

CHAPTER 1

Introduction

1.1 Introduction

... decision makers can satisfy either by finding the optimum solution for a simplified world, or by finding satisfactory solutions for a more realistic world. Neither approach, in general, dominates the other, and both have continued to co-exist in the world of management science.

Simon (1979)

Simon addresses the dilemma faced by economists, between working efficiently in an unreal world, or inefficiently in a real one. This general problem of inevitable compromise is, of course, found in many areas. In quantitative genetics, improvements in the estimation of breeding values, through, for example, an improved incorporation of the information from the records of relatives, refines the mechanisms used for differentiating between individuals on the genetic merit of a particular trait. Such improvements represent significant refinement in selection

methodology. To optimise the selection process there are still considerable developments necessary to make the use of estimates most efficient for those actually making selection decisions on real breeding stock.

An integral part of this refinement arises from a more efficient management of the risks associated with the decision making process. While risk is an integral part of both seedstock and commercial livestock production, not all the risks associated with such enterprises can be efficiently managed. While the more commonly addressed risks such as those related to price variation (input and product) are present, these will generally not be controllable, except through better market targeting. Further, any selection scheme minimising costs is likely to compromise the potential for genetic progress, thus, minimising costs must be a secondary objective subject to the achievement of other objectives.

More significant will be the direct impact of selection decisions on productivity and thus profitability - including the level and impact of inbreeding arising from selection decisions. These factors cannot all be handled simply, one reason is that performance and inbreeding are closely related outcomes. Improvement of predicted performance is central to most selection schemes, but a concentration on this as the sole objective of a breeding program could lead to longer term problems outlined below.

Conventional economic analysis relies on the mean value as an indicator of the outcome. Risk analysis, however, considers the likelihood, and implications, of different outcomes. In animal breeding, a similar separation can be noted. A reliance on the best unbiased estimate of the breeding value, the *ebv*, is frequently recommended. While this objective approach potentially offers considerable benefits through increased response, some refinement has been suggested by several researchers. This may be to allow additional benefits to be gained through better utilising the potential of less accurately recorded animals or through the reduction of the negative impacts associated with increases in inbreeding. Thus, there are perceived risks associated with a selection scheme entirely dependent on animals'

ebvs, with the adoption of a broader perspective on merit offering an approach by which many of the risks inherent in the selection process can be better addressed.

1.2 Risk in the Selection Process

Under random selection there is an equal likelihood of selection for all individuals. This is not a desired outcome where there are defined breeding objectives. However, what should be recognised in any selection scheme is whether the selection process is having effects other than those desired through the differential probabilities of selection of individuals. An early point, relating to the negative impact of directed selection, was made by Morley (1954) who suggested that in any population undergoing selection a positive correlation between inbreeding in progeny and merit in parents would be an automatic consequence of selection. His results, indicating a weak, but significant, positive correlation between inbreeding and genetic superiority in traits under selection, supported this contention.

Robertson (1961) considered the issues raised by Morley and found inbreeding under individual selection to be greater than that calculated by simple methods. He noted that this effect would be increased when selection was on a combination of individual and family measurements, except where there was significant non-genetic variation between families. The extension of this view relates to the co-selection of relatives. While Morley's work was prior to the use of BLUP estimates of breeding value, it does suggest potential problems in inbreeding arising from highly efficient selection mechanisms like BLUP. Recent interest in work which considers the relationship between selection using BLUP and resultant levels of inbreeding would appear to support such conclusions.

For those making selection decisions, appropriate use of information is a difficult process - there being a range of factors which can affect choice. With regard to the

use of the *ebv*, it is often suggested that decision makers base selection on the *ebv* alone, and where the accuracy of such estimates is available it is used on the basis of more accuracy is better (Freer & Sunstrom, 1991). This narrow perspective ignores factors such as the purchase price of animals, their potential performance and the future levels of inbreeding in the herd, all aspects which are likely to influence real world decisions. High accuracy animals continue to attract high premiums, producers being confident of the performance of the progeny of such animals. However, to have higher accuracies, such animals must have more extensive networks of relationships, meaning that there is also a potential for increased levels of inbreeding.

Van Raden, Freeman and Rothschild (1984) looked at different approaches to selection. They adopted a two stage method where, initially, animals of lesser merit were selected. In the second stage the optimal mating group was selected from this initial group. This method looked to the preferential selection of lesser known animals of lower merit over those with higher merit. Although some advantage was associated with this approach the additional cost associated with its application led to the conclusion that, in practice, it was not likely to be a viable option.

More specific consideration of the issue of using accuracy in the decision process has been more recently given by other researchers. Woolliams and Meuwissen (1993) applied a Bayesian framework to decision rules. They concluded that this framework could be used to provide a flexible means by which farmers might account for risk preferences in selection decisions. It was suggested that there could be some positive benefits from the use of less accurate animals. Although these animals may have lesser *ebvs*, their true breeding value could potentially be above that of marginally superior high accuracy animals due to the greater prediction error variance. Thus, the implications of lower accuracy could extend to lower prices, marginally higher returns and lesser inbreeding.

Another component of risk associated with the use of information in animal breeding programs is the methods used to select breeding stock. BLUP effectively utilizes the

information on relatives to maximize the accuracy of *ebvs*. However, there is increasing concern over the impact on inbreeding, or effective population size, of different methods of selection. Dempfle (1990), in considering animal breeding schemes, identified a conflict between maximizing short and long-term response. Recognising the implications of small effective population size in real breeding populations, he recommended that, to avoid reduced efficiencies in the overall selection process, restrictions on the selection process were needed to maintain reasonable levels of effective population size. He also noted that in the case of family selection, the selection criterion will be heritable - with individuals from more *successful* families having more *successful* offspring. Dempfle's concern relates to the correlation between the estimated breeding values and the effect on the effective population size.

The issue of the coselection of relatives has also been considered by Wray and other co-workers. Wray and Hill (1989) found that both the accuracy of selection on an index and the rate of inbreeding were higher when the index was based on larger numbers of records from relatives. Wray and Thompson (1990) noted that *in a population undergoing selection, families superior for the selected trait will contribute more offspring to the next generation than inferior families*. The obvious impact of this differential selection will be the potential for higher rates of inbreeding in selected population (see also Wray, Woolliams and Thomson, 1990).

Although there has been some concern about the dependence on BLUP estimates in selection schemes, this has continued to be recommended as the best approach. Quinton, Smith and Goddard (1992), assessing different methods of selection carried out with a fixed level of inbreeding, have further questioned this dependence. Where this constraint is placed on a selection scheme, the superiority of BLUP in quantifying merit is far less effective. Their work questions a basic approach currently adopted to selection. An increasing number of researchers are now recognising the relationship between methods of selection and the associated inbreeding rate.

Thus it is apparent that the objectives of maximising genetic gain and minimising inbreeding cannot be treated in isolation. As mentioned above, the accuracy of the estimation process for breeding values is also a factor in the achievable level of genetic progress. Accuracy and inbreeding are considerations through which decision makers can, at least to some degree, manage the price and production risks that they face. Although interrelated, accuracy and inbreeding are also far from interchangeable elements and must also be considered separately.

1.3 Objectives

How can the decision maker (in selection) most efficiently use available information to manage issues of risk? How can the preferences of decision makers be accommodated in current or enhanced selection practices? If risk is to be incorporated into the selection decision-making process there are clearly several issues which require consideration.

One assumption that underlying many decisions is the preference for higher accuracy. While the value of good information cannot be questioned, there can also be costs associated with the greater level of information. In the case of more accurate *ebvs* there are several possible costs. These issues are addressed in Chapter 3.

The single time period perspective adopted in Chapter 3 is useful to consider the issue regarding preference for accuracy. However, what is the impact over time from decisions where a consideration of risk moves from the traditional single objective of maximising expected response and also considers change in inbreeding? This is addressed in Chapter 4 through a consideration of the joint regulation of genetic gain and inbreeding.

While inbreeding and accuracy are the focus of considerable attention it is interesting to consider whether there is an earlier point at which the problem can be managed. Thus, is it most effective to address the problems arising from inbreeding, or is there a *problem* that in turn leads to inbreeding and which is the real point at which the problem should be addressed ? One possibility here is the network of relationships between individuals in population.

Finally, if the strategies developed in Chapters 3 and 4 do provide some mechanisms for addressing these issues, how do we decide what level of any strategy to apply ? Chapter 4 assesses a range of different levels of compromise between risk (of inbreeding) and returns (from genetic gain) and in Chapter 5 a mechanism for assessing and comparing such strategies is discussed and evaluated.

CHAPTER 2

Utility and Risk in Selection : Economic and Genetic Perspectives

2.1 Introduction

The estimation of breeding values represents a major step in the development of efficient selection techniques. However, there is growing concern as to the long term effectiveness of selection dependent entirely upon estimates derived from Best Linear Unbiased Prediction (BLUP). Such concerns relate primarily to the practical implications of such usage, of particular concern being the impact of selection schemes on inbreeding levels. Strong reservations regarding dependence of selection programs on BLUP estimates have been expressed by a number of researchers, including Dempfle (1990) and Quinlan *et al.* (1992) - both groups demonstrating the potential impacts of different selection processes on inbreeding levels.

While these concerns relate to the specific implications of applying BLUP estimates to the selection process, general reservations regarding the inevitable impact of intensive selection practices are not new. Morley (1954) saw increased inbreeding as

an inevitable consequence of more intensive selection - this arising from the unequal likelihood of animals being included in the following generation.

Considerable work has been carried out to identify techniques by which the increase in inbreeding associated with such selection can be managed. In addition, varied applications are being developed in which *ebvs* are incorporated into selection programs, providing greater flexibility in the application of *ebvs* by satisfying a range of objectives. Henderson's (1973) achievement through BLUP, while from one perspective representing an ultimate step in estimation can also be viewed as an initial step in the development of efficient selection practices optimising the usage of available information. The efficient application of information is of increasing significance in animal breeding, reflected in the perspective presented by Cartwright (1969), who looked to future trends in animal science, recognising the increasing importance of the information available to the specialist and the advice imparted from it.

To move from the narrow objective of maximising expected genetic response to optimising returns and outcomes through clearly defined bioeconomic selection objectives requires a refinement in the selection process. This objective should assist in maximising the benefits from the information available through the normal selection process. However, it is apparent that there is no easy selection objective, with Robertson (1977) concisely identifying the inevitable tradeoff in the overall selection process thus:

This perhaps is the moral of this paper. The individuals of one generation are the parents of the next - if they are accurately evaluated and selected in the first generation, the variation between families will be reduced in the next. You cannot have your cake and eat it too.

Before considering processes and methodologies by which such objectives are developed and evaluated, attention is directed to the objectives of the breeding programs - involving discussion of the concepts of merit, utility and risk in the animal breeding context. The final step in this review is a consideration of a particular application, the selection of mates.

2.2 Definition of the Breeding Objective

The overriding objective for any producer relates to returns from his herd, this perhaps best related to the maximisation of the expected performance. Cunningham (1974) suggested that, essentially, there were three factors involved in the profitability of beef animals, identifying:

- the probability of survival
- growth rate
- proportion of meat in the carcass

While these elements remain of central importance to current production and continue to be addressed in production enterprises, there are new issues which are taking centre stage in new breeding programs. Returns, for example, can only be implied from available information with a degree of uncertainty.

Anderson (1988), in addressing the issue of risk in livestock improvement programs, considered a range of potential areas where risk is a major factor. While he concluded that the benefits from dealing with risks may, in animal breeding, be rather minor, so justifying the lack of consideration by many researchers of this aspect, he did see some areas where consideration could have significant benefits. Such benefits would occur particularly where there are multiplicative interactions between variables in a profit function. While identifying limited areas of opportunity for the control of risk,

Anderson tempered this judgement with a recognition of the value of detailed case studies, such studies providing a practical assessment of his theoretical, outsiders impression of the area.

2.2.1 Profit vs Utility Maximisation

It is frequently assumed that the aim of producers is profit maximisation (Lin, Dean & Moore, 1974), however, this aim is neither well defined nor, frequently, clearly understood. The objective of profit maximisation implies the maximisation of the expected net return, ignoring the variation in this return and thus ignoring the many aspects of risk in the production enterprise. More commonly, decision makers act to maximise some broader objective, this encompassing both profit and personal preferences - including, for example, preferred physical characteristics, breed and risk elements in a production enterprise.

While profit maximisation aims at the achievement of the highest expected profit, a utility maximiser imposes constraints on the level of risk in the achievement of such returns. This may reduce the expected level of returns but better address the needs of the decision maker by providing greater certainty and consistency in such returns.

For many producers there is an increasing need to look to the risks in production and to apply the mechanisms available for handling the risk in product price. To do this effectively, the objectives of the production enterprise need to be clearly defined. Lin and Allaire (1977) identified a component of this problem in a discussion of the selection of dairy cows for profit, finding that maximising production was an inferior tool to a broader objective encompassing economic, environmental and resource aspects. Extensive work in this area has been undertaken through a range of approaches including the use of dynamic programming to address management and replacement policies (e.g. Van Arendonk, 1985a, 1985b).

The increasing application of utility in areas such as portfolio theory applied to selection strategies (e.g. Schneeberger, Freeman & Boehlje, 1982) has demonstrated the growing recognition of the value of extending the assessment of benefit to an inclusion of the risks associated with their achievement, and thus a move in the perception of decision makers from profit to utility maximisation. The presence of a wide range of marketing programs in agricultural commodities, providing mechanisms by which producers can hedge their price risk through the removal of some of the natural fluctuation, offers strong evidence of the basic risk aversion of agricultural producers.

2.2.2 Utility and Merit

Utility, in general terms, refers to the usefulness of an object (Garmonsway, 1979). From an economic perspective, utility, encompassing the concept of pleasure in circumstances or objects, can be defined *as the ultimate goal of all economic activity* (Bannock, Baxter & Davis, 1987). Although this extends the initial, more general definition above, it remains general and non-operational due to the broad nature of utility, which, like merit, refers to that which is preferred.

Falconer (1981) refers to merit as *the object of selection, whatever it may be*. As with definitions of utility, more merit will always be preferred to less. Comparison between degrees of merit are possible to make and, as with utility, producers are generally assumed to have the objective of maximising merit. One major difference between merit and utility is in the application. Utility is normally reflected in decision maker's preferences, while merit is used to provide a ranking on animals - thus merit can be viewed as a specific form of utility. It is not surprising that an increasing use is being made of utility in animal breeding, with the applications being similar to, but extending on those for merit.

Jansen (1985) provides a useful definition of merit, seeing it as *profitability, energetic efficiency or some other measure of the utility of an animal to the breeder*. Koopman, Smith and Dekkers (1992) also formally link merit and utility, although from the alternative perspective of merit as the principle objective, suggesting that *extra genetic merit has a higher utility when there is more competition for a limited market*. They assess the impacts of merit and risks associated with having no bulls in the top ranks, and consider the utility of achieving an increased mean merit in offspring through intense bull sire selection. The associated risks of alternative strategies were compared, leading to the conclusion that, while there was a strong risk associated with the strategy of maximising mean merit, the associated benefits compensated for these.

Utility functions are used by economists to provide a link between individual preferences and the decision making process. They provide a device for assigning numerical values to options or events, and so the decision maker with an objective tool by which to maximise his expected utility (Anderson *et al.*, 1977). There can be a wide range of utility functions, ranging from well defined mathematical functions to general specifications of utility.

Specific mathematical utility functions include linear, quadratic and cubic relationships. Lexicographic utility, essentially an empirical approach, is very different from such functions, the definition reflecting a non-continuous, frequently stepwise, change in utility commonly seen in real situations. Lexicographic utility is derived from a 'safety first' approach (e.g. Anderson *et al.*, 1977; Robison *et al.*, 1984) where a set of preferences must be satisfied for each level of utility, with sequential increases coming from the satisfaction of further steps. Unlike mathematical utility functions, no increase in utility occurs until a threshold is reached, and similarly no utility is associated with a lesser than required achievement.

Schneeberger and Freeman (1989) included a lexicographic function in their assessment of a crossbreeding experiment. In this they specified two goals, the first *survival*, the second, *profit maximisation*. Interestingly, the ranking derived from the lexicographic function differed more significantly from expected monetary value than did the ranking associated with the risk averse or risk prone functions and was closer to the behaviour of the Swiss farmers under consideration than were such functions.

Increasingly, definitions of merit are including a range of factors such as accuracy (Meuwissen, 1991; Klieve *et al.* 1993; Woolliams & Meuwissen, 1993) and inbreeding (Wray & Thompson, 1990; Wray, Woolliams & Thompson, 1990; Quinton *et al.*, 1992; Klieve *et al.*, 1994). In addition, risk is also being used to look at the impact of animal records on the estimation process (e.g. Geldermann *et al.*, 1986; Long *et al.*, 1990; Long *et al.*, 1991). Such functions provide the capacity to define a clearly specified measure of merit.

2.2.3 Applications of Utility to Animal Breeding

From selection index theory, it has been conventionally assumed that the total merit of animals is a linear function of measurable traits (Goddard, 1983), however, an increasing number of researchers in animal breeding have proposed more realistic, non-linear, functions (e.g. Wilton *et al.*, 1968; Allaire, 1980; Goddard, 1983; Allaire *et al.*, 1985; Smith & Allaire, 1985). Many of these researchers have applied such non-linear relationships in the area of mate selection, this according with the conclusion of Kinghorn (1987) that mate allocation will be of value in a case such as when merit is non-linear.

A common mechanism by which to include an economic perspective in genetic analysis has been through the use of profit equations (e.g. Soller *et al.*, 1965; Moav, 1966a; Moav, 1966b; Lin & Allaire, 1977; Woolliams & Meuwissen, 1993). These include simple linear relationships, quadratic profit functions (e.g. Wilton *et al.*, 1968) and more complex cubic profit functions in the selection index model (Ronnigen, 1971).

