection. Over time, this may reduce the effect of selection on inbreeding and subsequent loss of genetic variation (Verrier et al., 1990).

2.3.2 Inbreeding Depression

Inbreeding depression will only be exhibited if dominance or overdominance is expressed at loci controlling the trait of interest. In an idealised population under the assumption of no epistasis, the magnitude of effects of inbreeding depression due to loss in heterozygosity are linearly related to t/N_e (Hill, 1985a) and the average inbreeding coefficient F. Considerable evidence from animal breeding data exists for inbreeding depression in quantitative traits (Bereskin et al., 1968; Bereskin et al., 1970; Ehiobu et al., 1989; Davis, 1987; Takahashi et al., 1991), in particular for traits related to fitness. Inbreeding depression may affect selection response directly through reducing the mean phenotypic value of the population. Indirectly, inbreeding depression may reduce accuracy of selection, and reduce selection intensities through lowering reproductive rates (potentially of greater impact in uniparous species). The direct effect of inbreeding depression on the population mean is likely to be of greater magnitude than effects on reproductive performance (Davis, 1987). Literature clarifying the effect of inbreeding depression on accuracy of selection does not appear to be available, although it is recognised that predictions of additive genetic merit may be biased (Smith and Maki-Tanila, 1990).

The change in population mean (M) resulting from inbreeding depression is given by Falconer (1981) as:

$$M_F = \Sigma a(\bar{p} - \bar{q}) + 2(\Sigma d\bar{p}\bar{q})(1 - F) \tag{2.3}$$

where p and q are gene frequencies, a and d are genotypic and dominance values respectively, and F is the average inbreeding coefficient. Equation 2.3 shows that the population mean is determined by a linear summation of contributions from independent loci. As such, dominance effects would need to be directional for a high proportion of loci if inbreeding depression were to be exhibited. In addition, loci with intermediate gene frequencies would contribute most to inbreeding depression (Pirchner, 1983).

Animal breeding data generally confirm the linear relationship between inbreeding depression and F. However, significant curvilinear effects have also been found (Takahashi et al., 1991), the reasons for which may be numerous. Firstly, rates of inbreeding tend to be non-linear in early generations of selection (Hubbard et al., 1990) potentially resulting in non-linear changes in M due to non-linear changes in F. Where linear changes in F were ensured with specific matings (Hohenboken et al., 1991), non-linear effects are usually not reported. Secondly, epistasis, interactions between dominance effects of different loci (Crow and Kimura, 1970), or differences in previous selection and breeding history of populations may be indicated (Pirchner, 1983). Thirdly, selection favouring heterozygotes may reduce the degree of homozygosity below that predicted from the corresponding F, reducing the level of inbreeding depression from that expected. Fourthly, considerable variation may exist in the actual level of identity by descent within an individual due to linkage (Weir et al., 1980) and random segregation. This may be exhibited, in part, by differences in performance of highly inbred fullsibs. In addition, under selection removal of inbred lines and/or families which perform poorly is likely, and scale effects at the phenotypic level may assume some importance.

The effects of inbreeding depression at a particular F value may also depend on the rate of achieving that level of inbreeding within a population and/or the types of matings conducted (Biémont, 1991; Ehiobu et al., 1989). Differences in the effects of inbreeding depression due to these considerations may then be attributed largely to sampling processes (influenced by population size and breeding history), although Biémont (1991) supports non- additive gene effects which may relate the effects of inbreeding depression to the phenomenon of imprinting. Regardless of the underlying cause, quantifying the expected level of inbreeding depression associated with a breeding program, and its effects on selection response, may be complicated by these considerations. For this reason, it is usual to compare alternative breeding programs assuming that inbreeding depression effects are non-existent or strictly related in a linear fashion to F. Further discussion in this review is confined to the scenario where inbreeding depression is assumed absent.

2.3.3 Predicting the Effects of Inbreeding

The Inbreeding Coefficient and Rates of Inbreeding

The effects of inbreeding are usually related to the average inbreeding coefficient of a population at generation t (F_t) which is used as an indicator of the expected level of homozygosity within the population on average, and the extent to which individuals are related. Similarly, the coefficient of inbreeding of an individual i (F_i) reflects the probability of an individual having two alleles at any locus which are identical by descent, determined by the average additive genetic relationship between the individuals parents relative to a base population where all genes are assumed to be independently derived (Falconer, 1981). The difference between the average coefficient of inbreeding at generations t and $t+1$, averaged over all individuals produced in these separate generations, then indicates the accumulation of new inbreeding and subsequently the rate of inbreeding, $\Delta F = \frac{F_t - F_{t-1}}{1 - F_{t-1}}$. For examining the consequences of inbreeding relevant to breeding programs it is generally more valuable to compare ΔF for alternative schemes than absolute values of F, since the rate of inbreeding indicates the extent to which relatives are mated together, their average additive relationship, and subsequently the accumulated inbreeding. Inbreeding coefficients are only true indicators of loss in heterozygosity for idealised populations, a constraint overcome when comparing ΔF for alternative breeding programs (Falconer, 1981). Yearly rates of inbreeding are usually considered since generation intervals may be varied for alternative breeding programs.

Under an additive infinitesimal model, it is assumed that F_t, F_i and ΔF indicate the loss in heterozygosity for both selected and neutral loci, although the expectation of F is only strictly valid for loci neutral with respect to fitness (Pirchner, 1983). As such, coefficients of inbreeding may not indicate the true decline in heterozygosity. Considerable variation may exist around these values due to: differing true identity by descent between loci within an individual as a result of linkage; variation between pedigrees for individuals within a population (Weir et al., 1980); and random chance. The variation of inbreeding coefficients within an animal breeding population can usually be attributed to differences in pedigree even with structured mating systems. Variation around F_t also tends to decline with increasing population size (Weir et al., 1980). The variation around F_i due to linkage, however, is less easily quantified. Additionally, selection inducing changes in gene frequencies may alter homozygosity from that expected from inbreeding coefficients alone.

Effective Population Size

The coefficients and rate of inbreeding may be recursively derived from historical pedigree information available in animal breeding programs. However, predicting rates of inbreeding for proposed breeding alternatives is considerably more difficult. Early predictive methods relied primarily on using the relationship between N_e and ΔF. The rate of inbreeding in an idealised population is directly related to population size by (Falconer, 1981): $\Delta F = 1/2N$, where N is the actual number of breeding individuals and ΔF is considered constant. Under non-idealised situations N must be replaced by N_e, the effective population size as calculated from knowledge of the breeding structure of a population. The effective population size is then defined as that which would result in the calculated rate of inbreeding if bred in the same manner as an idealised population (Falconer, 1981). As N_e tends to decline over time with selection, the rate of inbreeding is no longer a constant. The difficulty is, of course, to calculate a valid N_e which describes the true rate of inbreeding within a breeding program over time.

Burrows (1984a) stated that N_e is a convenient summation of the genetic relationships within a selected group as well as the magnitude of drift effects. However, formulation of N_e must take into account the effects of selection on inbreeding. Ancestors of higher genetic merit may generate a selective advantage for their descendants, resulting in more variable family contributions under selection and an increased probability of selecting sibs. Robertson (1961), attempted to include this effect for predicting the rate of inbreeding under individual selection for one generation. Hill (1985b) found the formulae developed by Robertson (1961) considerably overestimated rates of inbreeding when intensity of selection and heritability were high. This was the result of a greater loss in genetic variation under these conditions, reducing the accuracy of selection and subsequently the influence of selection on the rate of inbreeding.

Burrows (1984a, 1984b) expanded the formulation for effective population size (individual or index selection) to include the influences of number of families, family size, selection intensity and intraclass correlations (r) for selection from unrelated families (1984a). This was further developed (1984b) to include relationships between families generated by regular mating systems (which will reduce r), as well as the influence of variable family size. As noted by Wray et al. (1990), for application to animal breeding programs the method of Burrows requires modification for dioecious populations. Moreover, this method tended to underestimate rates of inbreeding due to only considering the selective advantage parents generated for their offspring, ignoring the selective advantage indicated by more distant genetic relationships across generations.

Wray et al. (1990) reviewed various methods for predicting rates of inbreeding and found that one generation methods were inadequate for predictive formulations. Even if random mating was practised, predictions were biased due to (Wray et al., 1990): 1) changing genetic variances and covariances and 2) inherited selective advantage. Selective advantage is not only confined to parent-offspring relationships but also to grandparent-grandoffspring relationships, and so on. That is, grand-progeny of individuals with high genetic merit are likely to be advantaged at selection, the extent to which may not be solely indicated by the merit of their parents. Hence, inheritance of merit is not confined to a one generation perspective. Wray and Thompson (1990) developed a recursive method for predicting the asymptotic rate of inbreeding which accounted for the above two factors. Fundamental to this method was the partitioning of Wright's numerator relationship matrix to establish the additive genetic contributions of ancestors to their descendants, and hence the average genetic relationship between individuals over time. This relationship tends to stabilise and can be related to the asymptotic rate of inbreeding. For a specific breeding program with known hierarchical mating structures appropriate contributions could be predicted using this approach. Asymptotic rates of inbreeding were then recursively derived which accounted for the impact of selection on genetic parameters and increased competitiveness of contemporaries over time (Wray and Thompson, 1990).

The method of Wray and Thompson (1990) was found by the authors to be accurate when compared with simulation results. However, their method is complicated and not easy to apply in practice. Verrier et al. (1990) extended the formulation of Burrows (1984b) to recursively predict rates of inbreeding for dioecious breeding populations. This method allows for the effects of selection on genetic parameters, differing selection intensities between sexes, as well as the selective advantage from parent to offspring, although no higher order relationships are included. The method of Verrier et al. (1990) also proved to be a reliable indicator of rates of inbreeding when compared to simulation results. However, both Verrier et al. (1990) and Wray et al. (1990) concluded that only marginal improvements were obtainable with greater than one generation approaches, despite their theoretical superiority. Moreover, the above methods assumed constant family size prior to selection, a significant disadvantage from a practical viewpoint. Neither method was extended to cases where family index or BLUP EBVs were the selection criterion.

When inbreeding is considered for populations with overlapping generations, rates of inbreeding may be further increased when compared to corresponding populations with discrete generations. This is primarily due to the greater potential for increasing variation in family size should more unequal contributions of selected individuals to the following parental generations occur, and where the probability of mating related individuals is greater. This scenario is more likely when parents produce progeny over several generations, thereby creating the possibility of parent-offspring matings.

Where overlapping generations do not result in an increased lifetime variance of family size, and the same number of individuals enter the breeding population each generation to create a stable age distribution, Hill (1972, 1974) has shown that formulae relating to discrete generations remain valid for populations with overlapping generations. However, expected drift variance and rates of inbreeding are only approached asymptotically with overlapping generations (Hill, 1979).

Prediction of rate of inbreeding through considering calculation of N_e is valuable for several reasons. Alternative breeding programs may be compared in terms of the accumulation of inbreeding, and accurate prediction of response to selection requires knowledge of associated inbreeding. Further, identifying factors which influence rate of inbreeding provides an indication of methods which may be used to minimise the accumulation of inbreeding and it's undesirable effects on selection response. Of note is the paucity of literature recording attempts to predict rates of inbreeding when the selection criterion is not individual performance. However, Wray et al. (1990) postulated that use of family indices as selection criteria would improve the accuracy of predictions with current methods by allowing for environmental correlations between relatives. This has been supported by preliminary simulations (Wray, unpublished results; cited in Wray et al., 1990). Regardless, it is well recognised that the accumulation of inbreeding and hence it's potential impact on response to selection will become increasingly important over longer time frames, increasing selection intensity and accuracy of selection, and with decreasing population size (Keller et al., 1990). As such, deriving methods which allow accurate prediction of rates of inbreeding for these situations is a desirable objective.

2.3.4 Inbreeding Considerations for Selection Schemes

In animal breeding deliberate inbreeding as a selection aid is rarely carried out due to expected losses in response associated with decreasing additive genetic variation and accumulated detrimental effects (eg. inbreeding depression) over time. Specific selection programs incorporating deliberate inbreeding have been favourably evaluated with simulation studies (Berg and Christensen, 1990; Sirkkomaa, 1986). However, the relative efficiency of these systems over random mating was generally dependent on genetic properties (eg. degree of dominance) of the selected population and time scale (Sirkkomaa, 1986). That is, there was little value in pursuing systems using deliberate inbreeding in the absence of dominance and/or over short time scales. These conclusions were supported by Lush (1947), who noted that although cycles of deliberate inbreeding and crossing of selected inbred families increased the efficiency of family or index selection, the gains were insufficient to warrant this approach in animal breeding populations.

As such, where seedstock is produced in closed purebreeding herds, of primary interest to the breeder is the influence inbreeding has on response to selection rather than how deliberate inbreeding may be used as a tool for improving selection response (see Section 2.4.1). In this scenario, the accumulation of inbreeding is usually assumed detrimental and efforts are made to control rates of inbreeding within the selected population.

Control of Inbreeding in Populations Undergoing Selection

Methods for controlling inbreeding in order to alleviate inbreeding effects in a selection program are numerous. Choice of mating strategy applied to selected individuals for the control of inbreeding is carried out by many breeders, and is discussed in the Section 2.4.1. An alternative is to apply restrictions on the choice of individuals selected in order to maximise effective population size. These classifications are, however, somewhat arbitrary since decisions made at selection will impact on the possible mating alternatives, and may also be made jointly (eg. using mate selection strategies). Of concern to breeders is that methods which control inbreeding may not improve response to selection over the time frame of interest.