Lin and Allaire (1977) looked at the relative efficiency of selection methods for overall profit. They developed a number of indicators, including a profit function addressing both economic and genetic criterion, a selection index and a single trait estimate (milk yield) and compared the relative efficiency of selection based on these methods. They found the utility of an estimate of profit to be a more effective selection criterion for genetic gain in profit than the other methods assessed.

More recently, Meuwissen (1991) considered a range of formal utility functions and found that this method was effective in ranking breeding schemes. Woolliams and Meuwissen (1993) used utility functions to provide an approach to evaluate accuracy in the selection process. This move to formally include utility in such analyses reflects the increasing sophistication of the selection process.

With the incorporation of accuracy in selection, it is also important that further information is provided on its impact on the results of the selection process. The basic assumption that more accuracy is preferred (e.g. Van Raden *et al.*, 1984; Freer & Sundstrom, 1991) is becoming recognised as being subject to some qualification when the selection objective is broadened to reflect utility. This assumption was addressed by Klieve *et al.*, (1993) who assessed the response and utility range of functions having varying weightings placed on accuracy in a linear index for selection. This work showed that the preferential selection of animals of lesser accuracy would not necessarily result in a decrease in expected response. Similarly, Woolliams and

Meuwissen (1993), also recognising the potential value associated with the higher variance, suggested the possibility of an increase in response.

A link between the use of utility functions, which are frequently non-linear, and the genetic applications of selection practices occurs in research relating to non-linear definitions of merit. In many such applications utility is incorporated into the objective function (Lin & Allaire, 1977; Schneeberger & Freeman, 1980; Schneeberger, Freeman & Berger, 1982; Schneeberger, Freeman & Boehje, 1982; Smith & Allaire, 1985; Smith & Hammond, 1986; Rogers, 1990; Meuwissen, 1991). Linear merit, although frequently applied in merit functions, is not always a simple concept, as noted by Smith and Hammond (1987a) who provide an integration of the concepts of linearity and non-linearity in inferring that, to improve the additive genetic merit after several generations we are effectively dealing with a non-linear objective. This concept of non-linear impacts resulting from linear selection objectives in the parent generation can be found in earlier work. Morley (1954), for example, argued that, with any selection scheme, a positive correlation between the degree of inbreeding in progeny and merit in parents would be an automatic consequence of selection.

Goddard (1983), while deriving selection indices for non-linear profit functions, recognised that strategies to maximise merit in parents does not necessarily imply maximised merit in offspring. He concluded that, even for non-linear profit functions, a linear selection index leads to the greatest increase in profit. Bright (1991) raised the question of whether profit functions, acceptably linear over a single time period, would remain so where this was extended, as for example, across generations. This highlights the general problem that the implications of simple selection practices can extend from the direct objective to less desirable outcomes.

In a recent study, Wiener, Lee and Woolliams (1992) questioned the assumed linear relationship and inbreeding levels. While they found a significant detrimental impact on body weight, they also noted a non-linear effect, this arising above certain levels of F. Again this reinforces the view that, while linear relationships are both simpler to specify and apply, they frequently are a simple representation of more complex systems. While such simplifications frequently contribute to the overall understanding of an area, care must always be taken in the applications of findings arising from them.

While utility and merit appear similar in many applications, they differ in the conceptual base. The Expected Utility Model (EUM), discussed below, has been extensively used as a prescriptive tool - this inferring that the decision maker who obeys certain axioms, should choose actions which maximise their expected utility (Robison *et al.*, 1984). However, as well as this normative economic perspective (looking at what should be) utility is also of use at the positive economic level (of what actually occurs), being applied in the identification of decision making strategies which result in maximising utility. Broadly applied in a range of economic contexts, the EUM provides a unique mechanism by which to represent the goals of the rational decision maker.

2.2.3.1 The Expected Utility Model (EUM)

In 1738, Daniel Bernoulli, in presenting a descriptive model, proposed that people maximise expected utility not expected monetary value (Schoemaker, 1982). The EUM was formally developed by Von Neumann and Morgenstern (1947) through axioms classified under four areas - ordering, transitivity, continuity and independence - defining a rational and formal decision making process. While the EUM implies that decision makers will be rational and consistent, and so predictable, it is virtually impossible to capture all the elements involved in an individual concept of utility, particularly as these may not always be stable over time.

The EUM implies a very formal and rational decision making process with consistent and predictable decisions - given known level of utility. Naturally, as it is virtually impossible to capture all the elements comprising personal utility, particularly over time, any such model has limitations. Thus, while it is valuable to consider how decisions are made, and to assist in the provision of information for making such decisions, it is dangerous to suggest this or other models can replace the effectiveness of rational judgement - it can only contribute to its operation.

If the axioms of the EUM hold, then it follows that an optimal risky choice is based on the maximisation of expected utility. The assumption of rational behaviour in decision makers underlies a major failing in the EUM. Tests of the EUM have been directed at its specific axioms, this providing the most efficient test of its application, with, for example, evidence of contradictions on various axioms. (Von Neumann & Morgenstern, 1947).

While it may be reasonable to identify how a utility maximising decision maker should operate, real world decision makers may not be utility maximisers, and those who are, may be 'operating' on a utility function not consistent with that simpler form which is being modelled. It is therefore frequently accepted that the EUM provides a means of identifying optimal strategies for decision makers rather than predicting their optimal behaviour.

However imperfect the EUM may be as a predictive model, the concept of utility has been extensively applied in a wide range of approaches, providing a valuable, though imperfect, tool for the assessment of management strategies. Such compromise is also an integral part of quantitative genetic analysis as recognised by Kennedy (1981): *Trade-offs between what is conceptually ideal and what is practically possible are a fact of life in applied breeding work.*

2.2.4 Risk and Uncertainty

While in lay terms risk is often taken to mean that *the outcome is worse than expected*, the literature details quite fundamentally different concepts of risk, including (see Young, 1984):

- probability of loss;
- variance of profit; or
- size of the maximum possible loss.

Or, as Anderson *et al.* (1977) put it, *When a person is uncertain about the consequences of his decision, he faces a risky choice*. In this statement the importance of the uncertainty of the outcome of a decision (eg. management practices or breeding combinations) is highlighted.

There has been ongoing debate in agricultural economics about the distinction between levels of uncertainty or risk, with Knight (1921) delineating the degree of knowledge in decision making situations into the categories of perfect knowledge, risk and uncertainty. While the distinction between risk and uncertainty is focused mainly on the difference between objective and subjective probabilities (Sonka & Patrick, 1984), in practice, uncertainty and risk are frequently merged. Dillon (1977), for example, used the concepts interchangeably, and difficulties in determining true probability distributions supports this. In the area of animal breeding there has been very limited application of this concept, and thus extensive debate over this issue might more appropriately wait for the acceptance of the more general concept, and the development of appropriate methodologies to handle this factor in the context of animal breeding programs.

A major element differentiating risk and uncertainty is the distinction between the likelihood of outcomes - risk implying a known probability of outcome compared to uncertainty where this is unknown. While this definition implies that there is a clear distinction between the concepts, in reality this boundary is far more blurred.

Considerable development in the application of risk analysis occurred during the 1970's (Barry, 1984), with Anderson *et al.* (1977) taking a broader perspective of the definition of risk functions, incorporating *personal strength of belief about the occurrence of uncertain events and his personal evaluation of potential consequences*. More recently, Anderson (1988), in describing risk, referred to it as *uncertainty with teeth*. Thus, much that is unstable and/or variable might also be described as risky if the uncertain consequences cannot be predicted with complete precision (Quiggin & D Anderson, 1979).

There is a strong link between risk and utility. An individual's attitude to risk is apparent from the shape of the utility curve, this ranging from linear (neutral), concave (averse) and convex (preferring) and also combinations of these where different attitudes to risk are present in response to different situations.

2.2.4.1 The Use of Risk in Animal Breeding

Risk is now recognised as a key factor in most farming activities (Anderson, 1974). Although its application is well established in agricultural economics, animal breeders are only beginning to incorporate this perspective in their research. Anderson (1988), in assessing sources of risk in Livestock Improvement Programs (LIP's) through uncertainties in, for example, the performance of given genotypes, concluded that:

risk indeed represents considerable trouble to deal with and the advantages of dealing with it are rather minor. It can be reasonably be hypothesised that the optimal attention to risk amongst animal breeders generally is approximately zero ... one situation where this may not be true is in the case where there are multiplicative interactions between uncertain variables in a profit function.

Although Anderson's review of risk did not identify any valuable sources for future work, recognising many of the conventional uses as of minor significance to current work in animal breeding, he did inject an increasing awareness of components of risk in LIPs essential to the identification of more diverse and valuable applications.

A consideration of risk is becoming increasingly common in the animal breeding literature. The focus of such work, directed, for example, to risks associated with specific selection practices, differs from the enterprise directed focus of the traditional approach of agricultural economics.

Merit functions incorporating risk components are now being extensively applied in animal breeding, with risk variously defined as accuracy (Klieve *et al.*, 1993; Woolliams and Meuwissen, 1993), variation in net merit (Rodgers, 1990), variation in expected returns (e.g. the risk of losing money (Schneeberger & Freeman, 1980) or the standard deviation of the Predicted Difference (Schneeberger *et al.*, 1981)), or integrated functions addressing, for example, genetic response and inbreeding (e.g. Quinton *et al.*, 1992; Toro & Silio, 1992; Klieve *et al.*, 1994).

Rogers (1990), for example, developed a utility function for ranking sires. This function used a risk component related to accuracy (the variation in the expected net merit). Accuracy was also applied as the risk element in an evaluation of breeding plans by Meuwissen (1991). While this application - level of accuracy - differs from more conventional definition of risk such as the variation in expected returns, there are similarities. The level of accuracy is directly linked to the variation of the population (used by Van Raden *et al.*, 1984, to enhanced long term progress) both directly through the estimation process and also through the relationship between this variation and ΔF . Ruane and Thompson (1989) suggest that selecting with maximum risk aversion will partially account for a required decrease in ΔF , a similar view also expressed by Meuwissen (1991).

Another perspective (from Koopman *et al.*, 1992), not unrelated to the implications of accuracy, is that of the risk of having no bulls in the top rank. While selecting for high accuracy can be used to achieve consistency, there is a tradeoff with the injection of higher levels of variation.

Schneeberger, Freeman and Boehlje (1982) used portfolio analysis, another approach through which risk has been analysed, defining the optimal portfolio with respect to returns and their variability in dairy sire selection. They used a standard application, maximising the expected dollar return subject to the reduction of the variance in that return, providing a mechanism for the integration of benefits from returns with the risk of their achievement.

Thus, although risk is increasingly being formally accommodated in the area of animal breeding, and that application is extending the definition of risk there is still considerable scope to explore its contribution to the field of selection, and to capture the benefits from such a consideration in animal breeding programs.

2.3 Genetic Components of Merit

2.3.1 Introduction

Increasingly, utility functions incorporating economic, environmental and genetic factors, are being used to achieve desirable performance outcomes. Of particular interest in the improved use of available information is the attainment of enhanced performance - for example, the management of the interrelationship between achieved genetic potential and depression in this potential due to inbreeding.

BLUP estimates have an integral role in the development of mechanisms for selection, raising the question *how best to use information in the selection of breeding stock?* Similarly, the issue of inbreeding is of particular concern due to its link to the effective use of information on relationships. Manipulation of the coefficient matrix provides an important mechanism by which the interrelationship of inbreeding and selection can be managed to improve long term outcomes.

Central to the concern on the use of BLUP estimates is the difference between the achievement of short and long term objectives. Selection on *ebv* alone will maximize the response to selection observed in the following generation. However, the repeated use of this selection criteria will not necessarily result in a maximum response over a longer time horizon. This latter impact is due to the influence on the inbreeding in the next and subsequent generations resulting from the selection decisions in the present generation (Wray & Goddard, 1994).

2.3.2 Best Linear Unbiased Prediction

A cornerstone of recent advances achieved through genetic selection techniques is the development of BLUP (Henderson, 1973). This method, improving on the technique of selection index, provides a Best Linear Unbiased Estimate of breeding values (*ebvs*) evaluated using all available pedigree information.

Ebvs represent individual variation from the mean genetic merit of the group - that is, how much better or worse any animal is. From the basic input of phenotypic value, the method has to separate the individual's genetic component from other factors making up the phenotype - including environmental non-genetic elements. Information on relatives, incorporated through the Numerator Relationship Matrix (NRM) in the Mixed Model Equations (MME), provides a mechanism for the achievement of this.

Through the inclusion of all available pedigree information in the relationship matrix, the MME's provide an efficient means for the estimation of random genetic effects from individual animals. With the increased capacity of modern computers and the derivation of the simple method for inverting the relationship matrix (Henderson, 1975a, 1976; Quass, 1976) BLUP evaluations are increasingly feasible and now form an integral part of many widely applied genetic evaluation systems.

Extensive detail on the range of models used in BLUP applications are also found in Quass, Anderson and Gilmour (1984) as well as current research developed in a mixed model environment (e.g. Kennedy 1981; Belinsky & Kennedy, 1988; Schaeffer, 1976; Henderson, 1975b, 1976a, 1976b). Robinson (1991), in a review of BLUP involving commentary by other researchers, provides a useful overview of its application. While recognising the enormous contribution of BLUP to the area of animal breeding, he also identifies and discusses some of the controversial issues surrounding its application.

A range of models are used to estimate breeding values, with the basic model used in animal breeding applications being the Simple Breeding value Model (Quass *et al.*, 1984) detailed below:

$$y = X\beta + Z\mu + e \quad 2.1$$

where:

y is a vector of records

β is an unknown vector of fixed effects

Z is a known matrix relating breeding values to records (equalling 1 if 1 record/animal)

X is a known matrix relating the fixed effects to records

μ and e are non-observable random vectors, representing breeding values of animals and random residuals

It is also assumed that both $E(\mu)$ and $E(e)$ are null, and that

$$\text{var} \begin{bmatrix} \mu \\ e \end{bmatrix} = \begin{bmatrix} \alpha^{-1}A & 0 \\ 0 & I \end{bmatrix} \sigma_e^2 \quad 2.2$$

where $\alpha^{-1} = \sigma_a^2 / \sigma_e^2 \Leftrightarrow \alpha^{-1} = h^2 / (1 - h^2)$ and A is the NRM for the animals with breeding values represented in μ .

The Mixed Model Equations providing the best linear unbiased predictor of μ , $\bar{\mu}$, will be:

$$\begin{bmatrix} X'X & X'Z \\ Z'X & Z'Z + \alpha^{-1}A^{-1} \end{bmatrix} \begin{bmatrix} \bar{\beta} \\ \bar{\mu} \end{bmatrix} = \begin{bmatrix} X'y \\ Z'y \end{bmatrix} \quad 2.3$$

This model provides a mechanism for the use of information on relatives. However, the impact of differential levels of information on individuals is seen in estimates of differential accuracy. The *ebvs* of animals on which there more records are estimated with the greatest accuracy - that is, their *ebv* will be closest to the true breeding value. On the other hand, the *ebvs* of animals for which there are limited records available will be estimated with lesser accuracy (and a greater degree of error) - the extreme being those animals on which there is no information which will be estimated at zero.

Thus, in addition to the desired outcome of animals of superior merit having increased likelihood of selection in the next generation, this impact is also passed on to relatives resulting in increased likelihood of these also being including in subsequent generation.

2.3.3 Inbreeding

The generally negative impacts of inbreeding are, of course, well recognised. Inbreeding has the potential to reduce the returns to producers from their current and future stock through loss in fertility, reduction in genetic variance and genetic response rate (e.g. Morley, 1954; Dempfle, 1990; Quinton *et al.*, 1992; James, 1993; Wray & Goddard, 1994). Considerable research has been devoted to both the assessment of levels of inbreeding, the impact on inbreeding of various mating schemes and also the cost of inbreeding arising from depressed production and general decline in vigour.

Although there are negative effects associated with inbreeding in animal populations, including depressed production and fertility, it is not all detrimental. Dickenson (1973) commented on the use of selection to control and manipulate potential benefits available through levels of inbreeding and noted that Wright's results (1921,1922) indicated that *selection might be able to offset unfavourable effects of milder inbreeding and that inbreeding was a powerful tool for creating genetic diversity among lines.*

Much of the research associated with inbreeding considers patterns in an idealised population with a restricted and simplified mating structure, necessary in more theoretical research assessing different approaches to inbreeding (Wray *et al.*, 1990). Burrows (1984 a,b), for example, developed methods for the assessment of effective population size, and inbreeding levels, under defined family structures. The use of such simplified structures provides a convenient approach to facilitate the use of the mathematical investigation (e.g. Kinura & Ohta, 1971) for improved understanding of the operating mechanisms associated with mating patterns, and thus an insight into likely outcomes. However, a constraint in the application of the specific results of such work is the high level of deviation from the idealised situation, arising from aspects such as overlapping generations, variable mating ratios and family sizes.

In an idealised population, the inbreeding coefficient of individuals in generation t can be calculated as :

$$F_t = \frac{1}{2N} + (1 - \frac{1}{2N})F_{t-1} \quad 2.4$$

This being made up of an increment, $\frac{1}{2N}$, from new levels of inbreeding, and a remainder, $(1 - \frac{1}{2N})F_{t-1}$, attributable to the past (Falconer 1989). Using this increment, or ΔF , the inbreeding coefficient can be expressed as:

$$F_t = \Delta F + (1 - \Delta F)F_{t-1} \quad 2.5$$

which leads to

$$F_t = (1 - \Delta F)^t \quad 2.6$$

This equation, expressed in terms of ΔF and not F , is valid for any breeding system, and is not restricted to an idealised population. However, ΔF is only equal to $\frac{1}{2N}$ in an idealised population (Falconer, 1989).

The relationship between inbreeding and effective population size can be seen through this equation, where the relationship for a population deviating from the ideal is :

$$\Delta F = \frac{1}{2N_e} \quad 2.7$$

The concept of effective population size can be linked to the degree of deviation from the idealised breeding structure. Where there are high degrees of inbreeding, the effective population size may be far below the real number of animals in the population, and the impact potentially detrimental.