The most simple approach to lowering rates of inbreeding is to increase the proportion (p) of animals selected and therefore reduce intensity of selection (i). By maintaining a larger number of families the effect of selection on inbreeding, and subsequently loss of genetic variation, is reduced. In addition, at lower selection intensities loss in V_A due to disequilibrium is less (Keller et al., 1990). Increasing the proportion selected, however, may adversely affect selection response in the short term. For example, assuming inbreeding was the only factor reducing genetic variation over time, Robertson (1960) found that response to selection at the limit was maximised when the best 50% of the population were selected. That is, the effects of inbreeding on V_A were minimised at this value and hence response was maximised. Over intermediate time frames, however, the optimum proportion of individuals selected to maximise response at generation t is a function of t/T, where T is the number of individuals measured each generation (Robertson, 1970). As such, where t is relatively low, response to selection would be maximised by intensive selection as loss in V_A due to inbreeding is minimal over short time periods (Keller et al., 1990).

Further difficulties lie with choosing the optimum proportion to select over time when the effects of selection itself are considered. The optimum proportion may be higher than that indicated by t/T due to both the direct and indirect effects of selection which act to deplete genetic variation. Moreover, the choice of proportion may be limited if a particular family structure is to be maintained (Toro and Pérez-Enciso, 1990). Of additional interest is the relationship between i and generation intervals (L). The proportion of individuals selected for a given time interval is not necessarily independent of generation intervals, and both i and L influence rates of inbreeding but to different degrees (Wray and Thompson, 1990). De Roo (1988b) found that at the same proportion selected, choice of the number of boars to use concurrently had a significant impact on rates of inbreeding and selection response as a result of influencing generation intervals. In this study, lengthening generation interval decreased rates of inbreeding, but at the expense of genetic gain, and *vice-versa.* Reduced response was likely the result of failing to maintain expected selection differentials when boars were used for longer time periods. As such, unless selection differentials are maintained, increasing the proportion selected and/or manipulating generation intervals are not the best solutions to counteract the effects of inbreeding on selection response over short to intermediate time frames.

An alternative to increasing the proportion of individuals selected is to alter the genetic relationships between the selected individuals through changing selection practices. Toro and Pérez-Enciso (1990) evaluated the relative efficiency of deliberately lowering accuracy of selection or restricting family size on rates of inbreeding and selection response for index selection criterion. Accuracy of selection was lowered by reducing the emphasis placed on family information in the index. This indirectly reduced rates of inbreeding by decreasing selection between families, and subsequently decreasing variation in family size. Toro and Pérez-Enciso (1990) found that this method did not greatly reduce the efficiency of selection so selection response was largely maintained. Similar results were found by Grundy et al. (1994) for BLUP evaluations using heritability estimates biased above their true value.

In contrast, restricting family size through within family selection resulted in substantial reductions in selection response, despite maintaining higher levels of genetic variation (Toro and Pérez-Enciso, 1990). This was the result of reduced selection differentials imposed by altering family structure to control inbreeding, a consequence noted by Hill (1985a). As variation in family size increased, depending on the amount of within and between family selection allowed, increased rates of inbreeding and loss in genetic variation also occurred (Toro and Pérez-Enciso, 1990). As such, it was concluded in this study that in the short term, restricting family size to control inbreeding reduced selection differentials and response. De Vries et al. (1990) similarly noted that restricting selection decisions to within family may well negate use of family information in predicting genetic merit through reducing selection differentials.

Dempfle (1975) indicated that within family selection is most effective at increasing the selection limit when accuracy of selection is high, in the presence of inbreeding depression, and when significant non-genetic differences between families exist. In practical animal breeding programs, however, selection limit theory is rarely relevant and response is usually assumed to be determined under an additive model. As such, the results of Toro and Pérez-Enciso (1990) assume practical significance. Of interest to the breeder is whether a scenario exists where selection response could be maintained with lower rates of inbreeding using the above approaches. Both Dempfle (1975) and Toro and Pérez-Enciso (1990) showed that reductions in short term selection response, resulting from either within family selection or through reducing variation in family size, were less for traits of higher heritabilities. This was because selection differentials were reduced less at high heritabilities when family structure was altered. As such, these methods may have use in 'short term' animal breeding programs for selection programs aimed at moderate to highly heritable traits, despite the fact that their application will be most useful over very long time periods for maintaining genetic variation, or where inbreeding depression occurs.

Toro and Nieto (1984) proposed a method of selection and mating which combined components of the above-mentioned methods. Their procedure relaxed strict truncation selection to allow the selection of a larger proportion of individuals, increasing effective population size and subsequently reducing rates of inbreeding associated with the selection process. Selection differentials could then be maintained by allowing unequal contributions of selected parents to following generations, as defined by their predicted merit. Variation in family size, however, was fixed at a relatively low level, and matings were chosen to meet this requirement. The authors found that this procedure allowed selection response to be maintained while lowering rates of inbreeding in the short term. In the long term, greater use of superior individuals will reduce the effectiveness of this procedure. This method was expanded to allow for the impact of selection and mating decisions on inbreeding by Wray and Goddard (1994).

Generally it is considered that altering the genetic relationships between individuals of the selected population, at a given proportion selected, will only temporarily alleviate the problems associated with accumulating inbreeding. This is the case regardless of the method used to achieve reduced average relationships, i.e., at selection, mating or a combination of both, and is due to the fact that zero dominance covariance exists over generations. Hence, reducing rates of inbreeding in the short term will be offset in later generations by increased rates of inbreeding. Only through increasing the proportion of individuals selected can the rate of inbreeding remain constant over time. Fortunately for animal breeders, selection goals are usually relatively short term, and temporary alleviation of the effects of inbreeding may be justified, particularly when high selection intensities are desirable and herds are unlikely to remain permanently closed in the long term.

2.4 Mating Systems

Discussion in previous sections has generally assumed random mating systems. Within a random mating population, it is expected that a particular individual has an equal chance of mating with any other individual within the population, and that no specific (dis)similarity, either genetic or phenotypic, exists between mated pairs. For populations of infinite size, and in the absence of differing fecundity and viability of offspring, family size should then be relatively uniform allowing the potential for equal representation of progeny in future parents. Similarly, in a finite population, changes in additive genetic variation due to the effects of selection and inbreeding are usually predicted under the assumption of random mating systems. Classical selection theory encompasses this view.

If only additive inheritance is considered, expected progeny genetic merit is given by the mid-parent value, and the contribution of each parent to this merit is independent of it's mate(s). As such, to maximise total progeny value would only require the selection of genetically superior individuals for breeding, with no necessity to define specific mating pairs (Allaire, 1980). Hence, random mating should be as effective as any other mating system in obtaining response to selection provided general combining ability adequately represents progeny merit. For several reasons, however, differences in selection response will be achieved when random and non-random mating systems are employed. Mating systems may impact on selection response by changing components of variance in the progeny generation, influencing the level and effects of inbreeding, and potentially influencing the effectiveness of selection. Further, using specific mating systems may be useful when non-additive inheritance (eg. inbreeding depression) or economic considerations are important.

Falconer (1981) defines two broad categories of non-random mating. When mating pairs are: 1) related by common ancestry, or 2) preferentially paired according to specific phenotypic (dis)similarities, individuals no longer have equal probability of mating alternative partners. In animal breeding populations some mating of individuals related by common ancestry will be unavoidable even if non-random mating is not deliberately carried out. However, the breeder may also use knowledge of additive genetic relationships, or specific criteria for preferential pairing, for developing deliberate non-random mating systems. Further, mating pairs may be specifically selected according to criteria relating to the expected merit of their progeny (Allaire; 1977, 1980), which may incorporate additive and non-additive components of merit. This particular non-random mating system, incorporating both mating and selection decisions, is often called mate selection and will be discussed in Section 2.5. In this section the effects of non- random mating systems potentially available for use in animal breeding populations will be discussed. Emphasis will be mainly confined to mating systems used within purebreeding herds undergoing selection.

2.4.1 Mating Systems for Exploiting Additive Genetic Relationships

Knowledge of additive genetic relationships is useful for three reasons: 1) as an aid to genetic evaluation; 2) for determining mating pairs/groups to use differences or similarities between genetically related individuals or groups and; 3) for avoiding particular matings which will produce inbred progeny. Genetic evaluation will be discussed in Section 2.6. Aspects of points 2) and 3) follow.

Mating of Genetically Related Individuals

Mating systems which employ the pairing of individuals more closely related by common ancestry than expected under random mating include deliberate inbreeding or linebreeding, also commonly termed simply inbreeding. Linebreeding is a mild form of deliberate inbreeding where pedigrees may be traced back within lines to specific common ancestors who were considered exceptional in genetic merit. Inbreeding in general terms will be discussed as the effects of linebreeding specifically would be similar. A variant, topcrossing, will also be examined.

Inbreeding may be used to separate a population into several closed, unrelated lines, and manipulate additive genetic variation for future selection purposes. In the absence of selection, inbreeding will increase total additive genetic variation within the population from V_A to $(1+F)V_A$ (Falconer, 1981; Hohenboken, 1985). Genetic variation is redistributed between and within inbred lines according to $V_{A_b} = 2FV_A$ and $V_{A_w} = (1-F)V_A$ respectively (Falconer, 1981; Pirchner, 1983). Despite loss of variation within lines, selection and crossing of the best lines at the completion of inbreeding may then provide a large response to a single cycle of selection by using the enhanced between line variation. This result is under the assumption that permanent subdivision of the population into separate sublines allows fixation of desirable genotypes within lines. As such, the effectiveness of specific inbreeding systems is mainly through using differences between lines at selection following inbreeding.

Repetition of this cycle, however, is not likely to achieve rates of gain equivalent to continuous selection combined with random mating. The time lag required for reproducing inbred lines after each cycle of selection reduces the effectiveness of this mating system for improving efficiency of selection (Lush, 1947), although the rate at which differences between lines accrued would depend on the chosen degree of genetic relationships between mating pairs within lines. Further, as the cycle is continued it is likely that subpopulations will become related, reducing differentiation between lines for selection. Additional considerations are the deleterious effects of inbreeding on fitness traits, and the loss of genetic variation within lines for selection purposes. However, inbreeding systems would be expected to reduce the variation in inbreeding within a population due to producing specific pedigree types (Weir et al., 1980). This may be of value for selection purposes in the presence of inbreeding depression, since all groups of contemporaries would be expected to have similar levels of performance depression.

Deliberate inbreeding is unlikely to be appropriate for improving long term selection response in animal breeding populations. Large population sizes and minimal inbreeding within lines would be required to maintain fitness traits and selection differentials. In this scenario, only small gains in total V_A and V_{A_b} will be obtained, and selection between lines will be inefficient. A modification of these approaches is through topcrossing, the mating of highly inbred selected individuals to a randomly bred unselected population (Hohenboken, 1985). However, the value of this approach is also likely to be minimal since selection is only applied to the inbred subpopulation, in which the additive genetic variance is depleted, and consequently selection differentials would be greatly reduced from selecting within the entire population. Topcrossing, however, may be useful when particular progeny genotypes are desired, and are achievable with the use of prepotent sires.

Mating of Genetically Unrelated Animals

Crossbreeding or outbreeding (hereafter termed crossbreeding) between different breeds or inbred lines is the most obvious form of unrelated pairings. Gains in performance achieved from crossbreeding are partly due to alleviating the effects of inbreeding depression in purebred populations, as well as using the genetic diversity found among inbred families, lines and breeds (Dickerson, 1973). However, although progeny from these matings exhibit superior performance in many cases, effective within breed and/or line selection is required for continuous additive genetic gain. In this context, crossbreeding may be useful for producing base populations of greater genetic diversity for future selection purposes (eg. in the formation of synthetics). Of interest to animal breeders, however, may be mating systems designed to control inbreeding and maintain genetic variation when selection is confined to within closed purebreeding populations. In this situation it is perceived that reducing the effects of inbreeding will be beneficial for maintaining future selection response.

Initial impetus to evaluate mating systems for the control of inbreeding was provided by Wright (1921), who concluded that specific regular cousin mating systems led to the lowest decrease in heterozygosity over time. These systems involved the regular mating between the least related individuals, and were termed 'maximum avoidance' systems. Kimura and Crow (1963) noted that although Wright's maximum avoidance systems had the lowest initial rate of decrease in heterozygosity, specific circular mating systems had even lower rates of total decline in heterozygosity. However, the benefit of circular mating systems was unlikely to be realised until significant losses in heterozygosity, and therefore high levels of inbreeding, had already occurred. This was obviously not advantageous in livestock.

The work of Wright (1921), and Kimura and Crow (1963) primarily considered mating systems compared under equal family sizes and in the absence of selection. Additionally, both methods specify particular population structures, with the method of Wright (1921) resulting in permanent sublining of the population. Variable family size has already been seen to contribute to increased rates of inbreeding. When unequal numbers of parents of each sex were bred the efficiency of circular mating systems for reducing inbreeding declined (Kimura and Crow, 1963), as would be expected with random and avoidance mating systems. Unequal numbers from each sex also reduces the available alternatives for structuring the breeding population. Cockerham (1970) provided more general formulations to accommodate unequal contributions in populations subjected to avoidance mating systems. This work also considered population size and it's influence on achievable population structures, variance of family size and the degree of avoidance enabled.

Robertson (1964) generally concluded that there is little advantage gained by avoidance mating systems in the long term, since loss in homozygosity for avoidance systems will be equivalent to loss in random mating systems at the limit. Animal breeders, however, tend to operate over intermediate time frames, and may be advantaged by delaying the appearance of inbreeding. Further, the effects of selection, changing gene frequencies and non-additive considerations have been disregarded on the impact of these mating systems on selection response. De Roo (1988b) and Toro and Pérez-Enciso (1990) found, from simulation studies, that avoidance mating systems did not lower asymptotic rates of inbreeding, but delayed the appearance of inbreeding, resulted in a population of more equally related individuals, and reduced the likelihood of obtaining unexpectedly high inbreeding coefficients compared to random mating. Weir et al. (1980) also indicated that reduction in variation of true inbreeding is a likely consequence of inbreeding avoidance mating systems. In the presence of inbreeding depression, these features alone may be sufficient to encourage use of these systems in animal breeding.

In terms of selection response, however, avoidance mating systems may not improve additive genetic gain. De Roo (1988b) found that response to individual selection was reduced when matings between related individuals were avoided. He speculated that in order to avoid matings between related individuals, more progeny were produced from genetically inferior boars, who tended to have fewer relatives on average in the breeding herd. Further, with unequal contributions from sires, additive genetic variation available for selection was reduced. In contrast, Toro and Pérez-Enciso (1990) found that although avoidance matings greatly reduced inbreeding at generation t, the effects on response to family index selection were affected by trait heritability. At low heritability response was reduced, whereas at higher heritability response to selection increased. This contrast is likely the result of the greater weight on family information at low heritabilities not being supported by sufficiently accurate estimates of a families merit with avoidance matings. In either situation, selection response was more variable than that achieved under random mating, although variation in inbreeding would be expected to be reduced (Weir et al., 1980).

De Rochambeau and Chevalet (1982) proposed several circular mating systems, which incorporated concepts from both Wright (1921) and Kimura and Crow (1963), for reducing rates of inbreeding in small populations. The evolution of inbreeding was found to be significantly less with cyclical circular mating systems, at least within the first ten generations. Although not considering selection in this work, the use of within family selection, or selection within subpopulations, and the avoidance of mating relatives through circular mating systems may be useful in animal breeding applications. However, although levels of and variation in inbreeding may be lowered with these systems, within family selection or subdivision of the population for selection purposes is less efficient than the optimum use of combined within and between family selection. As such, response may not be improved despite a greater ability to control inbreeding.

An interesting feature of altering mating systems to lower rates of inbreeding is that they may have little effect on reducing loss of genetic variation due to genetic drift. Jacquard (1971) found that the exclusion of sib matings did not alter the rate of genetic drift, and that this rate was primarily dependent on the variance of family size. Toro and Nieto (1984) suggested that choosing an optimum distribution of family size, for a breeding population with unequal representation of progeny, would minimise drift in the long term without compromising short term response. Their method was experimentally verified by Nieto et. al (1986) and Toro et al. (1988), but can only be realised with a mating system confined to producing a particular distribution of family size. The benefits of this system are then realised through increasing effective population size, rather than the choice of mating particular individuals or groups who are more or less related.

2.4.2 Assortative Mating Systems

Assortative mating occurs when individuals mated together are more or less alike phenotypically than expected from random pairing. The genetic (dis)similarities between mating pairs, and therefore the genetic consequences of assortative mating, then depends on whether phenotypic (dis)similarity is determined by genetic components and not purely incidental, and whether mating pairs are genetically similar or dissimilar. Positive assortative mating (similarity of mates) in particular has been investigated by several researchers as a means for increasing response to selection, through increasing additive genetic variation and the efficiency of selection.

Positive Assortative Mating

Positive assortative mating (mating like to like) results in increased additive genetic variation in the progeny due to altering genotypic frequencies and increasing homozygosity of assortatively paired loci (Falconer, 1981). This is accompanied by a positive correlation between loci (Fernando and Gianola, 1986) and is analogous to positive gametic phase (linkage) disequilibrium (Crow and Felsenstein, 1968). The magnitude of these effects is dependent on the degree of genetic assortative mating and the heritability of the phenotypic criterion. The resultant positive covariances between loci contribute relatively more to additive variation than the other above mentioned effects.

The degree of assortative mating is reflected by the correlation (r) between phenotypic values of mates for the selection criterion. From this correlation, assuming an additive infinitesimal model, the degree of assortative mating based on genetic differences (the correlation between breeding values (m) for individual selection) may be related to r by $m = rh^2$, where the selection criterion has heritability h^2. The effect of one cycle of assortative mating, in the absence of selection, is then to increase progeny phenotypic and genetic variances by factors of $(1 + .5rh^4)$ and $(1 + .5rh^2)$ respectively, and subsequently heritability in the following generation (Falconer, 1981; Hohenboken, 1985). Positive assortative mating also increases the genetic and phenotypic covariances between relatives, above that which would be expected from an increased heritability alone, through changing genotypic frequencies (Falconer, 1981). These are reflected by increasing between family components of variance, as within family components of variation are unlikely to be affected unless locus number is small. The magnitude of this change is also dependent on r and m.

With recurrent assortative mating and for constant r and m, genetic and phenotypic variances stabilise to an equilibrium level above that found in the base population. If assortative mating ceases, and in the absence of other factors, genetic variation will return to it's original value exponentially, as occurs with gametic phase disequilibrium induced by selection (Bulmer, 1980). For discrete generations equilibrium values are reached rapidly, with greater increases in genetic variation occurring within the first few generations of assortative mating (Bulmer, 1980). However, in animal breeding populations, with overlapping generations and low rates of replacement of breeding stock, the expected equilibrium may not be reached (Kemp et al., 1986).

Positive assortative mating may also increase additive genetic variation for traits genetically correlated with the criteria for assortative pairing. Additionally, the correlation between these traits may be altered, the extent of this change depending on r, m, the equilibrium heritability of the criteria, and the original genetic correlation between traits (Gianola, 1982). As heritability, the genetic correlation and degree of assortative pairing increase, the magnitude of increase in equilibrium variances and correlations becomes larger. This process may be rapid with discrete generations although, as noted above, equilibrium correlations and variances may not be achieved in animal breeding populations even without selection (Kemp et al., 1986). The genetic correlation under positive assortative mating based on a single trait criterion may change in magnitude but not in sign (Gianola, 1982).

Fernando and Gianola (1984) investigated positive assortative mating applied to an aggregate genotype defined by a linear merit function. Assortative mating resulted in favourable sign changes of the genetic correlation, increased heritability, variances and covariances. These results would suggest that positive assortative mating may enhance response to selection for a variety of selection criteria. However, this conclusion may not hold for assortative mating carried out concurrently with selection.

Negative and Mixed Assortative Mating

In contrast to positive assortative mating, negative assortative mating (pairing of dissimilar individuals) may result in increased heterozygosity and reduced genotypic variation. However, negative assortative mating will have little impact on heterozygosity unless the phenotypic values of mates are highly correlated and only a small number of loci control the criterion trait (Crow and Felsenstein, 1968). Additionally, negative assortative mating has little effect on the genetic correlation between traits even when the criterion trait is highly heritable and r is high (Gianola, 1982). As such, little change in genotypic frequencies, correlations between relatives and additive genetic variance would be expected with negative assortative mating when gene frequencies are intermediate. However, Falconer (1981) indicated that negative assortative mating could result in changing gene frequencies to intermediate values when rarer phenotypes were preferentially favoured for mating.

An additional assortative mating system proposed by Gianola (1982) is that of mixed assortative mating. This involves the pairing of mates to produce phenotypic correlations between complementary sex limited traits (eg. growth rate in bulls with milk production in females). Without selection and under positive mixed assortative mating, the genetic correlation (either positive or negative) is always increased in a positive direction. In a similar manner, for negative mixed assortative mating the genetic correlation will always decrease. However, if the correlation is negative loss of additive genetic variation in both traits will occur. These mating systems thus provide means to reduce unfavourable positive correlations, or increase favourable negative correlations. The potential gains in response, however, will be reduced with associated loss in additive genetic variation (Gianola, 1982).

Assortative Mating and Inbreeding

Positive assortative mating may increase additive genetic variation to a greater extent than that accruing under inbreeding, although the increase in homozygosity is less. This is the result of inbreeding causing positive correlations within loci due to genes being identical by descent only, whereas assortative mating also causes correlations between non-homologous genes (Crow and Kimura, 1970). Assortative mating, however, may result in elevated levels of inbreeding over random mating systems, as pairing of like individuals for breeding may result in an increased probability of mating related individuals. It may be speculated that with the accumulation of inbreeding, the degree of homozygosity due to assortative mating may be further increased. The effects of inbreeding may then, in some part, offset gains in genetic variation due to positive assortative mating. Lande (1977) indicated that in the presence of natural selection, linkage and mutation, mating systems such as inbreeding and positive assortative mating have little influence on the long term maintainence of additive genetic variation. The degree to which this phenomenon is experienced in animal breeding populations undergoing selection is essentially unknown.

Assortative Mating and Selection Response

For selection purposes, assortative mating systems appear to have several useful characteristics. They may improve the effectiveness of selection through increasing additive genetic variation, and consequently heritability and selection differentials, or be employed for favourable manipulation of genetic correlations between traits (Fernando and Gianola, 1984). Further, with increased covariances between family members, and subsequently greater variability between family means, between family selection may become more efficient. Assortative mating may also be useful for increasing the precision of estimating genetic parameters from knowledge of changes in covariances between relatives (Falconer, 1981). However, the joint effects of selection combined with assortative mating must be considered to evaluate the impact of assortative mating on selection response. The above discussion has not included the effects of selection on assortative mating, and *vice-versa.* Of most interest to animal breeders is the effect of positive assortative mating on selection response, to which further discussion will be confined.

Several authors have shown that when selection is practised, positive assortative mating is most effective at increasing genetic (co)variances and heritability when the proportion of selected individuals is low, the phenotypic correlation between mates is high, and accuracies of component selection criteria are high (Fernando and Gianola, 1986; Shepherd, 1991; Smith and Hammond, 1987a; Tallis, 1989; Tallis and Leppard, 1987). Gene level simulations by Fernando and Gianola (1986) concluded that the advantages of assortative mating increase with increasing number of loci, and when frequency was low for the allele of highest value. Improvements in genetic gain over random mating systems under this scenario range from 10% (Fernando and Gianola, 1986) to 50% (Tallis and Leppard, 1987) for selection and mating based on individual performance alone. At higher selection intensities, depletion of additive genetic variation due to the magnified effects of selection and inbreeding hinders the potential of assortative mating to improve selection response. Advantages in genetic gain associated with assortative over random mating will then decline to no more than a 5% improvement under individual selection (Tallis, 1989). This decline is not the case for index or BLUP selection incorporating information from relatives (Smith and Hammond, 1987a; Shepherd and Kinghorn, 1994).

An alternative to reducing selection intensity, thereby increasing the efficiency of assortative mating, is to use assortative mating cyclically with selection. This method was shown to be very effective over short time frames by Smith and Hammond (1987a) for progeny index selection. Conversely, Tallis and Leppard (1987) noted that total genetic progress over a longer time frame was greater with continuous intense selection (individual performance) and assortative mating combined. Similarly, Shepherd and Kinghorn (1994) demonstrated that it was unnecessary to relax selection pressure (EBV selection) to obtain improved response with assortative mating. Thus, the greater efficiency of selection following a cycle of assortative mating alone would appear not to be maintained over repeated cycles of this approach.

In Section 2.3 it was noted that increasing the proportion of animals selected (to reduce the effects of inbreeding on V_A) did not improve selection response due to reduced selection differentials. In a similar fashion, reducing selection intensity to take advantage of assortative mating under individual selection is not likely to achieve higher genetic gain than more intensive selection under random mating. Further, Fernando and Gianola (1986) have shown that with low selection intensity, the greatest gains achieved by assortative over random mating systems are only obtained after a large number of generations have passed. This is unlikely to be of use to animal breeders interested in short term gains. Fortunately, the impact of assortative mating on selection response may be improved by increasing accuracy of selection.

Using stochastic simulation, Shepherd and Kinghorn (1994) found that improvements in genetic gain of up to 29% were achievable with assortative over random mating when selection was based on BLUP EBVs (10 generations). Further, for populations of infinite size the relative efficiency of assortative over random mating was independent of trait heritability under EBV selection provided sufficient historical data was available prior to selection. The improved efficiency of assortative mating from that predicted by other authors for mass selection (Tallis and Leppard, 1987) may be attributed in part to increasing the correlation between true and estimated breeding values within the selected individual, and by increasing the correlation between breeding values of mated pairs. Where the accumulation of inbreeding is high, however, the advantages of assortative over random mating are likely to decline with loss in V_A, the magnitude of which depends on characteristics of the selection criterion. Another factor which may reduce the relative efficiency of assortative over random mating is the potential for departures from normality in the offspring generation (Smith and Hammond, 1987a). Departures from normality are most likely at high heritabilities and under intense selection. However, it is difficult to extrapolate how non-normality may, if at all, affect the long term efficiency of assortative mating.