A major deviation from the idealised case in breeding populations of domestic animals is that of the number of males and females breeding. The number of males usually is less than that of females. Where there are different numbers of males and females, this number can be expressed as :

$$\Delta F = \frac{1}{8N_m} + \frac{1}{8N_f} \quad 2.8$$

where N_m and N_f refer to the numbers of males and females entering the population per generation, with the effective population size given by :

$$N_e = \frac{4N_mN_f}{N_m + N_f} \quad 2.9$$

A major concern arises where effective population size is small, with Weir, Avery and Hill (1980) suggesting that there is very little variation in inbreeding between populations unless N_e is small, then of course ΔF will increase substantially. Further, while the effective population size will be large if N_m and N_f are both large, if either is very small Equation 2.9 will be dominated by the smaller, with N_e approaching 4 as the lesser approaches 1. Thus, for populations with extreme mating ratios (generally associated with the use of a small number of males for breeding) rapid increases in ΔF will occur.

Overlapping generations provide another deviation from the idealised population. Hill (1972 and 1979) showed that, for such populations, the contributions of genes from animals introduced in a given year is $1/L$ (for the generation length of L).

An extension to the understanding of this concept has been provided by Hill (1979), who, in re-proving his earlier derivation (Hill, 1972) showed that the effective population size of populations with overlapping generations *equal the effective sizes of populations with discrete generations which have the same number of individuals entering the population each generation and the same variance of lifetime family membership*. He assumed that small disturbances either in age distribution or in the number born in each cohort did not substantially affect the results. Hill (1979) concluded that for general planning of animal breeding programs, or the study of long term populations in the wild, the asymptotic rates should be an adequate guide.

A further consideration is the impact of differential family size. While theoretical analyses tend to depend on the assumption of discrete generations (with size selected from a given distribution, for example, multinomial in Hill, 1972) this only approximates the variable family size found in real populations, and so will have an impact on the estimation of genetic response and inbreeding resulting from breeding.

Kimura and Crow (1963) recognised that, other factors being equal, the negative impact from family size will be least when family sizes are constant, hence, $\Delta F < \frac{1}{2N_e}$. Obviously with the selection practices, including overlapping generations, merit will impact on time retained in the breeding herd, and thus on family size.

Theoretical investigations provide a valuable insight into key issues which must be addressed to achieve more effective selection processes. Kinghorn, Smith and Dekkers (1991), in looking at the potential for future reproductive technology to impact on response, found the number of parents to be a highly significant factor on the resultant level of inbreeding, while the level of heritability, for example had little impact. The breeding strategy which they detail, while radical under current

reproductive technologies, has the potential to deliver annual increases in mean merit of an order of 3.7%. However, dependent upon the ability of female candidates to large numbers of viable offspring under different mating matrix, for selection and assessment at 13 months, this is unviable under current breeding capabilities.

2.3.4 Accuracy

Due to the differential levels of information, or records, used to estimate *ebvs*, such estimates are made with differential levels of reliability. While different approaches are used to address this factor they all target the efficiency with which such estimates are derived (for example, accuracy, the correlation between the true and estimated breeding value, (r_{AA} , see Van Vleck, 1987) or the Predicted Error Variance, $\text{var}(\mu - \hat{\mu})$ (Woods, Christian & Rothschild, 1991).

The application of BLUP leads to a minimisation of the PEV (Henderson, 1973). Robinson, Wilton and Schaeffer (1989), in commenting on the relative accuracy of selection based on Selection Index and BLUP, also found that both accuracy and genetic response increased under BLUP selection. However, while there are distinct advantages in the use of accurate estimates of genetic merit, disadvantages in the extensive use of high accuracy animals are increasingly being recognised.

The increased information on highly related animals means that relatives of a superior individual are likely to have similar *ebvs* (e.g. Belonsky & Kennedy, 1988). It is likely that such relatives will have an enhanced likelihood of selection - so increasing likelihood of coselection of relatives (e.g. Wray *et al.*, 1990). Thus, although accuracy and inbreeding are not directly related both arise from different levels of information and degrees of relationships between animals and impact on the level of variation in the population.

One method of addressing this negative impact of selection is to place an emphasis on low accuracy. Van Raden *et al.* (1984) incorporated an index of *ebv* and accuracy into a two-stage selection process, optimising long term improvement through a targeting of both *ebv* and accuracy. They compared this to the standard approach of maximising the mean of animals selected at any stage. The benefits in the proposed selection process depend on the greater variation associated with the selection of animals with both lower average *ebv* and less accuracy. While this work suggested that selection based entirely on *ebv* is not theoretically optimum, it also recognised that this is likely to be preferred due both to the small loss in genetic gain and the greater simplicity. Goddard and Fowarth (1994) concluded that, where there are multiple stages of selection, selection on *ebv* may not be optimal - dynamic selection and mating rules providing a mechanism through which factors such as cost, risk, inbreeding and heterosis can be incorporated into the objective.

The complexity associated with differential levels of accuracy is increasingly apparent. Klieve *et al.* (1993) assessed a range of weights on accuracy and found that for both the expected response and defined utility functions preferential selection for high accuracy was not always optimum. Meuwissen (1991), in looking at accuracy through a consideration of the variation in the expected response in a range of breeding schemes, also noted that maximum accuracy did not always lead to the best outcome.

In a consideration of decision rules applied in breeding schemes, Woolliams and Meuwissen (1993) discussed a situation of selection based on a percentile of the distribution of the individuals predicted breeding value. They found benefits for the 80% percentile - this occurred because the reward from underestimation of merit (ie. $\hat{\mu}_i < \mu_i$) outweighing the loss from the errors in prediction. Both the expected genetic progress and its variation was greater for the 80% decision rule than for lower levels. Where there is a high level of variation around an estimate (thus low accuracy)

the upside risk (benefit) of selecting better than expected animals, due both to the high levels of variation and the underestimation of $\hat{\mu}$, can outweigh the downside risks of selecting poor animals.

Recognising the implications of selection addressing differential levels of accuracy is one approach to directly manage the implications of such selection. However, managing the risks and rewards associated with the differential accuracy is only one component of optimal selection - acting to reduce the rate of increase in relationships and to maintain a productive level of genetic variance. This is a part of the establishment of more general selection criteria, as, for example, detailed by Wray and Goddard (1994).

In an interesting consideration of the impact of high levels of relationship, Woods *et al.*, (1991) identify that, while the accuracy of evaluation is improved given that relationships are included in the mixed model, one exception is that of closely related families. In this situation the limited numbers of off diagonal elements exhibiting close ties may result in the matrix losing diagonal dominance, potentially resulting in larger PEV from the evaluation. An additional aspect of this issue was considered by McClintock and Taylor (1982), who found that where homoscedastic variances have wrongly been assumed, there will be a decreased correlation between the estimated and true breeding value. Woods *et al.* (1991), further noted the need for care in the design of evaluation schemes particularly due to the impact of numbers of fixed effects included in the model.

Kemp and Wilton (1987), in looking at the effect of different Numerator Relationship Matrices, suggested that the benefits from the additional response associated with higher accuracy may offset the problems with the additional problems of animal identification required to obtain this higher accuracy. This strongly reflects the conventional view that more accuracy is better (Freer & Sunstrom, 1991; Van Raden *et al.*, 1984) - a premise now being questioned.

A final point which must be considered in the use of information is the integrity of the raw information. Concern has been expressed on errors in the identification of parents, Geldermann *et al.* (1986), for example, reporting from studies on cattle, that between 4 and 23 % of paternal identifications were false - potentially impairing the accuracy and precision of estimated parameters derived from progeny data.

2.3.5 Managing Response - the Impact of Selection

The estimation of genetic traits is of prime importance as an indicator of the expected returns from a selection scheme. There are several factors which appear to be indicators of likely uncertainty in the achievement of such response. These are related to the underlying levels of relationships within any group and the methods used to estimate genetic parameters used in the selection process.

For example, the accuracy with which such parameters are estimated is associated with the risk, or greater uncertainty, in the achievement of such returns, with less accurate estimates leading to variance. Similarly, inbreeding is associated with lower levels of variation among animals within lines and with the depression of their performance, and again is frequently associated with an uncertainty in the achievement of an expected level of production.

Some concern has been expressed at the impacts of selection methods, and particularly the estimation of merit used in such selection on effective population size and associated levels of inbreeding (e.g. Belovsky & Kennedy, 1988; Bunter, Long & Tier, 1992; Dempfle, 1990; James, 1993; Quinton *et al.*, 1992; Banos & Smith, 1991; Toro *et al.*, 1988; Toro & Perez-Enciso, 1990; Wray & Thompson, 1990; Leitch *et al.*, 1994).

In a population undergoing selection, families superior for a selected trait will contribute more offspring to the next generation than inferior families. While the non-random selection of succeeding generations is the objective of selection, and thus will always have an impact, the associated coselection of relatives is an inevitable problem arising from mechanisms to predict merit on which to make selection decisions. Such factors will always be present in otherwise efficient selection schemes (Morley, 1954; Robertson, 1977) thus it is important to clearly identify any negative impacts of selection and then develop strategies by which these can be better managed.

In addition to the impact of selection practices are concerns about the assessment and comparison of breeding schemes. Because of the nature of breeding schemes it is generally impractical to trial these on real populations, thus simulation modelling applications have been extensively used in this area.

Comparisons of breeding schemes have frequently been made on the basis of the expected genetic gain. Quinton *et al.* (1992) questioned such approaches, suggesting that such comparisons need to be made on a comparable basis. They modelled an idealised population and made comparisons on the impacts of selection based on phenotypic and BLUP selection with regard to genetic response and inbreeding. The model allows for variation in the number of sires selected, thus providing a differential selection intensity. From the results it was noted that, where schemes were compared at the same level of inbreeding, BLUP generally only achieved higher rates of response where greater numbers of sires were used. It was recommended that schemes should be assessed at the same resulting level of inbreeding, to identify significant underlying factors to enhanced response, rather than just on the basis of the expected level of such response.

This is one step through which the better use of available information can lead to some improvement in achieved response. Quinton and Smith (1994) looked further at

this problem, recommending that, in evaluating systems where such differential factors existed, a graphical presentation of the expected response and associated inbreeding would be appropriate to assess and evaluate breeding schemes. This would assist in understanding the impacts of such systems.

Leitch *et al.* (1994) considered the evaluation of selection methods and mating designs with respect to the resulting genetic response and inbreeding. They used simulation studies to consider three mating strategies (random mating, assortative mating and corrective mating) for a range of mating designs. While their work reinforced their concern over potential impacts of BLUP and the view that selection on BLUP may not be optimal, they concluded that the preferred strategy was to use BLUP estimates in conjunction with selection and mating strategies. Although their modelling considered only a limited range of such strategies, this and other work suggests that this is the most reasonable approach, and preferred to approaches which censor such information

The move in this area is to see a balance between genetic response and indicators of risk in the achievement of this response. Klieve *et al.* (1994) applied an adapted portfolio analysis approach to model and assess a range of alternative breeding strategies with regard to their ability to effect a joint regulation between response and inbreeding. Brisbane and Gibson (1994) also carried out simulation studies which utilised the maximal accuracy, *ebvs* and information on relationships. Such studies more clearly demonstrate patterns between response and indicators of risk such as accuracy and inbreeding, and so further our understanding of the mechanisms operating and thus our ability to manage the many factors impacting on effective selection processes and its outcomes.

The effect of factors such as selection intensity and heritability are also of importance. Toro *et al.* (1988) recognised that under artificial selection the inbreeding coefficient

will be greater than in comparable randomly mated populations. This is due to the differential probability of representation of different parents, with the magnitude of this effect being a function of selection intensity and heritability. Belonsky and Kennedy (1988), noted that inbreeding was higher with populations selected using BLUP than phenotypic estimates. As expected, they found that for phenotypic selection, inbreeding increased with increasing heritability but tended to decline under BLUP selection. The difference is due to the use of relatives' information at lower heritability under BLUP. At low heritability more weight is placed on relatives information causing animals to have similar *ebvs* and so greater likelihood of coselection.

It is, however, not just the inbreeding level in the following generation which needs to be considered, but increasingly it is recognised that the herd/relationship structure has a lagged impact on the resultant inbreeding level. Robertson (1964), in looking at the effect of non-random mating within inbred lines, concluded that *the mating together of close relatives within the line leads to greater initial inbreeding but a lower final rate of the approach to the limit. The converse will be true for maximum avoidance systems*. On the other hand, it must also be recognised that the impact in inbreeding arising from outstanding individuals may rise for several generations after their use (Robertson 1961). This suggests the need for a long term perspective with respect to the avoidance of inbreeding - a more efficient long term approach than reactive handling that looks to the underlying causal elements.

Attention is now being directed to the impact of mating schemes, these offering one mechanism by which to address the impacts of selection. Meuwissen and Woolliams (1994b) stated that *increases in genetic gains of breeding schemes are mostly achieved at the expense of the risk of breeding plans*, this leading to the recognition that *breeding schemes with high rates of gain and low risks may be preferred over schemes with very high gains and high risks*.

The relationship between the use of BLUP and resultant increase in the inbreeding level is taken further by Strandén, Maki-Tanila and Mantysaari (1991), who found that most of the variation in inbreeding could be explained by family structures, either as a consequence of mating strategies or from the sources on information used in making selection decisions. With regard to the latter they found that the greater the weight placed on pedigree information the higher the resultant rate of inbreeding. They highlighted the benefits of care in selecting mating strategies and identifying mating pairs at each breeding period.

This perspective reflects a stepping back from inbreeding to consider the relationships from which such inbreeding arises, and so understand the causal relationships. Woolliams and Thompson (1994) looked to this issue when stressing the need to consider the novel variation an individual is bringing into the population and assess its potential contribution. By decomposing the definitions of genetic gain and inbreeding into mendelian components they suggest that these factors can now be described through the NRM, and so, by implication, handled within the selection process.

Other approaches are also being developed to manage these issues. Meuwissen and Woolliams (1994a) reviewed approaches being developed to assess and manage the impact of selection, including the use of utility theory (Meuwissen, 1991) and bayesian rules for making selection decisions (Woolliams & Meuwissen, 1993). Meuwissen (1991) applied a quadratic utility function to achieve the trade off between response and its variance:

$$U(\Delta G) = \Delta G - a\Delta G^2 \quad 2.10$$

and the expected utility:

$$E(U(\Delta G)) = E(\Delta G) - a(V(\Delta G)) + E^2(\Delta G) \quad 2.11$$

where a represents the constant level of risk aversion.

In comparing a range of schemes they found the ranking of schemes similar for both linear and quadratic functions. They noted, however, that higher levels of response didn't always lead to higher levels of utility.

Woolliams and Meuwissen (1993), applied bayesian selection rules to define a profit function incorporating profit and loss aspects associated with error in estimation.

$$P(c) = c'\hat{u} + f(|c'u - c'\hat{u}|) + g(c'u - c'\hat{u}) + h(c'\hat{u} - c'u) \quad 2.12$$

where

c is a vector of animals

u is a vector of true breeding values

$f(x)$ is the loss due to the uncertainty of the mean of the true breeding values of the selected group

$g(x)$ is the extra profit when u was underestimated by \hat{u}

$h(x)$ is the extra loss when u was overestimated by \hat{u}

and where $f(x) = g(x) = h(x) = 0$, for $x \leq 0$

By using both linear or quadratic forms of f , g and h the profit functions analysed will include both forms. They found that with quadratic profit functions animals with low *PEV* were relatively favoured compared to results from linear functions. However, it was also found that a linear function could be derived which would select the same animals as under the quadratic form. It was therefore recommended that, along with estimates of merit, decile values (e.g. the 75% *ile*, 50% *ile* and 25% *ile*) should be published for decision makers. In looking at the divergence between long and short term benefits, they noted that in the long term high risk selection (ie. the use of 75% *ile*) yielded a marginally greater response due to a lesser reduction in genetic variance in one generation, and so greater levels of genetic variation in the next. This highlights the danger in concentrating on simple indicators of gain, without taking into account aspects which will ensure such benefits can be sustained in the long term.

2.3.5.1 Conclusion

Considerable work has been undertaken in this area to demonstrate both relationships between factors such as accuracy and inbreeding and also the constraints on the achievement of expected response. While these factors are only indicative of underlying causative elements impacting on response, they nevertheless provide a useful lead to more complete understanding of final response and the mechanisms through which action can be directed for desired outcomes.

In conclusion, it is increasingly apparent that inbreeding is one indicator of a source of production risk which can be effectively be incorporated in the selection decision process. The information available in the relationship matrix, and the resultant accuracy with which merit is estimated, provide linkages through which this can be achieved.

2.4 Methods of Analysis

2.4.1 Introduction

While considerable work has addressed the issues of the benefits in jointly regulating aspects such as response and inbreeding it is also important to identify approaches through which such integration can be achieved.

Many of the problems to be addressed have elements in common with those in other disciplines and so there are significant advantages to be captured from the innovative adoption of techniques developed to solve parallel problems in varied fields.

Operations research techniques, for example, have been applied across a range of disciplines, and offer opportunities in the form of new approaches to current problems in the area of animal breeding.

Two broad approaches, applied in various areas of animal breeding, are outlined here - linear programming and portfolio analysis. Although linear programming is very effective in handling broad problems defined with a range of formal constraints, it has limited capacity to handle risk. Portfolio analysis, on the other hand, developed in the area of financial management, is specifically designed to cater for a decision maker's preference for risk in investment choice. A final option discussed below provides some amalgam of these techniques.

While there are limitations in both linear programming and portfolio analysis, their application can contribute to the decision making process. As suggested by Wright (1983) in a discussion of the relative merits of approaches from management science and decision theory, there is the need for sensible and rational applications of any technique - all have implicit dangers and valuable insights to offer. The potential opportunity is to capture such benefits while managing the impacts of the constraints.