2.5 Mate Allocation and Mate Selection

Truncation selection of superior stock for breeding within a random mating herd is the traditional approach for obtaining genetic gain within animal breeding programs. The selection criterion is usually an estimate of breeding value, and merit of resultant progeny is then expected to reflect the mid-parent value of mating pairs. As such, the relative merit of progeny from alternative mating pairs will depict, with error, the superiority of each individual parent. In this scenario, contributions of individuals to their progeny merit can be considered independently from their mates (Allaire, 1980) and the traditional approach to selection and mating is effective for maximising total progeny merit. However, under traditional procedures it is assumed that inheritance is additive, the combination of additive genetic effects within progeny is linear, and the economic value of subsequent genetic gain is linearly related to additive genetic merit. These assumptions may not always be valid, and alternative approaches to traditional procedures may be required for maximising total progeny merit.

When total merit of progeny is not inherited additively, contributions from individuals to their progeny merit may not be factored into independent components due to interactions between mates (Allaire, 1980). As such, animals may re-rank from their expected superiority predicted from individual merit alone. Non-additive inheritance of merit may occur even under purely additive trait inheritance if economic interactions occur between mates either between and/or within traits (Allaire, 1980). Similarly, non-additive inheritance of component traits, due to interactions between mates in their expected breeding values (Kinghorn, 1987), will contribute to changing the mean genetic merit of the progeny for alternative selection and mating options. Evidence exists for a component of non-additive inheritance in several economically important traits (Bereskin et al., 1970; Dickerson, 1973; Sheridan, 1981; Tempelman and Burnside; 1991) and non-linear definition of total merit (Allaire, 1977; Smith and Allaire, 1985). Additional considerations which may introduce non- linearity into the breeding objective include: economic and production constraints (Jansen and Wilton, 1984); desired variation among progeny, and where costs associated with the use of particular breeding pairs and/or heterosis are important.

In the presence of non-linear effects, improvements in total merit may be obtained by considering pair-wise contributions of individuals at both selection and mating, rather than considering the merit of each breeding individual separately. Pair-wise merit enables interactions between alternative mates to be accounted for. It is possible to define both the individuals to be selected and their mating partner(s) in either independent two stage processes or a unified one stage process (mate selection) using mate selection rules. In this scenario, mate selection rules do not necessarily imply a regular system of mating, nor selection of breeding parents by truncation rules alone. In addition, mate selection rules are applicable to both selected and unselected breeding populations; i.e., selection of parents on individual merit would not exclude their re-evaluation for selection on paired-merit criteria. However, mate selection rules are only useful tools for manipulating response if choice of mating pairs or groups influences either the mean genetic (or economic) merit of the progeny, or the variance among the progeny in EBV if not in phenotype (Kinghorn, 1987).

Of interest to animal breeders are alternative situations where selection of particular breeding stock, mate selection or mate allocation may be beneficial in improving selection response or it's economic value. Discussion within this section will be confined primarily to the principles of mate selection rules within populations undergoing continuous directional selection. The discussion will be split into mate selection rules applying to either the traditional two stage selection and mating processes (which may include both mate selection and mate allocation), or a single stage procedure encompassing selection and mating decisions unified into one process, generically termed mate selection. The long term implications of these procedures are also discussed.

2.5.1 Mate Selection Rules Applied to Independent Two Stage Selection and Mating Decisions

There are many examples of traditionally orientated mate selection rules using independent two stage processes for selection and mating decisions. Selection followed by any form of non-random mating system implies that advantages in the progeny generation are to be gained from specific pairings or groupings of selected parents. Mating systems discussed in Section 2.4 will not be re-addressed here in detail, although it is recognised that specific regular mating systems are designed to impact on maximising progeny merit. Of interest in this section are the concepts of mate allocation and selection as defined above.

In the confines of traditional selection, where all selected individuals are expected to contribute to the progeny generation, individuals may be allocated to a partner in several ways: for example; at random; ranked on phenotypic performance; or pairs selected according to predicted progeny merit. Within this scenario, mate allocation typically represents the formation of mating pairs from all selected individuals since selection of an individual is not conditional on available partners, and therefore no individual is excluded from mating. However, if selected individuals are to be re-evaluated before breeding in a second stage of selection, conditional on characteristics of other available partners, mate selection is a more appropriate description of the selection and mating process. This particular terminology is considered most appropriate for the following discussion. However, it is important to note that mate allocation following selection may easily become a form of mate selection by removing the constraint that all selected individuals must breed. In contrast to unified procedures, however, this does not allow for individuals unselected originally to be subsequently eligible for allocation purposes.

Enhancing Additive Genetic Merit

Using mate selection rules to increase *additive* genetic merit of the progeny, following selection, in the absence of non-additive economic considerations, implies a long term perspective. The mean genetic merit in the progeny after one generation of selection is not expected to change regardless of the mating system if all contributions of selected individuals are equal and the mode of inheritance is strictly additive. Similarly, total economic merit of the progeny will not be influenced by the mating system if increasing economic merit is linearly related to increasing additive genetic merit. However, given that progeny genotypes are determined by pairwise contributions from the parental generation, the nature of parental contributions may influence average genetic merit of the progeny through differential use of parents, and also impact on genetic variation among progeny through altering genotypic frequencies, for future selection purposes.

For maximising progeny additive genetic merit, the objective function may be generally defined as (Smith and Hammond, 1987b):

$$Maximise \sum_{ij} x_{ij} E\{f(A_{ij})\} \tag{2.4}$$

where A_{ij} is additive merit of progeny with parents i and j, $x_{ij} = 1$ or 0 for male i to mate (or not mate) female j, and $f(A)$ is one of several possible functions which may be considered. When $f(A)$ is linear, no advantage is to be gained from specific selection of mating pairs as mean progeny merit is determined by mean additive merit, and this is unaffected by the mating system unless unequal parental contributions are allowed. However, when variation is included positively in $f(A)$, the function may become convex and choice of specific mating pairs to increase variation (eg. positive assortative mating) will maximise the objective. Smith and Hammond (1987b) consider the enhancement of additive genetic merit after several generations to comply with a non-linear objective, since total additive genetic merit of the progeny after several generations of selection is enhanced by increasing additive genetic variance. Conversely, concave objective functions would favour reduction in variation, and the specific selection of pairs (eg. negative assortative mating) may also enable this.

An additional consideration is that components of the chosen objective function may be antagonistic, particularly over different time horizons. Maximising genetic gain in the short term usually takes precedence over maintainence of genetic variation for longer term gains. These opposing objectives may not be met by the same selection and mating decisions. For example, mean progeny additive merit may be improved with increased use of superior individuals and therefore differential use of selected parents in the short term. However, disruptive selection and equal contributions from selected individuals are desirable for increasing genetic variation over a longer time period.

Moreover, the influence of inbreeding on genetic variation and phenotypic performance of inbred individuals cannot be ignored. The efficiency of any breeding program to improve selection response may be reduced if consequences of selection and/or mating practices include elevated rates of inbreeding, resulting in loss of genetic variation and/or inbreeding depression. Increased inbreeding was noted to be a factor reducing the efficiency of positive assortative mating in Section 2.4.2. These factors make it difficult to formulate an appropriate objective function, and also suggest that constraints may need to be applied to confine the optimum within a restricted solution space.

In contrast to selecting mating pairs based on additive merit, choice of specific mating pairs based on relationships may be warranted to minimise inbreeding. Avoidance mating systems are an example of applying mate selection rules in this situation, where it is perceived that lower inbreeding coefficients in the progeny generation are beneficial for maintaining future genetic variation and selection response. However, as with prior examples, these approaches do not necessarily facilitate maximising response to selection due to the potentially antagonistic relationships between factors which affect selection response and inbreeding. As such, extension of mate selection rules to more than one generation of selection and mating is difficult for joint selection and mating problems even when only additive merit is considered.

Enhancing Non-Additive Merit

Enhancing additive genetic merit, in the absence of non-linear economic considerations, essentially relegates mate selection rules to using knowledge of additive genetic considerations when selecting mating pairs. That is, either estimated additive genetic merit, or relationships, of selected individuals are the only factors influencing choice of their partner, and the mean genetic merit of their progeny reflects independent additive contributions from each parent. In contrast, the value of an individual parent for increasing non-additive merit is not independent of contributions made by alternative partners (Allaire, 1980) and knowledge of paired merit is required for allocation or selection of mating pairs. In addition, the effects of mate selection rules to maximise non-additive merit do not act in isolation of additive merit. Determining impact on gain in total merit, for both additive and non-additive considerations, is then significantly more complicated.

Non-additive merit may be defined for three alternative scenarios: 1) maximising total merit when interactions between mates occurs in their expected breeding values (Kinghorn, 1987) but economic increments are additive. To maximise total merit would then require maximising genetic merit; 2) maximising total merit when inheritance is additive but merit is defined by a non-linear profit function (Allaire et al. 1985, Smith and Allaire, 1985). Maximising total merit would then be a function of genetic and economic considerations, or; 3) in the presence of non- additive genetic and economic effects. Regardless of the scenario, in order to maximise total merit in the progeny it is necessary to derive the **paired** contributions of selected individuals to expected progeny merit (EPM) for alternative partners. This would then enable comparisons between alternatives and selection of the best combination of mating pairs. The problem may be formulated by an objective function, and solved subject to constraints, in a similar fashion to that mentioned previously.

To define EPMs for each scenario requires information from several sources. When inheritance is non-additive, knowledge of specific and general combining abilities is required to predict the expected genotype of the progeny for each mating pair. Additionally, where non-linear economic considerations are important or economic constraints exist, the economic value of alternative genotypes is required. This implies that both the most economically desirable genotype is known and that progeny genotypes may be predicted. The difficulty is to predict EPMs for each alternative pair when such information may be inaccurate or unavailable.

Allaire (1980) proposed that selection index theory was useful for predicting expected progeny merit when a non-linear relationship exists between merit and traits in the index. Selection of mating pairs based on the highest progeny index is then expected to increase total progeny merit. Similarly, Smith and Allaire (1985) describe a Bayesian selection rule to increase merit in progeny when applied to mate selection. Both examples, however, consider comparisons between very few pairs. When large numbers of pairs are considered the number of alternative combinations may increase exponentially. Simple ranking on paired merit is then not practical for maximising the objective function. Moreover, the opportunity cost of not making particular matings may not be adequately accounted for.

Following Kinghorn (1987), the simplest scenario is the truncation selection of m males and f females ($N = m + f$ breeding individuals), based on each individual's additive genetic merit, from which $M = f = m$ single pair matings are produced. With $M!$ possible single pair matings, evaluation of alternative mating pairs and combinations to maximise progeny merit (genetic and/or economic) may be difficult. The easiest method of choosing pairs is to rank parents of each sex on their own merit, and allocate mates sequentially according to rank. This reduces evaluation of possible mating pairs from $M!$ to $m = f$. However, ranking parents on individual merit does not account for interactions between mates. An alternative is to use information provided by the array of EPM values, from all possible mating pairs, to derive the optimal combination of mating pairs. Linear programming procedures provide the optimal solution for these types of problems (Jansen and Wilton, 1985; Kinghorn, 1987), improving total merit over that which would be achieved by random mating or ranking mating pairs on individual merit alone.

Linear programming (LP) procedures can be formulated to deal with a number of problems bounded by constraints and will always provide the optimum strategy, given the data provided, through exploration within the $M!$ combinations. Mate allocation solutions are derived by specifying that **all** selected individuals must be mated at least once. Alternatively, by relaxing this constraint a second evaluation of selected males may be carried out subject to the characteristics of selected females. This is a common scenario in animal breeding applications, where sufficient numbers of females are required to be mated in order to produce the desired number of progeny, and males may mate several females. The optimum solution may then exclude the use of particular males resulting in mate selection (Allaire, 1980). Analogously, Allaire (1977) has examined this situation from a multi-stage viewpoint for corrective mating methods using selection index procedures. By relaxing the constraint of one mating per male ($k = 1$) to ($k \geq 0 \rightarrow n$), where n is the maximum number of matings per male, the number of possible mating pair combinations increases to at least $f!/(k!)m$ for evaluation. However, this allows differential use of males and the potential to exclude undesirable animals from breeding, providing greater opportunity to use individuals which will produce progeny of higher merit. The benefits may then be realised through the ability to increase selection intensity for males as well as optimally allocating selected males to available partners.

As mentioned previously, components of the objective function may be antagonistic to maximising progeny merit over several cycles. Further constraints may be imposed by certain males being incapable of doing n matings, or if particular matings need to be avoided, for example due to inbreeding. Similarly, the use of embryo transfer would allow females to have greater than one mating, which increases the number of possible combinations above f. The complication of dependent EPMs is not dealt with in this study.

2.5.2 Mate Selection Rules Applied to Unified Selection and Mating Decisions

The procedures described by Kinghorn (1987) and Jansen and Wilton (1985) can also be applied to a strictly defined mate selection scenario. Selection and choice of mating pairs are unified into a one stage process using paired merit as the criterion for determining selected pairs. This approach is warranted under the assumption that preselection of parents, based on purely additive genetic merit, may eliminate desirable matings and reduce average merit of the progeny when non-linear components are important (Jansen and Wilton, 1985). Conversely, selection of parents conditional on available mates may then be expected to improve average merit of progeny.