2.4.2 Linear Programming

2.4.2.1 The Linear Programming Model

Linear programming (LP), widely applied in management science (e.g. Lee, Moore & Taylor, 1985; Dallenbach, George & McNickle, 1983), involves the definition of real world decision problems as mathematical models.

A standard Linear Programming formulation can be expressed as:

$$\text{Maximize } Z = \sum_{j=1}^n c_j x_j \quad 2.13$$

subject to

$$\sum_{j=1}^n a_{ij} x_j \leq b_i, \quad i = 1, 2, \dots, m \quad 2.14$$

$$x_j \geq 0, \quad j = 1, 2, \dots, n. \quad 2.15$$

where:

Z = the total value of the objective function (frequently profit)

x_j = the level of the j th activity;

a_{ij} = the technical requirements of the j th activity for the i th resource or constraint;

b_i = the i th constraint level;

n = the number of activities

m = the number of constraints;

c_j = contribution per unit of activity j .

The primary objective of most LP models is the identification of the allocation of resources resulting in the satisfaction of the profit maximisation (or cost minimisation) objective specified in the objective function. LP techniques have been applied in a range of areas in animal production including the development of least cost rations (Famula, 1992), and a consideration of factors in herd calving patterns (Jalvingh, Dijkhuizen & Van Arendonk, 1994). Extensive attention has been devoted to the application of mate selection processes in the management of inbreeding (Jansen & Wilton, 1984; Jansen, 1985; Jansen & Wilton, 1985; Kinghorn, 1987; Toro, Nieto & Salgado, 1988; Toro & Perez-Enciso, 1990; Bunter *et al.*, 1992; Toro & Silio, 1992).

In farm allocation problems the definition of an LP model can be a relatively simple process, involving the identification of the returns associated with activity levels and

the constraints used to define resource allocation limitations. Similar forms of constraints are used in animal breeding applications. Armstrong *et al.* (1990), for example, in maximising net returns in a beef production process, made a range of assumptions on the breeding structure and the price of inputs and products. Applications in mate allocation have used constraints in mating ratios, reproductive capacity and herd structure (Jansen, 1985; Kinghorn, 1987; Toro, Silio & Perez-Enciso, 1991; Bunter *et al.*, 1992; Toro & Silio, 1992).

2.4.2.2 Construction of the Model

The properties of the LP model provide an insight into the constraints applied in the model and thus the limitations of the approach (e.g. Lee *et al.*, 1985). At its simplest, a two dimensional LP problem may be solved graphically. However, more complex problems cannot be handled in this manner.

Linearity in both the objective function and the constraints is a major requirement of the LP model. Associated with this is the implication of the direct proportionality of relationships and thus constant rates of change. While interactions between variables do occur these cannot be represented by this model.

It is also assumed that all solution values are divisible - implying that variables cannot be constrained to integer values. While Integer Programming (IP) approaches have been developed and are widely used in situations where it is not feasible to allow for this assumption of divisibility thus the need to identify whole offspring, or complete matings) an integer solution is constrained by the level of the non-integer LP solution.

Finally, the LP model is static and deterministic, thus the value of parameters are known with certainty and assumed to be stable over time. Although the use of sensitivity analysis provides a mechanism through which the solutions from an LP

model can be tested for the impact of parameter change, this can only improve the information available to the decision maker for assessment, not add a stochastic element to the model.

Behind the basic structure of the LP model is the overlying assumption of profit maximisation. Lin *et al.* (1974), in a test of hypotheses of utility and profit maximisation, concluded that none of the models investigated predicted actual behaviour well due to a tendency to predict more risky behaviour than in fact is selected. They found that bernoullian utility maximisation was more accurate than either lexicographic utility or profit maximisation, with the latter being the least realistic. From this it was suggested that one reason for the poor application of the standard LP approach could be due to its tendency to recommend more risky strategies than are acceptable in real world situations, supporting perceptions of this method as unrealistic in definitively predicting optimal allocations.

While linear programming provides an excellent method to define the optimal solution to well defined linear problems, the assumptions of the method frequently conflict with real situations and so the solution defined must always be assessed in the light of such limitations. Of course although it is easy to identify limitations in this technique, such limitations are also evident in other methods. The issue for any researcher comes in accepting which form of compromise in method, or information, should be taken, rather than whether or not to accept a compromise.

2.4.2.3 The Primal Dual Formulation

In addition to the identification of strategies for optimal resource usage, further information can be provided through an LP analysis. For each normal LP model, defined as the *primal*, there is an alternate form, the *dual*. While the *primal* looks to the maximisation of profit, the value of the *dual*, directed to cost minimisation, is in

the economic interpretations which can be made from its solutions. These forms are closely linked and such links can be used to access additional information from LP analyses.

The following example, developed from an IP model specified in Jansen and Wilton (1984), demonstrates the two forms of an LP model, and the form of interpretations available from these.

Given the profit function:

$$c_j = 0.175(\mu_{milk} + \hat{g}_{milk,j}) + 5.0(\mu_{fat} + \hat{g}_{fat,j}) - 0.1(\mu_{feed} + \hat{g}_{feed,j}) - 7.5(\mu_{labour} + \hat{g}_{labour,j}) \quad 2.16$$

the *primal* form of the model, looking to define optimal allocations of males 1 and 2, is:

$$\text{Maximize } Z_p = 1,167.5x_1 + 1,270x_2 \quad 2.17$$

Subject to:

$$x_1 + x_2 \leq 45 \quad 2.18$$

$$5000x_1 + 6000x_2 \leq 250000 \quad 2.19$$

$$21x_1 + 24x_2 \leq 1000 \quad 2.20$$

$$\text{where } x_1, x_2 \geq 0 \quad 2.21$$

The constraints in equations 2.18 to 2.20 refer to limits on housing, milk cooler capacity and labour respectively. The optimal solution of \$54 416.67 occurs at the optimal levels of usage of males 1 and 2 (26.67, 18.33).

Moving to the *dual* form:

$$\text{Minimize } Z_d = 45y_1 + 250000y_2 + 1000y_3 \quad 2.22$$

Subject to

$$y_1 + 5000y_2 + 21y_3 \geq 1167.5 \quad 2.23$$

$$y_1 + 6000y_2 + 24y_3 \geq 1270 \quad 2.24$$

$$\text{where } y_1, y_2, y_3 \geq 0 \quad 2.25$$

representing the minimisation of costs (or constraints from the *primal*). The matrix used in this model is the transpose of that used in the *primal* above, the link between these forms.

The optimal point again occurs at 54416.67 (found at (450.0, 0.0, 34.17)), thus the solutions of the *primal* and *dual* converge at the optimal point where profits are maximised and costs minimised, demonstrating the 1st Duality Theorem (Chiang, 1984):

The optimal values of the primal and dual objective functions are always identical, provided that optimal feasible solutions do exist.

In addition to providing an alternative formulation, which may be more easily specified and solved, the *dual* solution provides the shadow prices, or opportunity costs, of the resources specified by the constraints of the *primal*.

In the *primal*, the constraints refer to a level of resource, however, these can also be used in the definition of, for example, mating ratios, providing the ability to assess not only the best mating structure but also comment on the marginal cost of increasing this parameter. The solutions to the *primal* and *dual* from the above analyses are specified below:

PRIMAL FORM

Variable	Optimal Value	Reduced Cost
x_1	26.67	0
x_2	18.334	0

Constraint	Level of Slack or Surplus	Dual Price
1	0	450.00
2	6 666.67	0
3	0	34.17

DUAL FORM

Variable	Optimal Value	Reduced Cost
y_1	450.00	0
y_2	0.00	6666.67
y_3	34.17	0

Constraint	Level of Slack or Surplus	Dual Prices
1	-0	-18.33
2	-0	-26.67

The limiting resources are the housing and labour. Cooler capacity, with a dual price of 0 is not limiting the system - any increase in this constraint would not increase profit, but would be an unused resource. It is useful to quantify the benefit associated with any increase in the limiting constraints and this can either be obtained from the dual price of the *primal* model or the solution to the *dual* model. Thus here the dual prices indicate no value with increasing cooler capacity, but suggests that profit will increase by \$450 for every increase in cows, and by \$34 if there is an increase in the time given to milking. The dual values of the *primal* are in fact the optimal solutions to the *dual*. Similarly we are able to obtain a measure of the marginal benefits from an increase in the capacity of males - the optimal solution in the *primal* or from the dual prices of the constraints in the *dual*.

Additional information from the sensitivity analysis of these models provides the decision maker with information on the ranges within which the weighting on the objective functions and the right hand side (RHS) constraints can be changed before there would be a change in the solution. Such analyses are a useful adjunct to the solution of the original model, aiding in better understanding and application.

2.4.3 Integer Programming (IP)

In many cases the solution of an LP model will not provide a realistic solution, this is particularly significant when the decision variable must be constrained to integer values.

One approach to this is through the use of IP, a form of LP, where the model is constrained to provide integer solutions to specified variables. While there may be some loss in the optimal solution through this restriction, with the LP solution providing the upper bound to that from IP, integer models provide a valuable tool for many real problems and offer a mechanism to manage a major practical constraint in LP. This is particularly true in mate selection algorithms where mating is a discrete event with many solutions requiring integer variables.

It is not surprising that many applications of LP in animal breeding have been integer models. However, an additional constraint on the dependence on integer models comes in the capacity of such models to handle large model specifications. For example, while the solution time for LP problems is generally predictable, increasing proportionally with the number of variables and with the square of the number of constraints, the time for an IP problem may even decrease with number of constraints and the solution time may increase dramatically with increased number of variable.

What may be a relatively small LP problem - 60 constraints and 60 variables - may be extremely difficult to solve as an IP problem (Schrage, 1991). Finally, the success of IP problems is more dependent upon an efficient specification of the model than are LP models.

The transportation model is a particular form of IP widely applied in animal breeding. In standard usage this defines positions of supply and demand and the cost of moving between these (e.g. Lee *et al.*, 1985). By defining the available males and females as the levels of supply and demand, and their merit as the cost of movement, the transportation model has been applied to the identification of optimal mating allocations (e.g. Jansen & Wilton, 1985, Kinghorn, 1987; Bunter & Long, 1991; Bunter *et al.*, 1992). This formulation has proved useful in the case of a relatively simple male/female allocation problems where the definition of a dummy male and female are used to exclude individuals from the final mating structure.

Toro and Perez-Enciso (1990) used IP to identify optimal mating combinations (thus mate selection) subject to restrictions on the rate of increase in inbreeding. Another application where control is placed on an objective (in this case a second trait) is given by Toro and Sillio (1992). Here, optimisation is directed at one trait while increases in a second trait are constrained. The associated constraints could define the mating ratios and Toro and Sillio (1992) have extended this general application by incorporating inbreeding in the model with a constraint placed either on the rate of increase in inbreeding or on the increase in the level of genetic merit. While this approach provides some increased level of control over the true objective, it does not necessarily provide an optimal level with no rationale for the choice with respect to its impact on the two components.

As recognised, although there are limitations associated with the use of LP and also IP, such approaches provide useful mechanisms through which problems such as

mate allocation can be addressed. One major limitation to their application addressed through various approaches, is the degree to which risk can be addressed by the analysis.

2.4.4 Portfolio Analysis

Portfolio analysis, originally applied in the area of financial management, provides optimal decision making framework where risk preferences are incorporated into the portfolio selection process. Moving from its original base, the general concept of portfolio management has been extensively applied to farm management issues (e.g. Robison & Brake, 1979). Cropping plans, for example, form diversified portfolios, generally reflecting a greater level of risk aversion than exists in a monoculture situation. Diversification allows the combination of enterprises which covary or exhibit differential levels of variation, so providing some protection against poor production, poor prices, or other risks.

At its simplest, a portfolio can be how one manages money. As recognised by Baumol (1970) the preference of many investors is for a diversified portfolio of investments as an effective risk reduction strategy. In animal breeding there are several benefits from a diversified portfolio of breeding stock. Practical considerations, such as viable mating ratios, ensure a basic level of diversification. The efficient allocation of mates can also be used to address factors such as inbreeding, and attractive levels of genetic diversity.

In defining a preferred portfolio, there are two elements common to most investors :

- a preference for more to less, thus the desire to maximise the expected mean return; and

- a preference for greater certainty, thus less variance in the return.

From the perspective of defining the best portfolio of breeding stock, there would be a preference to achieve the highest expected merit while, for example, attempting to achieve, the lowest levels of inbreeding. Portfolio analysis provides a mechanism through which the portfolio variance can be minimised (Musser, Mapp & Barry, 1984).

Mean-variance (E-V) analysis is a widely used form of portfolio analysis, providing a mechanism for incorporating levels of preferences in selecting the preferred asset combination, with a utility function being used to define the preference function. A frontier, or set, of E-V efficient portfolios can then be defined. These are combinations which, at a given level of expected return, have the lowest level of variance (or for a given level of variance, the maximum level of expected return). The best, or optimal portfolio can be identified as the point of intersection between the E-V efficient frontier and a defined utility function. Alternatively, the optimal or preferred point can be decided through a consideration of the different options along the E-V efficient frontier (see Figure 2.1).

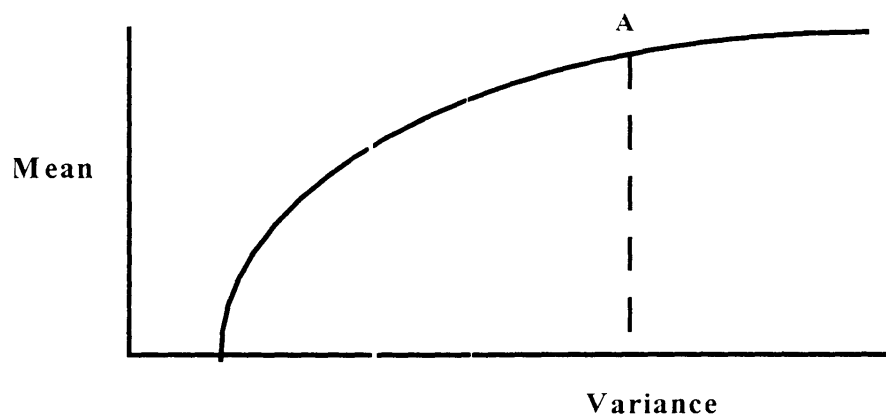


Figure 2.1 The E-V Efficient Frontier, where the point A has the same variance as all points on the line, but the maximum highest mean

Although portfolio analysis has been widely used in agricultural economics (e.g. Robison & Brake, 1979; Anderson *et al.*, 1977), it has not been widely applied in animal breeding. Smith and Hammond (1986 and 1987a) considered the theoretical aspect of this theory, concluding that portfolio analysis can be considered as an indirect process for rational decision making. Schneeberger Freeman and Berger (1982) in applying a portfolio analysis discussed the relationship between income and risk in the case of dairy sire AI selection. This problem was applied by Schneeberger Freeman and Boehlje (1982) who defined the generalised quadratic programming problem as:

$$\text{Maximise } U = px + lx'Qx \quad 2.26$$

$$\text{Subject to } Ax \leq b \quad 2.27$$

$$x \geq 0 \quad 2.28$$

Where:

U , utility, is a function of activities and risk

x is a vector of solutions

p a given vector with the expected incomes of activities

Q a given variance-co variance matrix

A the given coefficient matrix of constraints

b the matrix of right hand side values

the subjective weight for variance relative to the expected income (varying with risk preference)

The accurate definition of a decision maker's utility function will always be a limitation in identifying optimal decisions. It has been suggested that rather than defining the optimal point from the intersection of the frontier with the utility function, the options comprising that frontier can be tabulated, leaving the decision maker to select the preferred strategy from the details of this set (e.g. Anderson *et al.*,

1977; Rae, 1971; Schneeberger, Freeman & Boehlje, 1982). Certainly, Baumol (1970) recognised this refinement of the method provides an invaluable input from decision makers which can never be fully accounted for in definitions of utility and thus formally incorporated into a model.

It is normal to perceive a compromise between variation and expected return. The challenge for portfolio analysis is to provide a mechanism through which the management of risks such as inbreeding, differential accuracy or variations in return can be better handled in the selection process.

2.4.5 Mean Of Total Absolute Deviations (MOTAD)

Hazell (1971) developed a linear alternative to quadratic programming to allow a consideration of farm planning under uncertainty. This method sets as an objective the minimisation of the deviations from the mean rather than of the portfolio variance. The major constraint is the mean activity which is parametrised to allow a solution at each point. The method is referred to as the Minimisation of Total Absolute Deviations (MOTAD).

The following linear programming model (Hazell, 1971) is one form that can be used to apply this approach:

$$\text{Minimize } sA = \sum_{h=1}^s (y_h^+ + y_h^-) \quad 2.29$$

such that

$$\sum_{j=1}^n (c_{hj} - g_j)x_j - y_h^+ + y_h^- = 0 \quad (\text{for all } h, h = 1, \dots, s) \quad 2.30$$

and

$$\sum_{j=1}^n f_j x_j = \lambda \quad (\lambda = 0 \text{ to unbounded})$$

$$\sum_{j=1}^n a_{ij} x_j \leq b_i \quad (\text{for all } i, i = 1, \dots, m) \quad 2.31$$

$$x_j, y_h^+, y_h^- \geq 0 \quad (\text{for all } h, j) \quad 2.32$$

given

$$y_h = \sum_{j=1}^n c_{hj} x_j - \sum_{j=1}^n g_j x_j \quad (\text{for all } h, h = 1, \dots, s) \quad 2.33$$

$$y_h = y_h^+ - y_h^- \quad 2.34$$

and

$$y_h^+, y_h^- \geq 0. \quad 2.35$$

where

A is an unbiased estimator of the population mean absolute income deviation

y_h^- and y_h^+ are the negative and positive total gross margin deviations around the expected return

c_{hj} is the h th observation of gross margin from the j th activity

g_j is the sample mean of the gross margin s for the j th activity

x_j is the level of the j th activity

f_j is the expected (forecasted) gross margin of the j th activity

a_{ij} are the technical requirements of the j th activity for the i th resource or constraint m

b_i is the constraint level

λ is a scaler

There are several features which make the use of the MOTAD approach attractive, not the least being its computational accessibility, where it is an adaptation of the widely used LP approach.

Although MOTAD does not provide the flexibility that can be found in a portfolio analysis, it has been used as an operationally effective tool in handling portfolio analysis. While some deviations between the solutions from Quadratic Programming and MOTAD occur (Musser *et al.*, 1984) the approaches produce very similar results. Further, the use of the risk efficient frontier as a decision tool rather than relying on the identification of a single optimum point, provides a mechanism through which the preference of producers can be most efficiently handled.

2.5 Applications - The Selection of Mates

2.5.1. Introduction

The above discussion addresses issues associated with the integration of genetic and economic objectives in the selection process. In achieving such integration, we effectively are using the genetic information as an input into a bioeconomic assessment to achieve enhanced utility. This approach has been widely demonstrated in the development of mate selection algorithms. The importance of efficient mechanisms for mate selection is put into context by Allaire (1980), who refers to the selection of mating pairs for around 9 million cows annually.

2.5.2 Definition of Mate Selection

It is useful to separate the management of breeding into two steps. Allaire (1977) refers to the selection and mating phase, recognising the division between these two activities. The latter is normally by random means rather than specific allocations of individuals. However, specifications can be made, in, for example, corrective mating, (Allaire, 1977, Allaire, 1980).

Mate allocation and mate selection both imply a formal allocation of mating pairs. The major difference between these is that the former operates only during the mating phase (following selection) whilst mate selection is a process that incorporates selection and mating into a single step. Naturally, due to the additional assessment and management required such strategies will take greater resources than are needed with random mate allocation. Therefore, it is important to identify cost efficient applications for such strategies.

Allaire (1993) adds an additional term to this discussion, that of pair selection (also used by Jansen, 1985). This is defined as a single step where all possible pairs are ranked on an index of merit, with the best N pairs selected. Allaire defines mate selection as a two step process involving males and females initially being separately ranked, with the best N_F and N_M selected. This is followed by a step where the best combined pairs are selected. These two processes, mate selection and pair selection, will converge when the number of males and females to be considered in the second step include the entire population.

While this provides a clear specification of mate selection, there have been a range of similar usages of this term. Allaire (1980), in discussing this approach, stated that it is *a multi-trait selection method depending on the traits of the first preselected mate of a*

mating pair, and more specifically, recognising that in practice, selection will be based on the identification of a male that maximises the net worth of a dam's potential offspring. This definition suggests a distinction between the theoretical concept and its practical application. Such a distinction can be seen in the definition of Smith and Allaire (1985) who refer to it *as the synthesis of selection and non-random mating* or by Smith and Hammond (1987a) who define mate selection *as the selection of parents and the formation of mating pairs*.

2.5.3 Applications in Animal Breeding

Kinghorn (1987), clarifying the situations in which mate allocation will be of value, identifies this value as coming from the increased mean merit of progeny, or in the variance among these progeny. He outlines situations where these outcomes will occur: where there is crossbreeding; where merit is a non-linear function; where there are transportation considerations due to different locations of individuals; and where there are benefits in enhanced levels of variation among the progeny.

Jansen and Wilton (1985) demonstrated the use of the LP approach to the selection of mating pairs where the overall merit is defined as non-linear for one or more of the component traits. Jansen (1985), in assessing selection and mating strategies uses the simultaneous *mating pair selection* as one of the strategies assessed.

More recent uses generally present mate selection as a single step approach, (e.g. Toro *et al.*, 1991; Toro & Silio, 1992), this being particularly true where the mating and selection processes are simultaneously achieved through the solution of linear programming problem.

Assortative mating (mating of *like to like*) is one of the longest established methods of mate allocation (De Lange, 1974). This can be effectively applied as a mating strategy as demonstrated by Dekkers (1994) who identified an optimal breeding strategy for calving ease involved the selection of sires based on an index (incorporating *ebv* as well as various economic factors) and the subsequent assortative mating of such sires with cows in the herd.

With assortative and negative assortative mating (corrective mating) there is an increase in the level of homozygosity or heterozygosity respectively, thus the value of this method is through the greater control it provides over the level of variation in a population, with the ability to produce two diverse subsets (assortative) or a single more uniform group. The ability to increase the genetic variation (Smith & Hammond, 1986), will provide enhanced opportunities for increased genetic response from selection programs. However, while assortative mating strategies provide improvements in the mean level of genetic merit, these may not be the most appropriate strategies to apply where, for example, there are interactions between individuals, as will occur when one objective is a decrease in inbreeding.

With respect to variance, it is well recognised that assortative mating will increase the genetic variance among the offspring (e.g. de Lange 1974; Falconer, 1989; Fernando & Gianola, 1984). Fernando and Gianola (1984) considered how assortative mating (without selection) can be used to maximise the efficiency of selection. While they found that assortative mating based on linear merit functions could change the sign of a genetic correlation, and that it could increase selection efficiency, they suggested that these rules may not hold if assortative mating and selection are simultaneous processes. Most applications of mate selection take greater account of the impact of individual combinations, these being specifically defined, than occurs with paired rankings which occur in assortative mating.

Smith and Hammond (1987b) assessed the relative efficiency of mating and determined that *assortative mating is most useful when heritability is large, parent selection intensity is low and offspring selection intensity is high*. Using an index incorporating information on parents, they found that the influence on efficiency from the index was greatest at low heritabilities. The rationale for assortative mating is for increases in heritability in grand progeny, and thus merit in progeny (Smith & Hammond, 1987b). Mate selection to reduce inbreeding, on the other hand, may prove most effective at low levels of heritability where it is shown to provide a greater capacity to better manage the interactions between inbreeding and genetic gain in the situations where the estimation process is placing the greatest emphasis on family information (Belovsky & Kennedy, 1988).

Smith and Hammond (1987a) define mate selection as the selection of parents and the formation of mating pairs (also Allaire, 1980, Smith & Allaire, 1985) this identifying the single step process discussed above. It is suggested that non-random mating practices imply a non-linear objective, this being consistent with the rationale provided by Kinghorn (1987) where the instances of cross breeding and transportation costs can when included in definitions of merit, vary a formerly linear relationship.

While considerable discussion on the theoretical applications of mate selection has occurred (Smith & Allaire, 1985) actual results supporting its application are only now being presented. One of the developments which must be credited with this is the increasing use of programming techniques. LP, for example, provides a technique by which an objective (such as maximising merit) can be defined subject to constraints on the herd structure (Jansen & Wilton, 1984).

Portfolio analysis is a further step where this single step process can be identified, with the defined optimal portfolio satisfying the constraints for mating combinations and optimising results of expected return subject to level of risk. Schneeberger,

Freeman and Boehlje (1982) applied this technique to the selection of sires where variance of expected income was used as the measure of risk.

While early work on mate selection considered its application to non-linear merit functions (Allaire, 1980; Smith & Allaire, 1985) or where a linear merit function, over several generations, could be assumed to acting non-linearly (Smith & Hammond, 1987a) increasing attention is now being paid to the value of mate selection as a means whereby inbreeding specifically, can be controlled (Toro & Perez-Enciso, 1990; Bunter & Long, 1991; Toro *et al.*, 1991; Bunter *et al.*, 1992; Toro & Silio, 1992).

Bunter *et al.* (1992) used a mate allocation process to satisfy the objectives of increased genetic response and reduced inbreeding. While suggesting that mate selection is a powerful tool with applications to managing inbreeding, they feel that this method will only be of value for moderately to highly heritable traits. They incorporated mate selection in a two-stage process where the initial selection stage occurs followed by some selection/allocation in mating phase. This latter can be likened to the two-stage process used by Van Raden *et al.* (1984).

Toro and Perez-Enciso (1990) used an LP technique for the maximisation of genetic progress under restricted inbreeding. To restrict the level of inbreeding a rate of inbreeding was defined in the set of constraints. In an extension of this method, Toro and Silio (1992) look at a mate selection method maximising the level of a trait subject to the restriction that the mean of a correlated trait remains at or below 0. The next step in this development is the ability of true joint optimisation. For example, the achievement of some control over both genetic progress and reduction of inbreeding.

Inbreeding would appear to act as an effective non-linear trait in the definition of merit, and is particularly suited to mate selection applications. In addition to inbreeding, factors of relationship, such as accuracy, may well prove as amenable to

this form of analysis, these providing objectives which can best be obtained through the specific allocation of mates.

2.6 Discussion

In the development of enhanced approaches for the selection of breeding stock. Considerable refinement has occurred in the area of parameter estimation. However, there remains scope in the application of such parameters to better address breeding objectives incorporating not only genetic elements but also risk considerations..

The interface between the merit of animals and utility to the producer is one area where efficiently defined parameters can be applied to assist in better management decisions. The selection of mates provides a potential area for such applications for in this the needs of defining merit for outcomes is central to the decision maker involved.

Approaches such as linear programming, while highly applicable to the achievement of the desired objectives, are at a relatively early stage of development. Similarly, the identification and application of areas of risk in animal breeding, while still developing, are integral to the achievement of better mating strategies. The improved management of accuracy and inbreeding is central to this risk management perspective.

CHAPTER 3

The Value of Accuracy in Making Selection Decisions¹

3.1 Introduction

Selection on the 'best' estimate of a breeding value *ebv* of individuals should, in large populations, provide the maximal response in breeding value. However, many breeders deal with the selection of small numbers of animals from relatively small populations. In such circumstances it may be of value to also consider aspects of the risk associated with such selections.

Many genetic evaluation schemes provide breeders with information on the accuracy of estimates of breeding value (for example, in the Australian beef industry scheme, BREEDPLAN, see Schneeberger, Tier & Hammond, 1991), and many breeders take some account of accuracy when making selection decisions. It is not known what the most appropriate weight is to place on accuracy for breeders with different attitudes to

¹H.M. Klieve, B.P. Kinghorn and S.A. Barwick 1993 The value of accuracy in making selection decisions. *J. Anim. Breed. Genet.* 110:1-12.

risk. Here, the aim is to assess the gain in utility, defined by a function of the mean and variance of the estimated genetic merit, and the importance of any loss in genetic response from selection on an index of *ebvs* and their accuracies. Other issues include assessing how selection emphasising accuracy will alter the expected genetic response, evaluating the effects of different weightings on accuracy, and finding the relationship between the inclusion of accuracy in the definition of merit and the ranking of animals.

Meuwissen (1991) considered the expected genetic gain and its variance in different breeding schemes. Defining the variance of the selection responses an indicator of the risk associated with a breeding plan, he used utility theory to develop and assess a utility function of the expected genetic gain and used this to identify the circumstances when the expected utility would be maximised. The optimal breeding scheme was identified as a function of the level of risk aversion present. Similarly, the optimum number of sires to be used was dependent on the breeding scheme under consideration. Another application relevant to this research is the development of a utility function, incorporating a risk component, for use in the ranking of males.

Rogers (1990) defined risk as the variance of an estimate of merit - in this case the expected net merit, a value including economic and genetic components.

3.2 Method

Different weightings by which to combine accuracy with estimated breeding value are assessed empirically using a stochastic simulation. Figure 3.1 details the general simulation model. This involves deriving statistics describing the resultant genetic response and utility from a range of indices incorporating both the *ebvs* and their accuracies. An index with a positive weight on accuracy puts emphasis on reducing

the risk associated with an estimate and results in the preferential selection of animals with high accuracy. Conversely, an index with a negative weighting is more risky and requires that high accuracy animals have marginally higher *ebvs* to be selected.

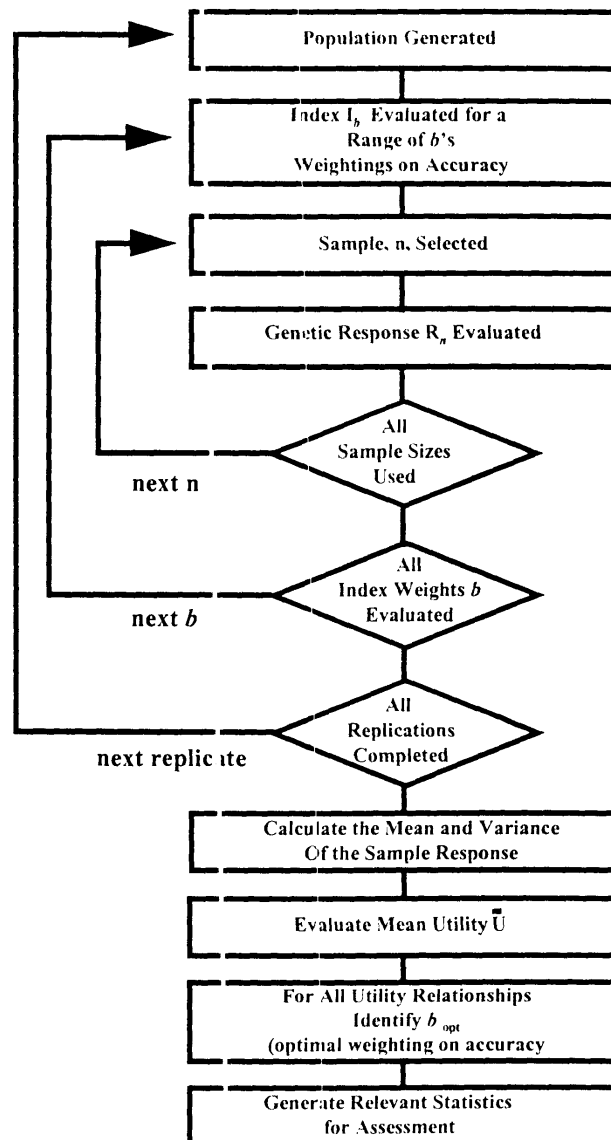


Figure 3.1. Flowchart of the simulation

3.2.1 The Simulated Population

A simulated bivariate normal distribution of 300 *ebvs* and their uncorrelated accuracies (population type A with accuracies in the range 0.0 to 1.0, population type B in the range 0.5 to 1.0) was generated, as in Figure 2.2. Type B was chosen because it reflects that commonly seen in genetic evaluation reports of sires, while type A uses the possible range of accuracies which could occur.

A vector of true breeding values (*tbv's*), $A_j \sim N(0.0, 1.0)$, was first generated. Uncorrelated accuracies, $r_{\hat{A}, A}$, were found for population types $A \sim N(0.50, 0.166^2)$, and $B \sim N(0.75, .076^2)$, these distributions being selected to provide accuracies in the range 0 to 1.0 and 0.5 to 1.0 (all simulated accuracies were within the stated range). *Ebvs* were then generated from *tbvs* and accuracies for each individual. Separate simulations were carried out for each population type.

The distribution of *ebvs* was obtained as follows. In the simple case where is derived as $h^2 P$ from the sole criterion of a single own phenotypic deviation, the regression of \hat{A} on A is:

$$b_{\hat{A}A} = \text{Cov}(h^2 P, A) / V_A \quad 3.1$$

$$= h^2 V_A / V_A \quad 3.2$$

$$= h^2 \quad 3.3$$

This provides a relation for the prediction of \hat{A} (thus $\hat{\hat{A}}$). The mean of this distribution of \hat{A} is $h^2 A$. The variance of \hat{A} "within individuals", where the mean $\mu_{\hat{A}}$ can also be defined as $h^2 E(P / .1)$, is:

$$V_{\hat{A}/A} = Cov(h^2(P - A), h^2(P - A)) \quad 3.4$$

$$= h^4(V_P - 2Cov(A, P) + V_A) \quad 3.5$$

$$= h^4(V_P - V_A) \quad 3.6$$

$$= h^2V_A - h^2h^2V_A \quad 3.7$$

$$= h^2V_A(1 - h^2) \quad 3.8$$

Generalising the selection criterion, by substituting the accuracy r for h , the distribution of the simulated $ebvs$ is:

$$A \sim N(r^2A, r^2V_A(1-r^2)) \quad 3.9$$

Thus the strategy for simulating ebv_j for animal j was to multiply a randomly sampled $N(0,1)$ deviate by $\sqrt{r_j^2V_A(1-r_j^2)}$ and add this to $r_j^2A_j$.

3.2.1.1 Indexes and their evaluation

Selection on an index of ebv and accuracy was simulated for a population size of 300 and repeated for differing numbers (s) of animals selected ($s=1, 5, 10, 25$ and 50). For each set of parameters, 500 replications were carried out.

Using the simulated population and index weightings on accuracy, b , over the range -10.0 to 10.0, an index value was calculated for each b , and all n observations as:

$$I_{b,j} = ebv_j + b \cdot r_j \quad 3.10$$

for the j^{th} individual, $j=1$ to n .

Selection was then carried out on the index value, I_b , leading to the retention of s of the 300 animals.

Rewriting equation 3.10 ;

$$b \cdot r_i = Ib_i - ebv_i \quad 3.11$$

$$r_i = (1/b) \cdot Ib_i - (1/b) \cdot ebv_i \quad 3.12$$

Equation 3.12 shows that the slope of the selection function operating on $ebvs$ and accuracies is $-1/b$, so that the function has a positive slope for a negative weight on accuracy, and vice versa. This can be seen in Figure 3.2 where animals selected using a weighting of 0 (vertical line) and a weighting of +3 (graph a) and -3 (graph b) are to the right of the associated selection lines. The difference between the average ebv of animals retained when $b \neq 0$ and $t=0$ is affected by both the slope of the selection function and the selection intensity applied.

For the animals retained, the genetic selection differential achieved, $S_{A,}$, was calculated from the true breeding value of the selected individuals, with the expected genetic response being equal to this. This process was repeated for all weights and number of animals selected, using the same population. By replicating the whole procedure, the sample mean and variance of the estimated response were found.