Allaire and Barr (1990) found that sire selection based on a progeny milk and type index, which accounted for available mates, was superior to sire selection using two stage processes. That is, sire selection based on a sire milk merit index followed by selection on a progeny type merit index resulted in lower total progeny merit than that gained using a unified approach. Kimura and Crow (1978) concluded that substantial departures from truncation selection did not greatly decrease the efficiency of selection processes for traits with purely additive control. This feature facilitates efficient mate selection when additive components of inheritance are also important in defining total merit of progeny.

Selection and allocation of m males and f females, from T_m males and T_f females available for selection, according to *paired* merit can be carried out using any procedure which allows for f selected matings to be defined within the appropriate constraints. Kinghorn (1987) found that selection itself had a significant effect on the efficiency of several procedures for allocating pairs concurrently with selection (mate selection). In this example LP algorithms again provide the best technique to obtain the optimum solutions. However, for single pair matings, sequentially ranking the next best remaining pair was increasingly efficient as selection intensity increased. The author speculated that with a larger number of options available for ranking, the elimination of later options was of less consequence as selection intensity increased. This may not be the case when parents are allowed unequal numbers of matings, as the opportunity cost of not making specific matings is then not adequately accounted for by ranking processes.

2.5.3 Impact of Mate Selection Rules on Selection Response and Total Progeny Merit

In classical theory, maximising total progeny merit over the time frame of a breeding program is analogous to maximising additive genetic gain (response to selection). This analogy does not hold in situations where mate allocation and/or mate selection are most appropriate. Therefore, the effects of mate selection rules on selection response, as opposed to total progeny merit, are difficult to define in a classical manner. Previous discussion has considered the theory by which gains in non-additive merit may be obtained through choice of specific mating pairs. Most of this theory incorporates the advantages to be gained only for the following generation. As such, it is not clear whether these advantages will accrue over several generations for all scenarios where use of mate selection rules would appear appropriate. That is, improving progeny merit on a generation by generation basis does not necessarily imply superior cumulative long-term gains over traditional procedures if non-additive components of merit are important. Key to expected cumulative gains is how total progeny merit is defined, and therefore the form of objective function which must be maximised.

Defining Total Merit in the Presence of Economic Interactions

Assuming that expected progeny merit may be calculated for all alternative mating pairs, total progeny merit may be maximised for a given objective function through optimising the combination of mating pairs chosen with mate selection rules. However, in certain situations re-ranking of selected individuals may not occur despite considering paired rather than independent contributions of individuals to progeny merit.

This is largely the result of inadequate interactions between candidates for mating. In such situations, additive genetic merit of selected individuals is a good estimate of their contribution to progeny merit, which is in turn inherited largely in an additive fashion. As such, no advantage may be expected from selecting specific mating pairs, and traditional methods are adequate to maximise both selection response and total progeny merit. There are several possible reasons for this phenomenon.

When total merit is defined as a function of additively inherited traits, but economic interactions exist between mates for traits of interest, then: potential mates must represent a wide range of genetic values for traits of importance; economic interactions should be strongly non-linear; heritability of component traits should be moderate to high (Allaire et al., 1985), and; high accuracy of predicted progeny merit is desirable (Allaire and Barr, 1990). These factors contribute to variability amongst alternative pairs in the merit of their progeny, and re-ranking of selected individuals and their partners. When one set of mates (eg. females) is predetermined, as is common, the frequency with which males are re-ranked according to paired merit then determines whether mate selection rules are appropriate (Allaire et al., 1985).

Where mate selection rules do result in re-ranking of individuals according to paired merit, and would therefore appear warranted, other considerations are important. Allaire and Barr (1990) found that mate selection rules which increased quadratic merit in the progeny were not efficient for improving total merit. In this example, non-genetic differences in phenotypes resulted in incorrect progeny index rankings, which reduced the potential for these rules to improve total merit. In addition, type traits, with merit defined non-linearly, were improved at the expense of additive genetic gain for milk traits. In this situation, reduced selection response for milk may be expected to reduce total merit achievable in the following generations. As such, these mate selection rules may disadvantage both selection response and total progeny merit over several generations, although the tendency was weak in the above example.

Allaire et al. (1985) produced a similar example, where no advantage was achieved through selecting sires on a quadratic progeny index as opposed to their own linear index of genetic merit. This was the result of high selection intensity of males and lack of re-ranking among selection candidates for alternative indexes. For example, when total merit was largely attributable to linear additive gain in milk, the top ranking sire for milk was also likely to be the top ranking sire from paired evaluation. Reducing selection intensity may modify this result somewhat since more combinations of mating pairs are possible.

An alternative to using paired merit indices for selection of specific mating pairs is the use of selection indices which describe non-linear merit for each individual. Wilton and van Vleck (1969) described several forms of indices for evaluating sire merit for selection purposes. Although not directly considering mating pairs to determine selection and mating decisions, herd means for component traits influencing economic merit indirectly indicated the average genetic merit of mates available. Profit was then described by a non-linear function as mean dependent, and therefore influenced by the genetic merit of available mates. In this example, sire selection on quadratic, linear and restricted indexes all provided an equivalent rate of economic gain, although due to different sources. The linear index provided the greatest additive genetic gains in milk, whereas non-linear and restricted indices reduced response for milk. Other component traits contributing to economic gain were correspondingly altered.

Similarly, Wilton et al. (1968) described quadratic selection indices for situations where total merit of an individual may be described by a quadratic function, and Moav and Hill (1966) considered the case where two or more traits contribute to a non-linear profit function. These authors found that when additive gain in traits was an important component of total merit, the efficiency of non-linear selection indices was not likely to be significantly higher than use of a linear index. This type of evidence prompted Goddard (1983) to suggest that selection of individuals based on linear indices, derived from knowledge of quadratic merit, was a more efficient method of improving selection response than either use of quadratic indices or mate selection procedures. This is under the assumption that improvement of progeny merit using mate selection must be recreated every generation and that variance considerations are ignored since specific phenotypes are the objective. It must be argued, however, that this will be very dependent on the function which describes total merit. As with mate selection rules, the optimum selection index for non-linear profit functions is dependent on selection intensity (Goddard, 1983).

Overall, it appears that when economic interactions between mates exist, mate selection rules in general may encourage a trade off between additive genetic gain and other components contributing non-linearly to total merit. In this scenario, cumulative merit may be reduced, although gains in other components of merit may adequately compensate for this in the short term. However, improvements in long term gain do not appear likely when the influence of these rules on additive merit is considered.

An alternative viewpoint is that mate selection rules may advantage breeders through altering selection intensities. In the work of Allaire and Barr (1990), the same level of merit was achieved by selecting more sires using the progeny index than were selected based on a sire index. As the use of several sires may be beneficial to future gains due to reduced risk associated with lower selection intensity and the effects of inbreeding, long term gain may not be as disadvantaged as indicated from the above studies. Moreover, Schneeberger et al. (1982) indicated, using portfolio theory, that variance in income was reduced by increasing the number of sires used. These other considerations may advantage mate selection rules.

Total Merit in the Presence of Genetic Interactions

Kinghorn (1987) has described a hypothetical situation where the breeding values of purebred mates interact, i.e., the genetic merit of their progeny is not described by the mid-parent value and inheritance of genetic merit is no longer fully additive. This feature is, of course, well recognised in reality through large non-additive effects of heterosis for crossbreeding applications, and within breed may be established by determining the presence of dominance variation (Tempelman and Burnside, 1991) and inbreeding depression. When inheritance is not additive, the selection and allocation of specific mating pairs is expected to increase progeny merit by maximising non-additive components of merit. However, this does not necessarily ensure cumulative gains.

For example, consider a trait controlled by one locus. If non-additive inheritance due to overdominance were the only source of non-additive effects, selection would always favour heterozygotes due to their superior performance. However, heterozygote parents mated together produce only 50% heterozygous offspring on average, the remaining 50% with inferior homozygous genotypes, resulting in progeny of lower average merit. Conversely, mating to maximise genetic merit in the progeny generation would require the selection and mating of homozygote extremes. In this situation selection opposes mating decisions, and the mean may change detrimentally following selection (Hill, 1969). Total progeny merit as such is determined by the proportion of hetero- to homozygous parents selected, genetic characteristics of the criterion (eg. gene frequencies and values), and use of a mating system to maximise dominance effects from the available parents. In this scenario, intermediate gene frequencies would always be favoured for maximising progeny merit (Hill, 1969) at the expense of increasing the frequency of genes of the highest value. It is well recognised, however, that cumulative genetic gain is impossible without the net effects of gene substitutions.

Most traits, however, have both additive and non-additive effects controlling their behaviour. Kinghorn (1986, 1987) has applied various mate selection rules (eg. ranking pairs and LP approaches) to determine the optimum procedure for selection and mating across breeds. These procedures reduce selection and mating policies to the level of each mating pair or group, where it is possible to optimise gain in both additive and non-additive effects within the progeny generation. The most simple approach ranks parents within breed on additive genetic merit, then mating groups with expected maximum progeny merit may be selected and mated (through mate selection) across breeds to exploit both additive gain and heterosis. Although cumulative gain in progeny merit is only achieved by increasing additive genetic merit within the purebreds contributing to the crossbred progeny, the extra emphasis placed on additive effects do in fact give increased long term gains (Kinghorn, 1984).

Increasing Total Merit through Controlling Inbreeding

In the discussion on increasing additive genetic merit, it was presumed that controlling inbreeding would enhance future selection response by reducing the effects of inbreeding on phenotypic performance and genetic variation. This is dependent on the method used for reducing levels of inbreeding, as particular selection and mating system alternatives may reduce overall response to selection despite reducing levels of inbreeding (De Roo, 1988b; Toro and Pérez-Enciso, 1990).

Toro and Pérez-Enciso (1990) applied the principles of mate selection for selection and mating of breeding stock to maximise additive genetic progress under restricted inbreeding. Progeny merit in this example was defined as a function of mid-parent additive genetic merit. However, the matrix of solutions was constrained to fit within the framework of maximum allowable rates of inbreeding. This procedure excluded the selection and mating of particular pairs, the combination of pairs chosen producing below the required rate of inbreeding. Repeating this process over five generations indicated, with deterministic predictions, that mate selection in this scenario was useful for maintaining selection response while accommodating other criteria important to progeny merit (eg. inbreeding). However, the effectiveness of mate selection for this application was critically dependent on the rate of inbreeding chosen to constrain the selection and mating of individuals. No advantages in response over independent selection and mating decisions were evident when rates chosen were suboptimal.

2.5.4 Some Additional Considerations

Mate selection has been shown to maximise total progeny merit under certain conditions. It has also been noted that short term improvements in merit are not necessarily associated with maximising selection response through additive genetic gain. In this situation, it is unlikely that cumulative gain will be equivalent to traditional procedures, particularly when profit objectives are included in total merit. However, additional considerations may be important in evaluating the performance of specific mate selection applications. Some of these may include:

1. Variation among progeny. For selection purposes, variation among progeny and associated additive genetic variation, are important factors influencing long term continuous response to selection. Variation will be influenced by the effects of selection and inbreeding, and the nature of paired parental contributions. Choice of mate selection rules to maximise total merit of the progeny for one generation do not necessarily imply maintainence of variation for future cycles of selection and mating choices.

2. Risk factors. Concerns also lie with the number of times an individual may be selected to mate, and for what reason. Mate selection rules may result in selection and mating of more or less males than would be selected for mating using traditional procedures. This would depend on the formulation of the mate selection problem. Reducing the number of individuals to be selected and mated increases the risk of obtaining higher inbreeding and more variable response (Schneeberger et al., 1982), which in turn is partially determined by the accuracy of selection and the number of possible matings per male. For maintaining long term response it is not desirable to use too few individuals per generation. Using more animals may reduce variability of response and inbreeding, as well as aid in maintaining additive genetic variation, although introducing more opportunity for the use of inferior animals. Risk for both short and long term gains is relatively poorly quantified.

3. Static Solutions. Linear programming (LP) procedures enable identification of the optimum solution for mate allocation or mate selection problems. However, formulation of the problem must be linear, ie. the objective function and constraints are presumed to denote constant returns to scale. LP methods also presume equal accuracy of the alternatives (data), and the problem and solution are only defined as static in nature Chiang (1984). This introduces uncertainty when variables do not change independently and data differ in accuracy (as occurs realistically in animal breeding applications). Quadratic and dynamic programming techniques may account for non-linear objectives and returns to scale. However, no known method allows for unequal accuracy of data, nor do they provide a strategy over time. For example, the impact of previous solutions will not be accounted for in later solutions.

4. Unequal Information under Additive Inheritance. The efficiency with which mate selection rules influence average progeny merit is determined by the accuracy with which paired merit reflects progeny merit. When economic non-linearities are well defined, and inheritance is additive, using the most accurate estimates of breeding value will facilitate the prediction of progeny merit and the appropriate choice of mating pairs. However, unequal information available for evaluating genetic merit of individuals may result in additional uncertainty on the outcome, since accuracy of estimates will differ between individuals, resulting in some inappropriate choices between mating pairs.