3.2.1.2 Utility Relationship

A utility function provides a link between a decision maker's risk preferences and the perceived value associated with a decision option (see Anderson, Dillon & Hardaker, 1977). In this research we consider the implications of extending a decision maker's choice from one based entirely on $ebvs$ to the situation where the accuracy of the measurement is incorporated in an index with $ebvs$. By identifying the utility-maximising weighting, the effect of differing attitudes to risk can be related to the

weighting on accuracy. The response associated with the use of such weightings can then be considered and the cost, in expected response lost, identified.

Here, utility relationships relate to the distribution of genetic responses, defined by the mean response and the variance of these responses. The increase in utility relative to small increases in response can be thought of as a measure of the perceived value of such improvements. For the risk preferrer, at upper levels of response, small increments in response or higher variances of response are rewarded by large increases in utility. In the risk averse situation, there is a decreasing rate of increase in utility leading to almost negligible changes under the same conditions. This can be interpreted as the risk preferrer setting a far higher value on the attainment of small improvements in superior animals than would the risk averse breeder.

Incomplete beta functions (Press *et al.*, 1986), specified by parameters X_A and X_B were used to define 6 utility relationships for use in the present analysis (see Figure 3.3). Values of X_A and X_B were chosen to represent a wide range of attitudes to risk, from very risk averse (curve A_3) to very risk preferring (curve P_3). The curves A_3 - A_1 represent a 'risk avoider', characterised by a decreasing marginal utility for X , while the curves P_1 - P_3 all represent the 'risk preferrer' who has an increasing marginal utility for X . The curves in each group provide degrees of attitude to risk. Curve N (a linear relationship) depicts a risk neutral relationship where Utility = Mean Response.

To use the incomplete beta function, response statistics (the X values in Figure 3.3) were scaled to a range 0.0 - 1.0. A three standard deviation bar around the maximum mean response was scaled to a width of 0.8, with the midpoint set to 0.5 - defining the distribution as a band from 0.1 - 0.9. Distributions of lesser mean response were centred below this (using the above scaling factor). Scaled response statistics were truncated outside the 0 to 1 range - excluding any extreme observations.

The mean utility was defined as the weighted average of the utility found at seven points on the distribution of mean response, with each point weighted by the ordinate from the defined normal distribution. This distribution is defined by the mean response and its variance for each index considered, with the points used being the mean and points at one, two and three standard deviations either side of the mean. The utility for curve N was obtained from the mean response, with no need to account for the variance of this response.

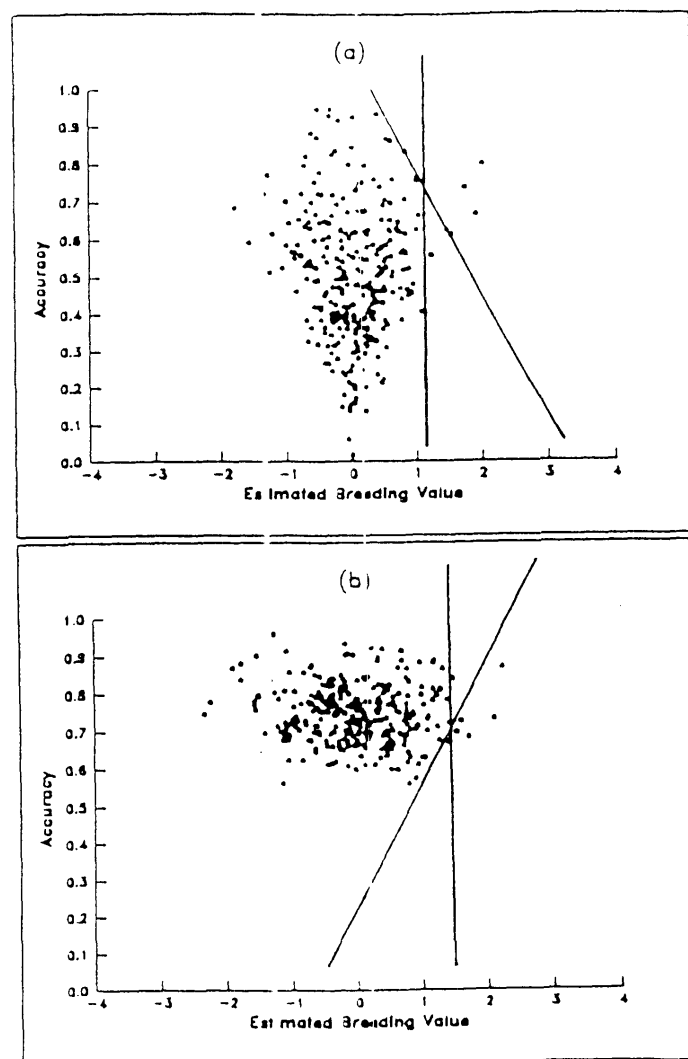


Figure 3.2. Illustration of the simulated populations ($N=300$) for (a) population type A (accuracy in range 0.0 to 1.0) and (b) type B (accuracy 0.5 to 1.0). Also shown are selection functions for (a) $b=0$, $b=+3$ and (b) $b=0$, $b=-3$, for six animals selected.

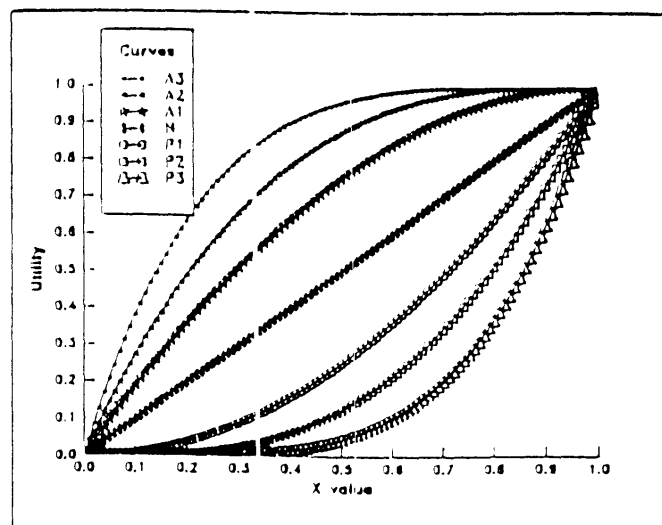


Figure 3.3. Risk averse ($A_1 - A_3$), risk preferring ($P_1 - P_3$) and risk neutral (N) utility curves used. The parameters X_A and X_B associated with curves $A_1 - A_3$ are $X_A = 1.0$ and $X_B = 2.0, 3.0$ and 4.5 , and for curves $P_1 - P_3$, $X_A = 2.0, 3.0$ and 4.5 and $X_B = 1.0$.

The maximum utility was found for each number of animals selected and each utility curve. This utility, $U_{b,opt}$, allows identification of the optimal weighting for accuracy in each of these circumstances. The utility of all weightings on accuracy were compared to the utility at $b=0$ ($U_{b=0}$) by deriving the summary statistic, 'relative utility', ie.

$$U_{relative} = (U_{b,opt} - U_{b=0}) / U_{b=0} \quad 3.13$$

3.3 Results

3.3.1 *The Effect on Response*

To assess whether there is a range of weights on accuracy over which there is little falloff in mean response (\bar{R}_b) over the maximum attainable (\bar{R}_{\max}), the ratio \bar{R}_b/\bar{R}_{\max} was calculated for all indices. The index weightings on accuracy were then identified for which the levels of response were within 1% and 5% of the maximum identified. These values are presented in Table 3.1. In all cases the defined range included $b=0$ as a relatively central point, although, for population type A, the range of positive weightings was generally wider. For the 1% case, this defined region had a total width of about 1.0 for population type A and 2.5 for population type B.

The effect of the weighting applied to accuracy on the mean response, for the case where one animal is selected, is illustrated in Figure 3.4. Three definitions of expected response are illustrated : $\bar{R} + \sigma$, \bar{R} and $\bar{R} - \sigma$. For these curves, the weighting associated with the maximum response are, for population type A, $b=-1.15$, -0.15 and 1.45 , and population type B, $b=-1.35$, -0.15 and 1.05 for $\bar{R} + \sigma$, \bar{R} and $\bar{R} - \sigma$ respectively. These results show increases in the index weightings associated with the response as its definition moves from $\bar{R} + \sigma$, \bar{R} and $\bar{R} - \sigma$.

For both population types there was a slightly greater variance in response for negative index weights, while for population type A there was a stronger decrease in mean response with increasing negative weights than for positive weights. The strong decline is associated with the greater chance in that population of selecting animals of lesser *ebv* and much reduced accuracy (that is, animals with accuracy around 0).

Table 3.1. Index weightings on accuracy defining a plateau response region within 1% and 5 % of the maximum response. The range is defined by lower (L) and upper (U) bounds.

No Selected n	Population Type A				Population Type B			
	L(5%)	L(1%)	U(1%)	U(5%)	L(5%)	L(1%)	U(1%)	U(5%)
1	-1.6	-1.2	.5	2.2	-2.7	-1.3	1.3	3.9
5	-1.4	-.9	.5	2.0	-3.2	-1.4	1.6	4.3
10	-1.3	-.6	.6	1.7	-3.2	-1.5	1.7	4.1
25	-1.2	-.6	.6	1.6	-3.0	-1.2	1.6	3.7
50	-0.9	-.4	.6	1.4	-3.1	-1.4	1.4	3.4

3.3.2 The Effect on Utility

Optimal index weights for each population type, utility curve and number of animals selected are represented in Table 3.2. The major pattern apparent is that, for both population types, the optimal weightings on accuracy for risk averse relationships (curves A_3 - A_1) are positive while the weights for risk preferring relationships (curves P_1 - P_3) are negative. A few exceptions occur but these have weights of small magnitude and are associated with the selection of larger numbers of animals. The optimal weights also tend to be larger when the number selected is small.

Figure 3.5 shows the relationship observed between the index weightings on accuracy and relative utility for the four extreme utility curves (excluding A_2 and P_2 , the intermediate curves). Curve P_3 , applying to breeders who are most prepared to

Chapter 3 - The Value of Accuracy in Making Selection Decisions

Table 3.2. The optimal index weights for the simulation.

Population Type A							
Size n	- AVERSE		- Utility Curve -		PRONE -		
	A ₃	A ₂	A ₁	N	P ₁	P ₂	P ₃
1	0.50	0.50	-0.15	-0.70	-0.70	-0.70	-1.15
5	-0.55	-0.55	-0.55	-0.55	-0.45	-0.45	-0.40
10	0.35	0.35	0.25	0.05	-0.35	-0.35	-0.35
25	0.15	0.10	0.10	0.10	0.10	-0.45	-0.45
50	-0.05	-0.05	-0.05	-0.05	-0.05	-0.10	-0.10
Population Type B							
Size n	- AVERSE		- Utility Curve -		PRONE -		
	A ₃	A ₂	A ₁	N	P ₁	P ₂	P ₃
1	1.05	1.05	-0.15	-0.15	-0.15	-0.55	-0.60
5	0.45	0.50	-0.30	-0.30	-0.60	-0.60	-0.60
10	-0.10	-0.20	-0.20	-0.20	-0.50	-0.50	-0.55
25	0.25	0.25	0.25	0.25	0.25	0.25	0.25
50	0.20	0.20	-0.10	0.05	0.05	0.05	0.05

take risks, leads to more extreme decreases in utility both for large positive and negative weights than occurs for other utility relationships. Results are similar between population types, except that the decrease in relative utility for negative weights is far more extreme in population type A than B.

For both (a) and (b), the maximum for curve P_j occurs before the decline associated with increasing negative weights. For positive weights, curve A_j is consistently high suggesting that there is a large range of positive weights over which utilities will be near the optimum, for breeders who are most risk averse.

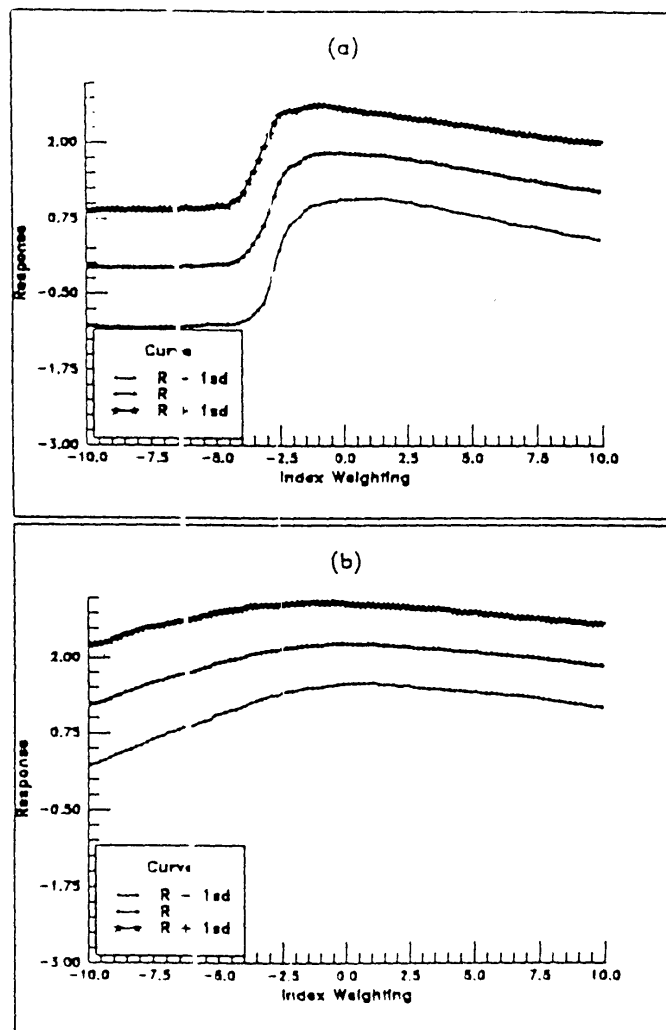


Figure 3.4. Mean Response and mean $\pm \sigma$, for population types A (a) and B (b) with the selection of 1 animal from 300 candidates.

3.3.3 The Effect on Ranking

To provide an indication of the effect of differing indices on rankings for *tbv*, populations of size 300 and population type A and B from the simulation were examined. Rankings were compared for weightings on accuracy of +1.0, -1.0 and 0. The values of ± 1.0 were chosen because they are \pm one standard deviation of the true breeding value predicted. Figure 3.6 illustrates the changes in ranking occurring by plotting cumulative *tbv* against the rank order for pairs of indices.

Note in Figure 3.6 that an index which is a better indicator of *tbv* will have a greater area under its curve. Where curves overlap, the animals being compared by the two indices have identical mean genetic merit. When a ranking is a poor indicator of true merit, animals of low *tbv* will be included earlier than they would under a more efficient index, so that the rate of increase in cumulative *tbv* is less and the turning point lowered. Thus the closer two curves are at any point the greater the similarity in their ranking is likely to be.

For population type B, rankings with weights on accuracy of 1.0 or -1.0 were both close to that for a weighting of zero. The main differences in ranking occurred in the middle of the distribution. This is consistent with the earlier result that only very small decreases in response occur for weights on accuracy of this magnitude. The impact on ranking is far greater for population type A, particularly for larger numbers of animals selected. This reflects the fact that weights of ± 1.0 are outside the range of weights corresponding to the plateau response region shown in Table 3.1.

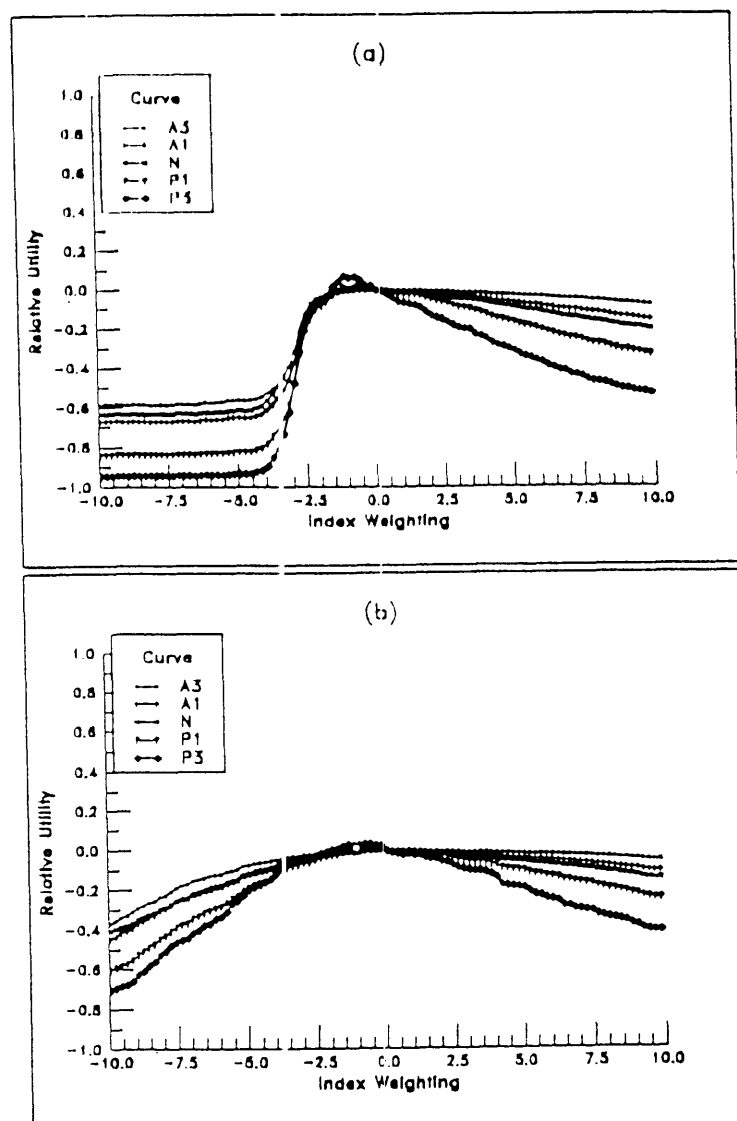


Figure 3.5. The relative utility for the major utility curves (medium levels U_2 and U_5 excluded) for one animal selected and population Types A (a) and E (b).