5. Non-Additive Inheritance of Component Traits. It may be very difficult to define and predict progeny merit when specific combining ability is important within a purebreeding population as this is complicated to estimate with precision. Tempelman and Burnside (1991) have suggested that optimising mate allocation may be appropriate when dominance genetic variation, in combination with additive genetic variation, is apparent for component traits. However, heterogeneity of variances between sexes (Tempelman and Burnside, 1991) makes accurate evaluation difficult even with appropriate mixed model methodology. Placing appropriate emphasis on additive and non-additive components may also be difficult to define when considering short-term and long-term gain for a population undergoing continuous selection.

6. Non-additive vs Additive Genetic Merit. Any economic considerations imply that phenotypic merit is the prime determinant of progeny total merit. Non-additive genetic considerations imply that phenotype mediated by non-additively determined genotypes is of importance. In both situations total progeny merit may not adequately reflect permanent cumulative genetic gain, since this can only be achieved through directional selection for additive genetic effects. As such, meritous matings for advantageous phenotypic outcomes may mask deficiencies in additive gain at the genotypic level, which will then reduce the efficiency of maintaining rates of improvement in total merit over later generations.

The effectiveness of mate selection rules for improving long term merit is thus an area where considerable research is required. It may well be that this approach is only efficient over selection followed by mating in certain situations. However, this would depend on the objective function formulated, which may incorporate any number of issues important to animal breeding (Kinghorn and Shepherd, 1990).

2.6 Genetic Evaluation and Selection Procedures

As mentioned in Section 2.2, response to selection can be improved by increasing the correlation ($r_{\hat{u},u}$) between true and estimated breeding value, thereby increasing accuracy of selection. The impact of alternative selection and mating decisions on genetic gain will ultimately be mediated by accuracy of selection, since this relates to the efficiency with which selected animals for breeding represent genetically superior animals. It is often difficult to estimate each individual's genetic worth with equal accuracy, and there are several methods available for predicting breeding values which may be used. In this section, some common methods of genetic evaluation are described, and their impact on selection response noted. In Section 2.6.4, additional considerations for multiple trait genetic evaluation will be discussed following establishment of principles for single trait evaluations.

2.6.1 Individual Performance

The simplest criterion for selection is based on a single objective measure of an individuals own phenotypic performance for the trait(s) of interest. The predicted breeding value for individual i ($\hat{A}_i$), for a given trait, is then $\hat{A}_i = h^2 P_i$, where h^2 is the trait heritability and P_i is the phenotypic value of individual i expressed as a deviation from the population mean (Falconer, 1981). With unity inheritance and in the absence of fixed effects, phenotypic performance would be the best indicator of an animals genetic merit. For constant heritability and phenotypic variation, and assuming no correlation between environmental and genetic effects, the accuracy of truncation selection based on phenotypic performance is then given by the correlation between the genotype and phenotype for the trait, $\sqrt{h^2}$, Hazel (1943). Thus at high heritability, phenotype is a good indicator of an animal's breeding value and accuracy of selection may be expected to be high.

In animal breeding populations, however, accuracy of individual selection may be considerably lower than that predicted. The efficiency of selecting on individual performance is reduced when animals are selected across genetic groups or fixed effects. For example, candidates available for selection may depict the effects of birth types (single, twin, multiple births), management practices, generations of prior selection and contemporary groups. As such, the population mean reflects both the genetic mean and additional fixed effects relevant to the trait of interest, requiring the correction of phenotypic records to account for these sources of variability. Moreover, it is usually not possible to compare animals for selection decisions across contemporary groups, since individual performance testing does not enable the breeder to distinguish between contemporary groups with different genetic means. This could be overcome to a degree using unselected control lines as a benchmark for environmental trends. However, this is not usually a realistic possibility for animal breeding enterprises. For breeding populations with several contemporary groups available for selection and mating, it may be difficult to make valid comparisons.

Additionally, the requirement for correcting records for fixed effects assumes that appropriate correction factors are known with certainty. A single estimate of the mean of the fixed effect does not account for the variability in fixed effects over time. For example, correction factors for single versus multiple births may be different between years due to diverse nutritional status. As such, correction factors generalised over time to adjust records for fixed effects, allowing comparisons of animals across fixed effect groups, may result in inadequate representations of an animals phenotypic and therefore expected genetic worth. In simulation studies, Wood (1991a, 1991b) noted that the influence of fixed effects on the efficiency of individual selection was an important factor reducing selection response. For populations undergoing continuous selection, accuracy of selection will further decline due to the effects of selection and inbreeding. Phenotypic differences become reduced over time due to changing (co)variances, and it is less easy to differentiate individuals on the basis of their own records. These types of effects are not accounted for with individual selection.

However, the major disadvantage of selecting on individual performance is that several sources of information available to aid in the prediction of genetic merit are not used. In addition to an individual's own performance for a trait, repeated records and information from several types of relatives may provide a better prediction of an individual's genetic merit, particularly for lowly heritable traits. In this scenario the expense of performance testing for selection on individual performance alone may not be justified since selection accuracy and response may be low. Additionally, there are several categories of traits which may not be measured on individuals available for selection. Some examples include sex-limited traits, carcass traits, and longevity or traits associated with reproductive performance in sexually immature animals. The only information available for these types of traits is that obtained from relatives. In both these cases additional use of information would be useful and/or necessary for genetic evaluation purposes.

Despite these factors, however, selection on individual performance is easily implemented and will achieve selection response in many situations where heritability is moderately high (Kuhlers and Jungst, 1990). Alternative methods of genetic evaluation and selection must be recognised to incur higher costs to the breeder, which should at least be offset by greater gains.

2.6.2 Index Selection Procedures

Use of information from relatives can be applied to selection decisions in a number of ways. The simplest approach would be to use both the information provided by the phenotypic value of the individual as well as the difference between family means. This information may be used to constrain selection decisions to either between or within family selection policies, or optimally weighted through combined indexing procedures to take advantage of both sources of information and variation. Additionally, it is possible, using selection index theory, to combine information from several types of relatives rather than confining information use to that provided by specific family structures. The efficiency of these alternatives is dependent on the genetic and phenotypic parameters of the trait of interest. Combined indexing and selection index theory incorporating information from relatives will be discussed in this section. Discussion of selection decisions between and within families is outside the scope of this review.

Combined Index

The phenotypic value of an individual, P_i, expressed as a deviation from the population mean, may be factored into two components: the deviation of the individual from it's family mean (within family deviation, P_w), and the deviation of the individual's family from the population mean, P_f. Selection on individual performance gives equal weighting to these two sources of information (Falconer, 1981). Should individuals have the same phenotypic value, it would not be possible with individual selection to differentiate between their genetic merit without using additional information provided by family means, or other information from relatives. This illustrates the necessity for alternative criteria on which to base selection decisions.

To incorporate information from relatives in selection indices, and obtain appropriate weighing for P_w and P_f, requires the partitioning of phenotypic and genetic variances into observational components between and within families. Fisher (1918) fused biometry and Mendelian inheritance concepts for quantitative traits, which enabled the computation of covariances between relatives. This procedure was somewhat simplified by Wright (1922) using path coefficient methods, which also allows extension of these calculations to situations where inbreeding is important. From Falconer (1981), the intraclass phenotypic correlation (t) between members of families allows the partitioning of the observed total phenotypic variation (V_P) between (V_{P_b}) and within (V_{P_w}) families such that $V_P = V_{P_b} + V_{P_w}$, $V_{P_b} = tV_P$ and $V_{P_w} = (1-t)V_P$. Similarly, the correlation of breeding values between family members (r) enables the partitioning of additive genetic variance (V_A) between ($V_{A_b} = rV_A$) and within $V_{A_w} = (1-r)V_A$ families. For half and fullsib families $r = \frac{1}{4}$ or $\frac{1}{2}$ respectively, in the absence of factors influencing (co)variances and assuming large family sizes. By considering equal family sizes of n members, further partitioning of variances into causal components, accounting for sampling effects, is possible (see Falconer, 1981, for detail).

From this partitioning it is possible to derive the heritability of both family means (h_f^2) and within family deviations (h_w^2), which are analogous to partial regression coefficients on family mean and within family deviation respectively (Falconer, 1981). These two sources of information may be combined, weighted by their partial regression coefficient, into a single index value for predicting genetic merit. The prediction, given the data, of an individuals genetic merit is then $\hat{A}_i = h_f^2 P_f + h_w^2 P_w$, where phenotypic values (P) are expressed as deviations from the population or within family mean respectively. Accuracy of, and response to, selection for a combined index criterion may be increased by a factor of $1 + \frac{(r-t)^2}{1-t} * \frac{n-1}{1+(n-1)t}$ when equal information is available for all individuals and (co)variances remain constant (Falconer, 1981; Lush, 1947). However, as covariances between relatives increase the relative efficiency of combined indices over individual selection would decline.

Combined indices are the simplest method available for the partitioning of information from relatives into separate genetic and environmental components. They are, however, rather limited in their application to animal breeding. Combined indices require repeatable specified population structures and do not use all information available for predicting an individuals genetic merit. However, extended pedigree information is not required for genetic evaluation, so additional expense to the breeder would be expected to be minimal.

Selection Index

Selection index has been the standard procedure of genetic evaluation for several years in animal breeding. It is analogous to the multiple regression of breeding value on all sources of information available, or included, for predicting an animals genetic merit (Falconer, 1981). For a single trait measured, the construction of selection indices incorporating information from relatives or repeated records of the individual is useful in many scenarios for increasing the accuracy of genetic evaluation, particularly when individual performance is unknown or a poor predictor of genetic merit. Selection index theory has two other main applications in animal breeding: firstly, to use information from correlated traits to increase the efficiency of predicting genetic merit, and; secondly, optimally weighting the economic importance of several traits in the breeding objective, along with appropriate use of genetic relationships between traits, to maximise the correlation between aggregate breeding value and the selection objective. These two applications will be discussed in Section 2.6.4 for multiple trait evaluations.

Selection index theory provides the means by which both individual performance and information from relatives can be unified into an index for selection decisions. Selection decisions are then based on the truncation selection of individuals according to their computed index value. The index of an individual (I_i) is:

$$I_i = b_1 P_1 + b_2 P_2 + \ldots + b_n P_n$$

where b are weighting factors, P is a source of information (eg. the phenotypic value of an individual or group of relatives, or repeated records), and subscripts refer to each component source (up to n sources). The most appropriate b values are found by maximising the correlation ($r_{I,A}$) between the index and the breeding value (Henderson, 1963). This is equivalent to maximising the correlation $r_{\hat{A},A}$ between estimated and true breeding value, ie. the accuracy of selection. In order to maximise $r_{I,A}$, it is necessary to have estimates of population phenotypic and genetic (co)variances. Multiple regression equations may then be derived, and solved simultaneously, to provide solutions for the b values, which optimally weight the chosen sources of information (Falconer, 1981). The computed index value is then the best linear prediction of an individuals genetic merit (Henderson, 1963) given the information made available. Some of the desirable properties of classical selection indices, as noted by Henderson (1963), include:

1. The maximisation of $r_{I,A}$ corresponds with minimising the average squared deviations of criteria from true breeding values, thereby minimising prediction error variance.
2. The computed index value is the most appropriate selection criterion given the data.
3. The probability of correctly ranking any two animals on their computed index value is maximised.
4. Under conditions of equal information, unknown means will not affect the correct ranking of individuals.

With several sources of information available it is possible to derive extremely complicated indices for evaluating genetic merit. These, of course, vary in efficiency depending on the amount and usefulness of information incorporated into the index. However, unless $r_{I,A}$ is substantially increased above the value of $\sqrt{h^2}$, it is unlikely that use of additional information from relatives will greatly increase response to index selection over that achieved by individual selection. In addition, time lags may become excessive if information from particular relatives, for example progeny, is required.

Henderson (1963) provides several examples of application of selection index theory to prediction problems, which the reader is invited to refer to.

Assumptions which apply to the derivation of selection indices include multivariate normality, purely additive inheritance, constant genetic and phenotypic (co)variances, known fixed effects, and equal information for all selection candidates. Additionally, when data is available in the form of group means, it is presumed that all individuals within the group are all related to the same degree (Henderson, 1963). In animal breeding populations, the above assumptions may be difficult to satisfy. The effects of selection and inbreeding, and adjustments made to records for fixed effects, may influence genetic and phenotypic (co)variances. Selection particularly is not accounted for in the computation of index values, so individuals with differing prior selection history may not be validly compared. For inbred populations, calculation of covariances between relatives is further complicated if non-additive components of genetic variation are present. As mentioned previously, fixed effects are also not usually known with certainty, and variation in fixed effects is not accounted for. In addition, variable amounts of information may be available for different selection candidates. When true means are unknown, it is then not possible to always rank individuals correctly when their index values are computed with differing amounts of information. Individuals with less information tend to be regressed towards the mean, the extent to which is determined by the value of the information they have available. Further, accurate estimates of genetic parameters may not be available for specific populations. These considerations may reduce the efficiency of selection indices for genetic evaluation.

Several authors have shown index selection to be an effective procedure (McKay, 1990; Sorensen, 1988; Toro et al., 1988). However, it is also noted that selection index becomes less effective as genetic changes occur due to: 1) biased construction of the selection index; 2) bias in fixed effect estimators with genetic trend (Sorensen, 1988); and 3) potential for increased rates of inbreeding (Toro et al., 1988). The more efficient use of family information in an index increases the likelihood of selecting related animals, thus resulting in increased rates of inbreeding resulting from selection. Toro et al. (1988) indicated that in the presence of inbreeding depression, selection response from index selection may be considerably reduced from that predicted due to the accumulated effects of inbreeding and phenotypic depression. This effect was also noted by Quinton et al. (1992). Further, it has been noted that index values may hide important variation both among animals and traits (Brascamp and De Vries, 1992). This consideration may be particularly important as a factor hindering the identification of outliers or favourable mutations.

2.6.3 Best Linear Unbiased Prediction (BLUP)

The properties of BLUP have been outlined by several authors (Henderson, 1975; Kennedy and Sorensen, 1988; Robinson, 1991) for animal breeding and other applications. It is not the aim of this review to detail BLUP procedures as these may be applied to a multitude of prediction problems. Instead, the general theory behind BLUP will be outlined, and factors influencing it's use in animal breeding applications will be discussed.

As with selection index, BLUP is a statistical procedure by which contributions to an individuals phenotypic performance, from genetic and non-genetic influences, may be partitioned appropriately for predicting an individuals genetic merit. Mixed models are used to describe phenotypic variation in the population as a linear function of both fixed and random effects. As such, for a single trait the observed phenotypic variation within a population may be represented, where all genetic variation is additive, by the mixed linear model:

$$y = Xb + Zu + e$$

where y is an observation vector of phenotypic records, X is a known design matrix relating records to their fixed effects, b is an unknown vector of fixed effects, Z is a known design matrix relating records to their unobservable breeding values, and u and e are unknown uncorrelated random vectors, with null means, of additive genetic effects (breeding values) and environmental effects respectively. The second moments are:

$$Var\begin{bmatrix} u \\ e \end{bmatrix}\begin{bmatrix} G & 0 \\ 0 & R \end{bmatrix} \tag{2.5}$$

where $G = A\sigma_a^2$, A is the numerator relationship matrix (NRM), R is a matrix of residual terms (non-additive genetic, environmental and error terms) given by $R = I\sigma_e^2$ where I is an identity matrix, and σ_a^2 and σ_e^2 are the additive genetic and environmental variances respectively (Henderson, 1975; Kennedy and Sorensen, 1988; Quaas and Pollak, 1980). For multi-trait BLUP procedures, G and R are matrices of additive genetic and environmental (co)variances respectively. Key to mixed model procedures is the NRM, which allows information from all known relatives to be included in BLUP analyses for predicting genetic merit.

From Henderson (1975), when fixed effects (b), G and R are known the best linear predictor (BLP) of $k'b+m'u$ is $k'b+m'GZ'(R+ZGZ')^{-1}(y-Xb)$. This is equivalent to classical selection index but using information from all known relatives for predicting an individual's breeding value. However, when b is not known, as is usual, predictions may be biased. In the absence of selection, biasedness may be overcome by obtaining generalised least squares estimates for $\hat{b}$ and substituting these estimates into the above equation. However, Henderson considered this method to be computationally demanding and biased under selection. Alternatively, $k'b+m'u$ may be predicted from $k'\hat{b}+m'\hat{u}$ using the solutions of the mixed model equations proposed by Henderson (1950):

$$\begin{bmatrix} X'R^{-1}X & X'R^{-1}Z \\ Z'R^{-1}X & Z'R^{-1}Z + A^{-1}\sigma_a^2 \end{bmatrix} \begin{bmatrix} \hat{\beta} \\ \hat{u} \end{bmatrix} = \begin{bmatrix} X'R^{-1}y \\ Z'R^{-1}y \end{bmatrix} \tag{2.6}$$

Mixed model procedures then allow the simultaneous estimation of best linear unbiased estimates (BLUE) for fixed effects concurrently with best linear unbiased predictions of breeding values. The major properties of BLUP are easily recognised from it's acronym: *Best* meaning BLUE and BLUP estimates of the variables (fixed and random respectively) have minimum mean squared error, corresponding to increasing the correlation $r_{\hat{u},u}$; *Linear* since effects are defined by linear functions of the data; *Unbiased* as the expectation of the estimate is equivalent to the expectation of the quantity being estimated; and *Prediction* for predictors, distinguishing prediction of random effects from estimation of fixed effects. In addition to the properties of selection index, BLUP allows correct ranking of individuals in all generations by accounting for fixed effects and the effects of selection and inbreeding. In the absence of fixed effects, BLUP may be considered simply as a set of custom index weights for each animal.

Henderson (1975) indicated that BLUE estimates of fixed effects are equivalent to generalised least squares (GLS) estimators in the absence of selection. As such, variation in fixed and random effects fully explains observed phenotypic variation within the population. Under selection, Kennedy and Sorensen (1988) showed that inclusion of the NRM in the mixed model equations accounted for changes in genetic variation due to selection disequilibrium and inbreeding, through accounting for changing covariances between relatives. Further, the NRM accounts for increasing drift variance under selection (Sorensen and Kennedy, 1983). However, changes in genetic variation as the result of gene frequency changes, for traits controlled by a finite number of loci, is not accounted for, although mixed model methods ensure good approximations of this effect (Kennedy and Sorensen, 1988). As such, estimates of fixed effects from mixed model procedures would be expected to remain unbiased, unlike GLS estimators of u or b (which are considered as fixed effects), in the presence of selection. These results only apply, however, if all sources of information relating to selection decisions are included in the analyses. This enables individuals to be validly compared across different time frames and fixed effects. Additional properties of BLUP as noted by Robinson (1991) include:

1. Predictors of u are 'shrunk' towards the mean compared to GLS estimates obtained by considering u as a fixed effect.

2. BLUP leads to the recovery of inter-block information. This is most useful when sub-classes are unequal and for improving the efficiency of estimating fixed effects.

3. BLUP is supported by a number of viewpoints from classical statistical theory (eg. BLUP is Bayesian with flat priors), although exponents of different schools may argue finer points. That is, BLUP is a valid statistical method for animal breeding applications.

There is little value for this review to detail alternative models to which BLUP procedures may be applied. The animal model, in which a u is fitted for each animal, or equivalent (eg. reduced animal model fitting parents only), is currently considered the most efficient model available for animal breeding applications. Extensions to consider non-additive effects in BLUP analyses will have important impact in the future. Of most importance is that the model chosen accurately reflects genetic and non-genetic determinants for the traits of interest. It is only through appropriate modelling that data are turned into information, which will be of little value if the model is incorrect.

Of interest to animal breeders, in terms of genetic evaluation and selection decisions for additive traits, are some of the potential deficiencies of BLUP. All above-mentioned properties have assumed random mating. There are few studies investigating the efficiency of alternative BLUP procedures for predicting genetic merit under different mating systems. Hudson and Schaeffer (1984) indicated that the animal model was efficient for predicting genetic merit with a non-random mating system, although sire and modified sire models were considerably less efficient. In this example, however, a considerable amount of 'pseudo-random' mating was simulated, so data structure may not have been greatly affected. Kennedy and Sorensen (1988) suggested that the animal model was suitable for non-random mating systems by accounting for contributions by mates. This may not be the case for less complete models or where data is very unbalanced. As such, there is need for work in this area.

Additionally, when selection is not solely based on information provided by the analyses (eg. criteria other than estimated breeding values when data are not included in the analyses) BLUP may no longer be unbiased. This effect has received little investigation by researchers, although it is recognised that selection decisions are not usually confined to EBV's alone, particularly when multiple stage selection procedures are present. Unless information from other correlated traits is available, there may be no benchmark by which this effect can be accounted for. The degree to which this factor influences the efficiency of BLUP is unknown.

Of further concern is that additive BLUP procedures do not account for the effects of inbreeding depression, although the NRM (correctly used) allows for increasing covariances between relatives due to inbreeding. As such, in the presence of inbreeding depression, accuracy of genetic evaluation for additive merit may be reduced. Various methods have been proposed to deal with non-additive genetic considerations when predicting additive genetic merit. Maki-Tanila and Kennedy (1986) included a dominance relationship matrix (D), in addition to the NRM, into the MME but found that predictions of additive genetic merit, although improved, remained biased in the presence of inbreeding. Kennedy and Sorensen (1988) suggested that including F as a covariate in the model (with D) would aid in accommodating the effects of inbreeding depression. This proposal was tested by Uimari and Kennedy (1990) who found that estimates of additive genetic merit were unbiased in the presence of selection, and for complete dominance at all loci, only when the model included additive and dominance effects and F as a covariate.

Uimari and Kennedy (1990), however, computed D from elements of A while ignoring inbreeding. Hence the need to include F as a covariate. Smith and Maki-Tanila (1990) parameterised dominance models under conditions of inbreeding using six genetic parameters to describe additive and dominance effects and inbreeding depression. This gametic model properly accounts for additive and dominance effects as well as inbreeding depression, but is computationally demanding. The applications of such mixed models would undoubtedly improve estimates of additive merit, although their real virtue may lie in enabling the development of breeding programs which capitalize the use of dominance variation, in addition to additive variation, while accounting for inbreeding effects. Moreover, the theory may be extended to crossbreeding applications. However, further development of theory is desirable, and computing resources usually limit the feasibility of applying more complicated models to practical situations.

For breeders selecting within closed purebreeding herds, two points need to be addressed from an appropriate perspective when considering these apparent deficiencies of commonly used additive BLUP models. Firstly, no alternative methods to BLUP evaluation exist which account for non-additive genetic effects. Secondly, relatively low levels of inbreeding in many populations reduce the necessity of using more complicated mixed models. This is illustrated by the fact that many practical applications ignore the effects of inbreeding altogether (Hudson and Kennedy, 1985; Sorensen, 1991; B. Tier, pers. comm.). Hence, although practical applications of

BLUP may operate at a lower accuracy than is theoretically possible, BLUP is still the most accurate genetic evaluation procedure currently available to animal breeders.

The efficiency of BLUP procedures, like selection index, is dependent on obtaining good estimates of (co)variances. Characteristics of the data are also important determinants of the efficiency of BLUP analyses. Henderson (1974) has shown that ranking of individuals is largely unchanged when parameters of variable accuracy are used to define G and R. BLUP tends to be more robust than selection index in this situation since the structure of the mixed model equations 'smooths' inequalities of the data. In addition, data structure, content and use for BLUP analyses have been investigated by several researchers (Long et al., 1990a; Satoh and Nishida, 1990; Wood et al., 1991a, 1991b). For example, the advantages of collecting additional data over that required for a particular selection index depends on the impact, or value, of that data on BLUP solutions. Satoh and Nishida (1990) have shown that increasing the amount of data available for analyses has more impact on improving the accuracy of genetic evaluation for traits of lower heritability, where accuracy in prediction is lower and less stable. Where pedigree errors exist, Long et al. (1990a) showed that the efficiency of BLUP was reduced, more so for traits with low heritability, although response obtained was still greater than that obtained for selection index.

Since all available information may be used in BLUP analyses, overall data structure may also influence the accuracy of selection. Wood et al. (1991a) showed that accuracy of prediction may be improved by increasing family size (families unrelated) and establishing genetic ties across fixed effects. However, within the same contemporary group, closely related animals tend to be evaluated less efficiently relative to unrelated individuals due to dependencies within the mixed-model equations. These factors may influence the accuracy of predicting each individual's breeding value, ranking individual animals and therefore selection decisions. However, as shown by Klieve et al. (1993) it is not generally necessary to consider accuracy of the EBVs when making selection decisions. Ranking for selection is sufficient to make use of BLUP for improving selection response. Moreover, data structure may be manipulated by the breeder with appropriate breeding program design.

Regardless of the above considerations, substantial evidence exists for improved response to selection using BLUP procedures over alternatives from simulation. Mabry and See (1990) showed that selection on phenotype, within contemporary group, was less effective than selection on within herd BLUP estimated breeding values. Belonsky and Kennedy (1988) also noted the superiority of BLUP over individual selection, although relative differences between selection alternatives decreased with increasing heritability. Sorensen (1988) and Roehe et al. (1992) showed that BLUP was superior to selection index for both single and multiple trait selection schemes respectively. Quinton et al. (1992) additionally indicated that BLUP was superior to individual selection over several heritabilities and achievable selection intensities. As such, it is generally concluded that the superiority of BLUP is well established, although the relative superiority of BLUP will depend primarily on the trait(s) in question, data structure (Sorensen, 1988) and attitudes to inbreeding.

Such consistent research results have led to the development and implementation of BLUP procedures into breeding programs, both within herd and at the national level (Hudson and Kennedy, 1985; Long et al., 1991; Sorensen, 1991). The main criticism levelled at the use of BLUP for animal breeding applications has been in the area of accumulated inbreeding with the use of more accurate selection alternatives (Quinton et al., 1992). This is an area where much work needs to be done.

2.6.4 Multiple Trait Genetic Evaluation Procedures and Selection

Selection decisions are not usually confined to a single trait in animal breeding populations as several traits of economic importance may be of interest to the breeder. The principles of genetic evaluation must, therefore, be applied to predicting an individual's aggregate genetic merit for selection decisions. When several traits are to be used as selection criteria, the most efficient method of selection is to combine them into a single value on which to base selection decisions (Hazel, 1943). The emphasis placed on each trait to maximise aggregate genetic merit is defined by the breeding objective, which indicates the relative economic value of objective traits. Given this, and identification of measurable traits, the most appropriate selection criteria may also be identified. Combined with knowledge of the relationships between objective traits and criteria traits, the appropriate selection criterion may then be derived.