3.4 Discussion

Selection decisions by the breeder involve a broad range of considerations. Objectives, whether or not they are defined formally, will include not only the maximisation of genetic merit in the animals to be selected but also a minimising of

associated costs. So, while the best genetic option will always be to select the top sires, associated costs, personal preferences and the competition with other breeders for these sires may alter the selection decision made.

Traditionally it is suggested that if accuracy is taken into account, a positive weight should be placed on it (e.g. Freer & Sundstrom, 1991) - leading to a preferential selection of higher accuracy, better known animals. This is a risk averse approach for which breeders will pay through higher prices. Our results allow an assessment of the cost, in terms of the loss in genetic response, of preferentially selecting animals of either high or low accuracy. Using low accuracy, some risk is taken by selecting lesser known animals, with potential rewards coming in the form of lower purchase prices and the possibility of the animals proving to be notably better than their present information would suggest.

There are several features to emphasise from the results. As expected, the maximum mean response occurred at, or close to, an index weighting on accuracy of 0, although for both population types this weighting was negative. There is, however, a range of weightings from which only small reductions in response will be expected - and so where there is a perceived benefit from either low or high accuracy animals, the cost of this in terms of response is not necessarily high. The decision to adopt either a mildly risk averse or preferring approach to the selection of animals is unlikely to significantly reduce the expected response.

To take a strongly positive attitude to the value of accuracy will reduce expected response. From a consideration of the results presented in Tables 3.1 and 3.2, particularly for the selection of small numbers of animals, the curves A_3 and P_3 can lead to the identification of points outside the range defined as close (within 1%) to the maximum response, while the ranges defined using the less extreme curves A_2 and P_2 consistently include the optima. Thus, the adoption of a medium level strategy of either risk preference or aversion will lead to only a small change in expected response, due to only small changes in the ranking of animals. High accuracy animals

allow a producer to have greater consistency of production. Where very positive emphasis is placed on accuracy (curve A_3) there will be loss in response from the exclusion of less known animals having higher *ebvs*. If a heavy emphasis is placed on low accuracy (curve P_3) there will as with curve A_3 , be lost utility, but, potentially some benefit from the generally lower levels of relationships existing in the pedigrees of selected animals. Lower levels of inbreeding are likely as is a higher variance in the mean utility. While the emphasis defined as optimal under P_3 may be too costly in the achieved outcomes, reasonable benefits might be achieved using the optimal weightings for curves P_1 or P_2 (similarly for A_1 or A_2 in the above case).

A further benefit of placing a negative weighting on accuracy is in the area of inbreeding. Animals of high accuracy are also likely to be those which have large numbers of offspring, and so a high future representation in the herd. Morley (1954) noted that 'in any population undergoing selection, a positive correlation between degree of inbreeding of progeny and merit in parents is an automatic consequence of selection'. With the increasingly efficient selection procedures currently practised the impact on inbreeding can be increased. Robertson (1961) also considered this problem, recognising that under artificial selection all parents will not have an equal chance of selection, so leading to future problems of inbreeding.

In the approach considered here, the use of a positive index would be expected to lead to a positive correlation between accuracy and inbreeding, so increasing the rate of increase in inbreeding. However, with a negative weighting on accuracy, the negative correlation between accuracy and inbreeding should place some constraint on increasing F .

The following example (Table 3.3) of 12 Poll Hereford sires (from the Semen Buyers Guide, 1991 Australian Poll Hereford Genetic Evaluation Report) demonstrates the effect on ranking of different weightings on accuracy. The price per registration is included here although there are several factors which affect price, for example, *ebv*, accuracy and whether imported. With such a small sample covering both a range of

accuracies and *ebvs*, the rankings of animals are relatively distinct. Variations in ranking will thus not occur as frequently as in larger samples where animals of similar merit exist. However it allows an example of the levels of weighting on accuracy required for any change in ranking to be presented. These are shown in Table 3.4 for pairs of animals ranked on 600 day weight *ebv*_{600day} along with the change in dollar value accompanying each alteration. It is apparent that where there are large differences in *ebv* but only small differences in accuracy, the weighting required for a change in ranking to occur is extremely high. Also confirmed is the tendency for the rankings of superior animals to generally remain unchanged due to their high *ebvs* and accuracies. Thus, even if a weighting of ± 23 is used (around the standard deviation of *ebv*_{600day}) there is no change in ranking for the top three animals. Animal D, however, very rapidly is moved from fourth position with the use of a positive index whilst a negative index of this order leads to H and K dropping in merit.

The question of the best weight to place on accuracy is a function of both the degree and direction of risk preference. For type A and type B populations weights of around $\pm 0.5\sigma$ and $\pm 1.5\sigma$ respectively, appear to be appropriate. Here, the sign on the weight is defined by the form of the risk preference (-ve for risk preferring and +ve for risk averse) and the position in the defined range by the degree of the preference. The relative price which might be paid for high ranking animals can then be considered in making selection decisions. This can also be done more objectively by incorporating purchase price in an index following the approach of Kinghorn (1986).

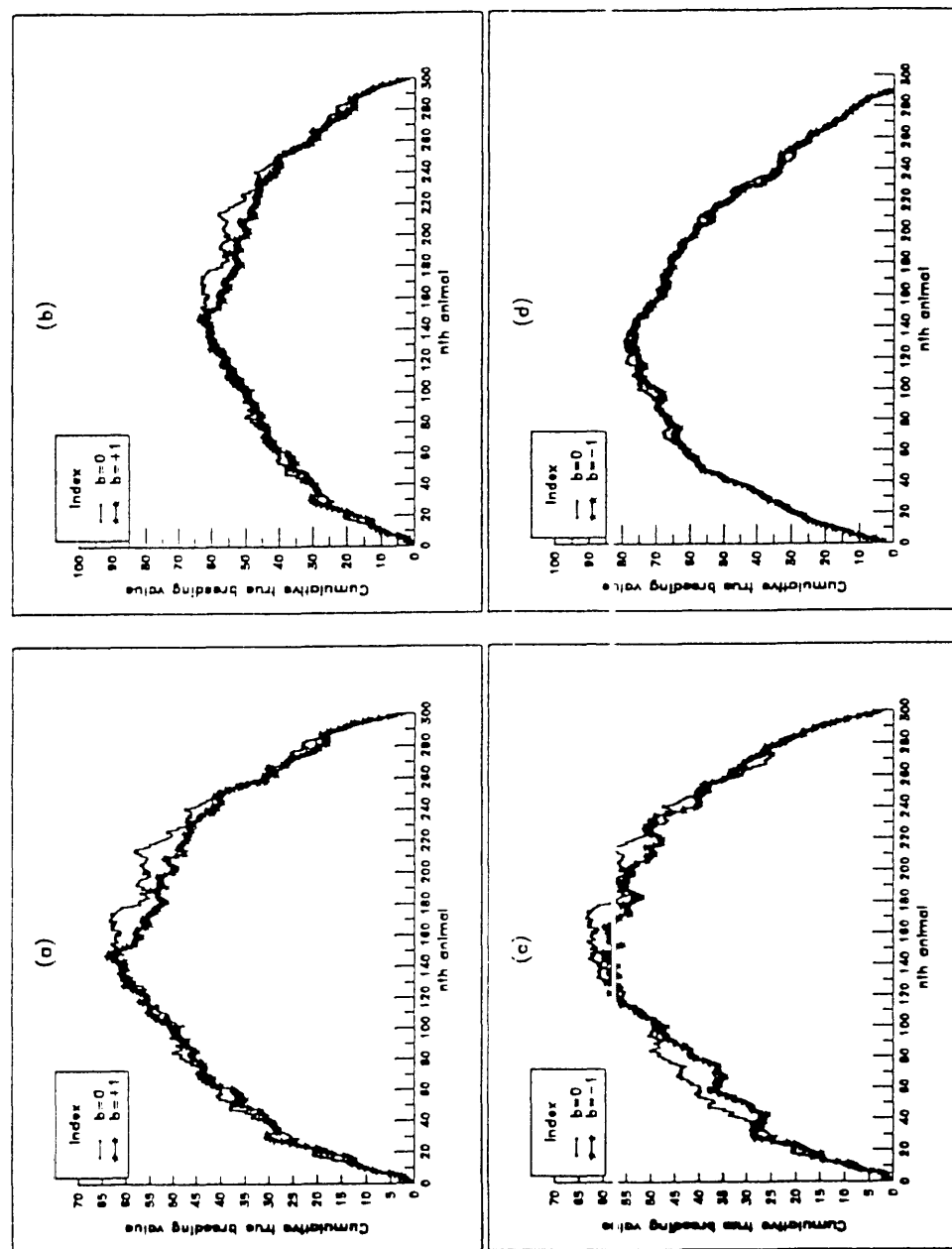


Figure 3.6. Illustration of the extent of change in ranking of animals for true breeding value when ranked on indices with weightings on accuracy of 0, 1.0 or -1.0 for population types A (a and c) and B (b and d).

Table 3.3. Sires from 1991 Poll Hereford Genetic Evaluation Report Semen Buyer's Guide, showing ebv_{600day} , accuracy, r , and price/registration (dollars).

Sire	Code	ebv	r	Price per Registration
<i>Floral View Navigator</i> *	A	82	.97	550
<i>Academy Challenge</i>	B	79	.89	400
<i>Graystone Granite</i> *	C	66	.96	500
<i>Pontiac Achiever</i>	D	53	.57	65
<i>Inverary Groom</i>	E	51	.69	300
<i>GK Voyageur</i> *	F	51	.68	300
<i>PRL Case</i> *	G	47	.94	250
<i>Sevenbardot Indigo</i>	H	46	.91	160
<i>Wat GK Discovery</i> *	I	44	.83	300
<i>Remitall Stetson</i> *	J	43	.94	250
<i>Magador Sculptor</i> *	K	38	.88	300
<i>Inverary Ellis</i>	L	36	.59	166

* Imported bull

Table 3.4. Example showing the index weighting required to change the ranking of pairs (above diagonal) and the associated price change (below diagonal) of such a variation.

A	B	C	D	E	F	G	H	I	J	K	L	
A		-38	-1601	-73	-111	-107	-1167	-601	-272	-1301	-489	-122
B	150		186	-82	-141	-134	641	1651	-584	721	-4101	-144
C	50	-100		-34	-56	-54	-951	-401	-170	-1151	-351	-82
D	485	335	435		17	19	17	21	35	28	49	851
E	250	100	200	-235		-1/1	17	23	51	33	69	151
F	250	100	200	-235	0		16	22	47	31	66	-167
G	300	150	250	-185	50	50		-34	-28	0**	-151	-32
H	390	240	340	-95	140	140	90		-26	-101	-267	-32
I	250	100	200	-235	0	0	-50	-140		10	121	-34
J	300	150	250	-185	50	50	0	-90	50		-84	-21
K	250	100	200	-235	0	0	-50	-140	0	-50		-7
L	384	234	334	-101	134	134	84	-6	134	84	134	

* equal ebs, thus any weighting leads to change

** $r_1 = r_2$ - therefore no impact from a weighting

CHAPTER 4

The Joint Regulation of Genetic Gain and Inbreeding Under Mate Selection.²

4.1 Introduction

Animal breeders are normally faced with a range of selection decisions. Techniques exist allowing attention to be directed at several traits simultaneously, including when estimated breeding values *ebvs* are available for each trait (Schneeberger *et al.*, 1992). However, methods for the joint consideration of *ebvs* and other information available on animals are not well developed. This other information includes the level of inbreeding of individuals, crossbreeding effects, operational costs and the accuracy of *ebvs* (e.g. Van Raden *et al.*, 1984; Kinghorn & Shepherd, 1990; and Klieve *et al.*, 1993).

² Klieve, H. M., Kinghorn, B. P. and Barwick, S. A 1994, The joint regulation of genetic progress under inbreeding *Journal of Animal Breeding and Genetics* 111: 81-88.

This paper describes a method in which the advantages of portfolio analysis (see, for example, Schneeberger *et al.*, 1992) are integrated in a mate selection strategy to achieve more control over otherwise competing objectives. The strategy minimises inbreeding subject to a defined acceptable loss in the achievable additive genetic merit.

An approximate quadratic programming method, MOTAD (Mean Of Total Absolute Deviations), is adapted to the problem of selecting the most suitable portfolio of breeding pairs or groups from the frontier of efficient portfolios, where the selected portfolio is defined by the level of allowed sub-optimal genetic response.

Kinghorn (1987) examined strategies for the formal allocation of mates and suggested they have value when either the mean merit of progeny is affected (for example, where merit is a non-linear function of parental breeding value and other characteristics of interest) or when the allocation will affect the variance among progeny. Smith and Hammond (1987a), Goddard and Smith (1990) and Bunter *et al.* (1991) examined mate selection strategies which utilised linear programming (LP) techniques as a means of reducing inbreeding under selection. Each of these studies applied a constraint on inbreeding through an adjustment to the *ebv*,

$$ebv_{adj} = ebv - f(F) \quad 4.1$$

where $f(F)$ is a '*sufficiently large cost*' subtracted from the *ebv*, related to the level of inbreeding (Smith & Hammond, 1987). Toro and Perez-Enciso (1990), using a different mate selection approach, maximised genetic merit subject to a constraint on the rate of increase of inbreeding. While such approaches did include both inbreeding level and genetic response, the patterns of relationship between these variables are not captured by the function. In the present study, the portfolio approach allows constraints to be formulated after joint consideration of the additive genetic merit possible and the risk (inbreeding) associated with differing levels of merit.

4.2 Methods

4.2.1 Portfolio Analysis and the Breeding Value - Inbreeding Frontier

In portfolio analysis (see Anderson *et al.*, 1977), a frontier of Expected value and Variance (E-V) efficient portfolios - those portfolios which have the lowest level of variance for a given level of return - is defined (see Figure 4.1 for a typical example). For the present application this can be adapted to be a frontier of the genetic merit and inbreeding level of specified portfolios - thus a BV-F frontier. In this case the measure of genetic merit for each portfolio is the sum of *ebvs* of selected parents. Similarly, the inbreeding level of portfolios is found from the sum of inbreeding coefficients of prospective offspring from selected parents. The problem is to minimise inbreeding subject to achieving at least a minimum level of additive genetic merit, denoted λ .

In deciding on the point on the BV-F efficient frontier at which to operate (those points which have the minimum level of inbreeding for a given level of genetic merit) it is important to have information on the associated level of inbreeding expected for each level of *ebv*. Figure 4.2 shows BV-F frontiers at five year intervals, generated for the population and age structure of this analysis, using a simulation model which targeted maximisation of mid-parent *ebvs*. At each time period the BV-F 'frontier' was generated by varying λ .

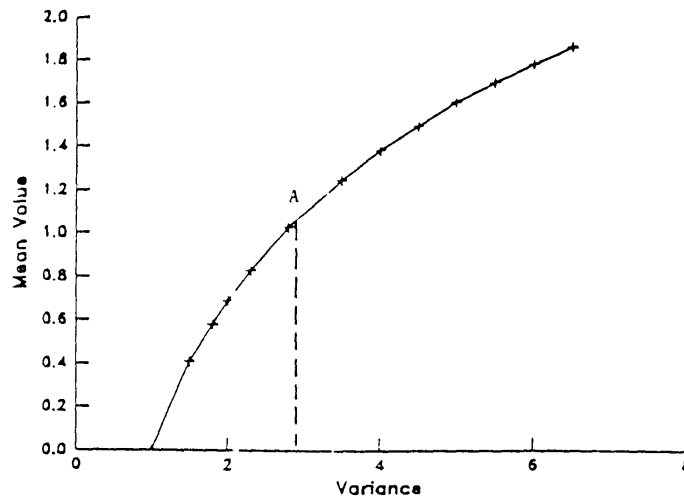


Figure 4.1 An example of an E-V efficient frontier for a portfolio analysis. Here, point A represents a portfolio with maximum value for a set level of variance. Portfolios with the same variance but lesser means are shown on the dashed line.

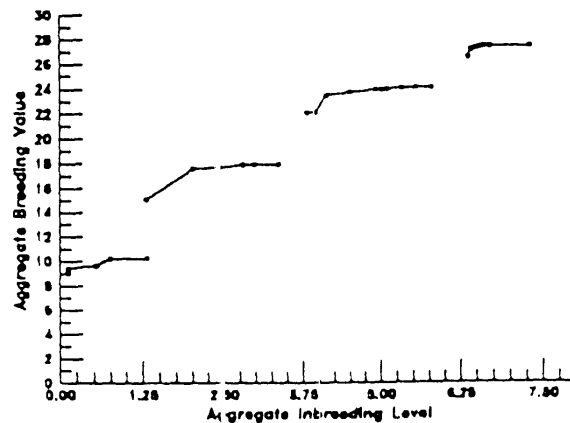


Figure 4.2 The BV-F frontier at 5, 10, 15 and 20 years. The right hand point on each curve is the maximum level of aggregate breeding value, and the associated aggregate inbreeding level, from the best combination of matings, where inbreeding is not considered. Very small allowed reductions in aggregate breeding value and resulting levels of inbreeding are shown for other points on the curve.

At all time periods in the simulation, aggregate breeding values differ little over a considerable range in level of inbreeding (Figure 4.2). By accepting a marginal reduction in the level of genetic merit aimed for, considerable reductions in inbreeding can be gained.

4.2.2 Adapted MOTAD

An approximation of Quadratic Programming, MOTAD (Mean Of The Absolute Deviations method, see Hazell, 1971) was used to describe the E-V efficient frontier and to select the most efficient position on that frontier with respect to the objectives. The aim was to minimise the level of inbreeding subject to a defined sub-optimal level of merit.