In addition to combining information from different traits into a single selection criterion, of importance is the use of information provided by correlated traits for genetic evaluation. Correlated traits provide an additional source of information which may enable the accuracy of genetic evaluation to be improved. The principles of selection index and BLUP, reviewed above, may be applied to multiple trait evaluation and selection procedures. Only brief mention will be made here of additional considerations required for multiple trait selection programs.

Multiple Trait Genetic Evaluation Procedures

Analyses of animal breeding data have shown several examples of correlations between traits. When traits are correlated genetically and/or environmentally, information is available from several sources to improve the accuracy of genetic evaluation through the use of multiple trait evaluation procedures. The extent to which this information improves the accuracy of genetic evaluation is dependent on the magnitude of the correlations between the traits in question, and how much additional useful information they can provide.

Both selection index and BLUP procedures can be simply expanded to include information from other traits for genetic evaluation purposes. Statistical properties are as mentioned previously, the additional requirement being that genetic and environmental (co)variances between and within the traits are known. Multiple trait BLUP procedures, as expected, make much better use of the information from correlated traits by including all known records and solving simultaneously for both fixed and random effects. The effects of selection and inbreeding are also accounted for within and between traits for all traits included in the BLUP analyses, with no knowledge of relative selection emphasis on the component traits required. Unlike selection index procedures, multiple trait BLUP may also account for prior selection, or sequential culling procedures, using information from correlated traits (Henderson, 1975; Pollak and Quaas, 1981; Quaas and Pollak, 1980).

For traits which are genetically uncorrelated, there is no advantage to a multiple trait evaluation procedure unless strong environmental correlations are present. In this situation, information on environmental correlations may improve the BLUE estimates of fixed effects and, correspondingly, increase the efficiency of genetic evaluation. With no fixed effects, secondary traits act as covariables to improve accuracy of evaluation. In the absence of any correlation, no additional information can be used. In this situation, separate single trait procedures are adequate, and desirable from a computational viewpoint.

Defining Aggregate Genetic Merit

As noted above, predictions of genetic merit for individual traits used as selection criteria must somehow be combined into a single value on which to base selection decisions. However, estimated breeding values for different traits may vary in accuracy due to differences in trait heritabilities and the amount of information available. This problem is accommodated to some extent in BLUP EBVs, although difficulties may arise in selection index should animals be compared with unequal observations. Additionally, traits differ in relative economic importance, and hence their emphasis in determining aggregate genetic merit. Selection index theory is the traditional approach used to combine economic and genetic information into an linear index which defines aggregate genetic merit. This application is usually confined to situations where the same type of genetic evaluation procedure has been used to predict breeding values for all traits included as selection criteria. Non-linear functions of merit were discussed in Section 2.5 and will not be addressed further. Moreover, economic values are assumed known, as the derivation of economic values for objective traits is outside the scope of this review.

Hazel and Lush (1942) tested several selection strategies for improvement in aggregate merit. Their discovery that selection response was greater for 'total score' methods of selection, compared to multiple trait selection with independent culling levels or tandem selection procedures, was incentive for Hazel (1943) to develop selection index theory which was applicable to multiple trait selection schemes. Selection index theory could be applied to the multiple trait selection problem given knowledge of the relative economic values for each trait and phenotypic and genetic (co)variances (Hazel, 1943). In this situation, the appropriate emphasis for each uncorrelated trait in the index to maximise aggregate genetic gain (i.e., maximise $r_{I,A}$), is equal to $a_i h_i^2$, where a and h^2 are trait i's economic value and heritability respectively. Aggregate genetic merit is then defined by a weighted linear combination of additive criteria. This theory may be extended to correlated traits if genetic and environmental (co)variances between the traits are known. Assumptions relevant to multiple trait selection index theory were described in Section 2.6.2.

The work of Hazel (1943) dealt with combining phenotypic measures of merit for each trait where all selection candidates had equal information contributing to their selection index values. In this situation selection index values are of equal accuracy. However, when aggregate merit is to be evaluated from BLUP estimated breeding values, it is well recognised that the accuracy of each individual's EBVs will vary depending on the amount and value of information available for each individual. Lin (1990) provided a method to compute index weights in the restricted case, assuming (co)variance matrices of estimated breeding values and true breeding values are equivalent (ie. accuracy = 100% and the breeding values of all individuals are equally well estimated). This is not common from standard BLUP analyses. Consequently, Schneeberger et al. (1993) considered the influence of accuracy and found that provided all individuals had EBV's for the same criteria, b values were the same for all animals. As such, b values only depend on economic values of the objective traits and the genetic (co)variances among the selection criteria and the traits in the objective.

Both Lin (1990) and Schneeberger et al. (1992) showed that an index of EBV's was analogous to classical selection index theory for phenotypic measures. This was under the assumption that BLUP estimates already account for genetic and environmental (co)variances between criteria fitted in the model. As such, the procedure for indexing EBV's will result in maximum additive genetic gain. Achievable gains in aggregate merit and component traits may be simply predicted for selection index from theory. However, for BLUP EBVs prediction of achievable gains requires assumptions to be made on the population structure (Schneeberger et al., 1992).

2.7 Conclusions

Where breeding programs are to be compared in terms of selection response, simple classical response theory may be adequate in the simple case and over short time periods, but increasingly inaccurate with greater design complexity and time scale. The main shortfall of simple classical response theory lies in it's failure to account for the effects of small population size and selection on genetic parameters, and hence response to recurrent selection over time. Population size and structure have important consequences for selection response through genetic drift, inbreeding and calculation of selection differentials. Further, disequilibrium resulting from the selection process itself must be accounted for. Moreover, these factors may act jointly to influence genetic parameters (Keller et al., 1990). As such, selection response is usually reduced from that predicted under simple theory (Gallego and Caballero, 1990). Although accounting for these factors reduces bias in predictions under a purely additive model, some authors have shown that generally breeding program alternatives do not rerank in their relative merit when response is predicted using either classical or more theoretically correct approaches (Wray and Hill, 1989). This may be the case for simple scenarios, but is unlikely to be the situation where complex alternatives are to be compared, particularly for substantial differences in selection intensity, effective population sizes or accuracy of genetic evaluation.

Of the factors noted above, disequilibrium resulting from selection, and inbreeding contribute most to reductions in response through depleting genetic variation. The effects of drift and adjusting selection differentials for population size and structure were found to be relatively minor when predicting selection response (Keller et al., 1990; Verrier et al., 1990). Both disequilibrium and inbreeding effects are of greater consequence when selection intensity, trait heritability and accuracy of selection are high. However, disequilibrium has greater impact on selection response in the short term, is relatively unaffected by population size at a given selection intensity and stabilises over time, whereas inbreeding effects accumulate over time and are of greater importance in the long term. Hence, although several common factors contribute to disequilibrium and inbreeding, these effects are of concern over different time scales.

Further, population size has an important impact on the effects of inbreeding even at the same selection intensity.

In addition to depleting additive genetic variation, inbreeding was also seen to reduce selection response in the presence of inbreeding depression, where traits are controlled by loci with directional dominance and/or overdominance. Inbreeding depression can directly reduce response by decreasing the population mean, introducing bias to genetic evaluation procedures (Maki-Tanila and Kennedy, 1986) and reducing selection intensities through lowering reproductive rates. Moreover, considerable evidence exists for inbreeding depression in animal breeding data (Bereskin et al., 1968; Takahashi et al., 1991). From classical theory and analyses of data, the effects are usually presumed to be linearly related to the mean inbreeding coefficient, although some non-linear effects have been noted (Takahashi et al., 1991). Regardless, predicting the effects of inbreeding depression may be as, if not more, difficult than predicting the effects of inbreeding on additive variation, particularly in the presence of selection. Hence, it is usually ignored in studies on the efficacy of breeding programs.

Little can be done to alter the effects of selection disequilibrium on selection response. However, much research has attempted to address the effects of inbreeding, both examined favourably as a tool for increasing between family genetic variation (Berg and Christensen, 1990; Lush, 1947) and as an unfavourable effect which must be minimised. Using deliberate inbreeding programs in livestock populations would not appear to be of much use due to accumulation of the above-mentioned detrimental effects of inbreeding and the long time lags required between cycles of inbreeding and selection (Lush, 1947). However, alternative methods which could be used to control inbreeding may also reduce selection response in the short term through decreasing the efficiency of selection and/or reducing selection differentials. As such, their value to breeders is somewhat limited, particularly when future gains are discounted to current values (Goddard, 1983).

For example, within family selection (Dempfle, 1975; De Vries et al., 1990), increasing the proportion of individuals selected (Robertson, 1970), increasing generation intervals (De Roo, 1988b), avoiding matings between relatives (De Vries, 1990) and reducing accuracy of selection and/or variation in family size (Toro and Nieto, 1984; Toro and Pérez-Enciso, 1990) have all been shown to reduce the accumulation of inbreeding. However, very few methods were shown to correspondingly increase, or even maintain, selection response over alternatives despite maintaining higher levels of genetic variation. Where selection differentials were deliberately maintained, through differential use of selected individuals, the likelihood of maintaining selection response while reducing rates of inbreeding was much higher (Toro and Pérez- Enciso). Undoubtedly, however, methods which control inbreeding may be more beneficial than noted in the presence of inbreeding depression.

The impact of assortative mating systems on selection response, in particular positive assortative mating (PAM), was also examined. Under normal conditions of intensive individual selection, the relative efficiency of PAM over random mating was very low, in the order of approximately 5% (Tallis, 1989). However, with more accurate selection criteria (eg. BLUP EBVs) the relative efficiency could be considerably higher, making PAM a valuable tool for increasing selection response. Shepherd and Kinghorn (1994) found that the relative efficiency of PAM over random mating exceeded 25% for EBV selection over ten generations (ignoring inbreeding). However, PAM increases rates of inbreeding above that of random mating, through increasing selection between families and the frequency of matings between related individuals. Hence the effects of inbreeding are likely to offset, in part, the value of assortative mating systems for improving selection response.

Mate allocation and mate selection (achieved using mate selection rules) were considered as alternative methods to traditional selection and mating systems. Where mating pairs are specifically selected using mate selection rules, total merit is altered only where such action results in changes to the progeny mean or variation among the progeny, including progeny EBVs (Kinghorn, 1987). Moreover, such rules are only appropriate where individuals re-rank in superiority according to their comparison for individual versus paired merit (Allaire et al., 1985). Further, the relative efficiency of mate selection rules over traditional alternatives is very dependent on the type of formulation which describes total merit. For example, where paired merit is strongly attributable to merit for additive gain, total merit is unlikely to be improved with mate selection rules (Allaire et al., 1985). Hence, merit should be described by strongly non-linear functions, and sufficient differences between alternative pairs must exist if selection decisions are to be altered.

Of the mate allocation and mate selection scenarios reviewed, the greatest attribute of these procedures was in increasing the flexibility of formulating, and accounting for, components of non-additive progeny merit mediated through characteristics of selected individuals and their potential mates. However, when non-additive merit was the result of economic interactions between mates and/or traits, or due to non-additive modes of inheritance alone, mate selection rules did not appear to facilitate improved cumulative gain. A consistent tendency, in these scenarios, was for non-additive gain to be improved at the expense of additive gain, resulting in minimal changes in total merit (Allaire et al., 1985; Allaire and Barr, 1990). In contrast, where additive and non-additive genetic components of merit were considered, mate selection rules aided in improving total and cumulative merit (Kinghorn, 1984; Toro and Pérez-Enciso, 1990; Toro and Silio, 1992; Wray and Goddard, 1994). Once again, however, it must be noted that the results of mate selection rules are very dependent on their formulation and objective. Further, high selection intensity and low accuracy of selection tend to hinder the ability of mate selection rules to alter selection response (Allaire and Barr, 1990; Kinghorn, 1987).

Of more predictable impact, genetic evaluation systems were found by several researchers to have a significant influence on response to selection through altering the correlation between true and estimated breeding values. The superior accuracy of BLUP procedures, using an animal model or equivalent, is well recognised, although the relative efficiency of selecting on BLUP versus alternative criteria (eg. individual performance or selection index) is dependent on trait heritability and data structure (Sorensen, 1988). Of concern to breeders, however, may be elevated rates of inbreeding seen from selection on BLUP criteria (Belonsky and Kennedy, 1988; Quinton et al., 1992; Sorensen, 1988; Wray, 1989). This phenomenon is related to the increased use of information from relatives in predicting genetic merit, resulting in greater selection between families. As such, with high rates of inbreeding the efficiency of selection on BLUP criteria may be reduced. Moreover, the effects of inbreeding may accumulate to unacceptable levels, reducing the relative efficiency of selecting on BLUP over alternative criteria (Quinton et al., 1992). Hence, practical implementation of more accurate genetic evaluation systems may be undesirable for breeders operating under conditions of intensive single trait selection and small closed herd size unless consistent procedures are developed which maintain the advantages of BLUP while reducing rates of inbreeding.