Following Hazell's standard formulation, the problem is a Linear Programming problem framed to minimise the level of inbreeding (risk) subject to a set level of genetic merit:

$$\text{Minimize } \sum_{i=1}^{n_{fc}} \sum_{j=1}^{n_{mc}} x_{ij} F_{ij} \quad 4.2$$

such that

$$\sum_i \sum_j x_{ij} A_{ij} \geq \lambda \quad 4.3$$

$$\sum_j x_{ij} + n_{fm} K_j \leq n_{fm} \quad 4.4$$

$$\sum_j K_j = rno \quad 4.5$$

$$\sum_j x_{ij} \leq 1 \quad 4.6$$

$$\sum_i \sum_j x_{ij} \leq n_{fs} \quad 4.7$$

where n_{fc} is the number of female candidates; n_{fm} the maximum number of females per male; $x_{i,j}$ reflects the usage of matings (1 if used, 0 if not); $F_{i,j}$ and $A_{i,j}$ are the inbreeding coefficient and mid-parent *ebv* associated with mating animals i and j ; and K_i is a dummy variable, for males, used to identify those excluded. Both $x_{i,j}$ and K_i are defined as binary. Equation 4.3 defines the minimum level of aggregate breeding value, λ , to be targeted. Equations 4.4 and 4.5 use the dummy variable K_j to identify the males to be excluded (*rno*) by the mate selection process in any year; equation 4.6 defines a single mating per female and equation 4.7 defines the maximum total number of females selected (n_{fs}).

In a formal MOTAD model an additional constraint, not included here, is used to handle variations in data accumulated from several time periods:

$$\sum_{j=1}^n (c_{h,j} - g_j)x_j + y_h^- \geq 0 \quad 4.8$$

where:

$$y_h^- = \left| \sum_{j=1}^n (c_{h,j} - g_j)x_j \right| \quad 4.9$$

In the application detailed here, Equation 4.9 would measure the sum of the deviations of the inbreeding coefficients, c_{hj} , from a 'mean' g_j of 0, weighted by x_j , the usage of the mating. As y_h^- is always positive and inbreeding coefficients must be equal to or greater than 0, Equation 4.8 is equivalent to $2 * y_h^-$. Equation 4.8 is thus always satisfied and is not required.

In most MOTAD applications the input data are gross incomes achieved from a range of activities, with information coming from several time periods. Here, the data on inbreeding are effectively from a single time period. The MOTAD framework can be used to place several sub-objectives into the objective, as long as all are scaled to comparable ranges (avoiding the domination of the objective by any one sub-objective). When there were two sub-objectives, say inbreeding and levels of relationship, over which control has to be achieved, the objective function could be specified as:

$$\text{Minimize } \sum_{i=1}^{noF} \sum_{j=1}^{noM} x_{i,j} * F_{i,j} + x_{i,j} * R_{i,j} \quad 4.10$$

where $R_{i,j}$ is a measure of the amount of information, through relationship, available on an animal, and $F_{i,j}$ the measure of inbreeding. In this case both would be appropriately scaled to ensure comparable data, not dominated by either objective.

For the present application, the Mixed Integer Programming method from GAMS (General Algebraic Modelling System, Brooke *et al.*, 1988) was used. The mate selection process was repeated annually, over the 20 year time frame used, as the means for selecting and allocating breeding pairs. Thirty replications were run and the mean and standard error of results for each strategy were calculated.

4.2.3 The Simulation Model

A stochastic simulation was used to model a breeding population over a 20 year period. A base population of 3 males and 15 females, with each male mating with 5 females, was generated as follows, for animal i :

breeding value:

$$a_i = X_{1i}\sigma_a \quad 4.11$$

phenotype:

$$y = a_i + X_{2i}\sigma_e \quad 4.12$$

where X_1 , X_2 are independently sampled from $N(0,1)$, and $\sigma_a^2 = 1$, $\sigma_e^2 = 4.0$ ($h^2 = 0.2$).

The time animals remain in the breeding structure was dependent upon their continued definition as mates - all animals not included being culled after each mating period. While all animals became available for mating at sexual maturity, the number of offspring contributed by any female is dependent upon how long before that animal is culled and the success of her offspring (with one per year with a given mortality rate).

After the initial generation, breeding values were generated using the following relationship:

$$a_i = 0.5(a_s + a_d) + X_{1i} * \sigma_a * 0.5 * \sqrt{(2 - F_s - F_d)} \quad 4.13$$

where a_s and a_d (F_s and F_d) are the breeding values (inbreeding coefficients) of the sire and dam of animal i .

From Equation 4.13 it can be seen that the impact of reduced genetic variance from increased levels of inbreeding is included in the model, but effects of inbreeding depression on performance are not. The phenotype of animals was then defined as

$$y_i = a_i + e_i \quad 4.14$$

where $e \sim N(0, \sigma_e^2)$. BLUP estimates of the foundation population breeding values were then derived for use in the selection process.

The model united selection of breeding stock and the definition of mating pairs into a single step - thus mate selection. The female breeding population size was kept constant over years at $n_{fs} = 15$ females, and with maximum females per male set at $n_{fm} = 5$, and with replaced \leq by $=$ in equation 4.4, this gave 3 males used equally in each year. Mature animals not selected were culled, and each breeding female produced one offspring per mating.

4.2.4 Treatments

Treatments were chosen to demonstrate the impact of the method and included 'controls' in the form of selection on BLUP $ebvs$ (E_r) and on phenotypes (P_r), under random mating. A linear programming mate selection model which maximised the sum of the $ebvs$ of offspring from selected parents was first run subject only to a defined breeding structure.

Treatments were then chosen which varied the allowed reduction in the predicted attainable genetic response, where this was defined from the difference between the best achievable average ebv of selected parents and the average ebv of all parents before selection. In both cases, averages were calculated giving equal weighting to the two sexes. With the exception of E_r and P_r , all treatments used mate selection (MS^*) and aimed to minimise inbreeding. Treatments were:

MS_0 selection on BLUP $ebvs$ - no decrease allowed in genetic response

MS_1 selection on BLUP $ebvs$ - 1% decrease allowed in genetic response

MS_5 selection on BLUP $ebvs$ - 5% decrease allowed in genetic response

MS_{10} selection on BLUP $ebvs$ - 10% decrease allowed in genetic response

*MS*₂₅ selection on BLUP *ebvs* - 25% decrease allowed in genetic response

E_r selection on BLUP *ebvs* - random mating

P_r selection on phenotype - random mating

4.3 Results

Figures 4.3 and 4.4 show results for average breeding values and inbreeding coefficients over the time period of the simulation for the strategies analysed. The breeding values, inbreeding coefficients and associated standard errors for years 5, 10, 15 and 20 are presented in Tables 4.1 and 4.2.

Figure 4.2 suggested that considerable reductions in inbreeding level can be associated with very small reductions in aggregate *ebv* and Figures 4.3 and 4.4 show that such decreases in inbreeding were in fact realised. Figures 4.3 and 4.4 show treatment *MS*₅ to result in considerably lower inbreeding than *E_r* and with equivalent genetic merit. The genetic response from mate selection alone (*MS*₀) was consistently above that of *E_r* , probably due to increased genetic variation resulting from the markedly reduced levels of inbreeding which also occurred. Compared to *MS*₀ , treatments *MS*₁ and *MS*₅ gave only slightly less genetic merit but further considerable reductions in inbreeding

Interestingly, for treatment *MS*₅ there was a consistent increase in the standard error associated with the breeding value. The mean breeding value for *MS*₅ , while increasing at close to the same rate as that for *MS*₁ until year 15, surpassed this by year 20, *MS*₅ then having a level of genetic merit just above *E_r* but an inbreeding level below that for *MS*₁ (Tables 4.1 and 4.2).

The simulation results are presented on BV-F axes in Figure 4.5. The results demonstrate a pattern similar to that of Figure 4.2. The strategy selecting on $ebvs$, E_r , can be identified as a high return/high risk option. A point corresponding to this strategy would not occur on a true EV-F efficient frontier as the MS_0 strategy shows both higher genetic response and lower inbreeding and is thus preferred on bases of both returns (BV) and risk (F).

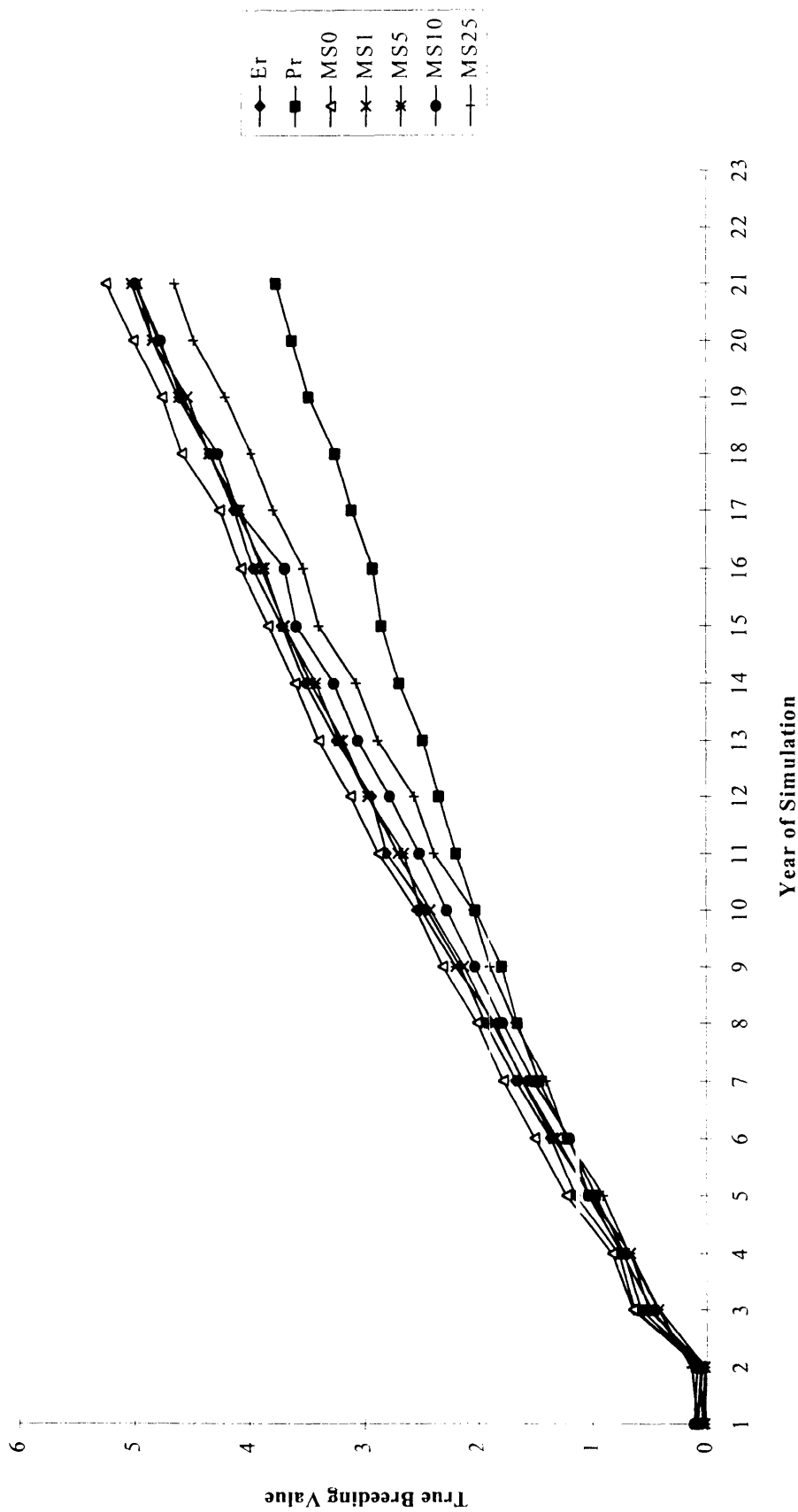


Figure 4.3 Simulated change in mean true breeding value for different selection strategies

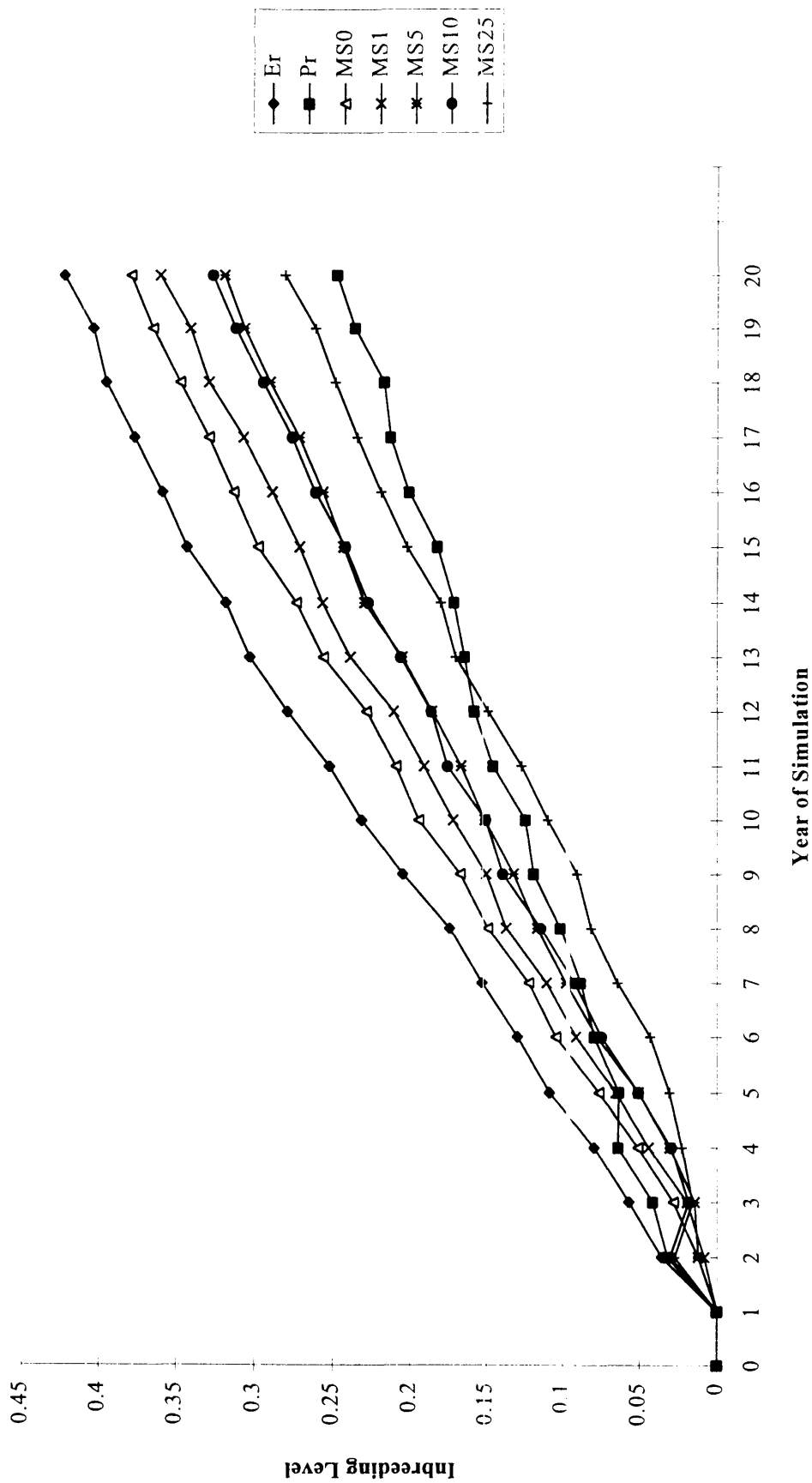


Figure 4.4 Simulated change in mean inbreeding level for different selection strategies

Chapter 4 - The Joint Regulation of Genetic Gain and Inbreeding Under Mate Selections

Table 4.1 Average breeding values (standard errors), at 5 year intervals for simulated selection strategies¹

Simulation		Treatments					
Year	E_r	P_r	MS_0	MS_1	MS_5	MS_{10}	MS_{25}
5	1.3601	1.2142	1.5005	1.3078	1.3400	1.1961	1.2236
	(.0822)	(.0805)	(.0921)	(.1269)	(.0753)	(.0923)	(.0709)
10	2.8003	2.1914	2.8711	2.7001	2.6518	2.5145	2.3864
	(.0923)	(.1064)	(.1127)	(.1006)	(.1143)	(.1054)	(.0807)
15	3.9595	2.9195	4.0631	3.8853	3.8588	3.6850	3.5217
	(.1094)	(.1336)	(.1131)	(.1102)	(.1431)	(.1126)	(.1005)
20	4.9870	3.7611	5.2380	4.9620	5.0155	4.9825	4.6432
	(.1310)	(.1528)	(.1038)	(.0983)	(.1501)	(.1081)	(.1067)

¹See text for definition strategies.

Chapter 4 - The Joint Regulation of Genetic Gain and Inbreeding Under Mate Selections

Table 4.2. Average inbreeding coefficients (standard errors), at 5 year intervals, for simulated selection strategies * ($h^2=.2$).

Simulation		Treatments					
Year	E_r	P_r	MS_0	MS_1	MS_5	MS_{10}	MS_{25}
5	.1085	.0633	.0762	.0651	.0505	.0507	.0305
	(.0054)	(.0049)	(.0053)	(.0058)	(.0053)	(.0052)	(.0035)
10	.2314	.1244	.1944	.1719	.1513	.1507	.1099
	(.0088)	(.0063)	(.0067)	(.0072)	(.0067)	(.0073)	(.0068)
15	.3432	.1822	.2979	.2710	.2431	.2420	.2020
	(.0105)	(.0069)	(.0083)	(.0070)	(.0069)	(.0071)	(.0076)
20	.4225	.2472	.3792	.3605	.3192	.3268	.2805
	(.0103)	(.0079)	(.0072)	(.0080)	(.0069)	(.0067)	(.0082)

¹See text for definition strategies.

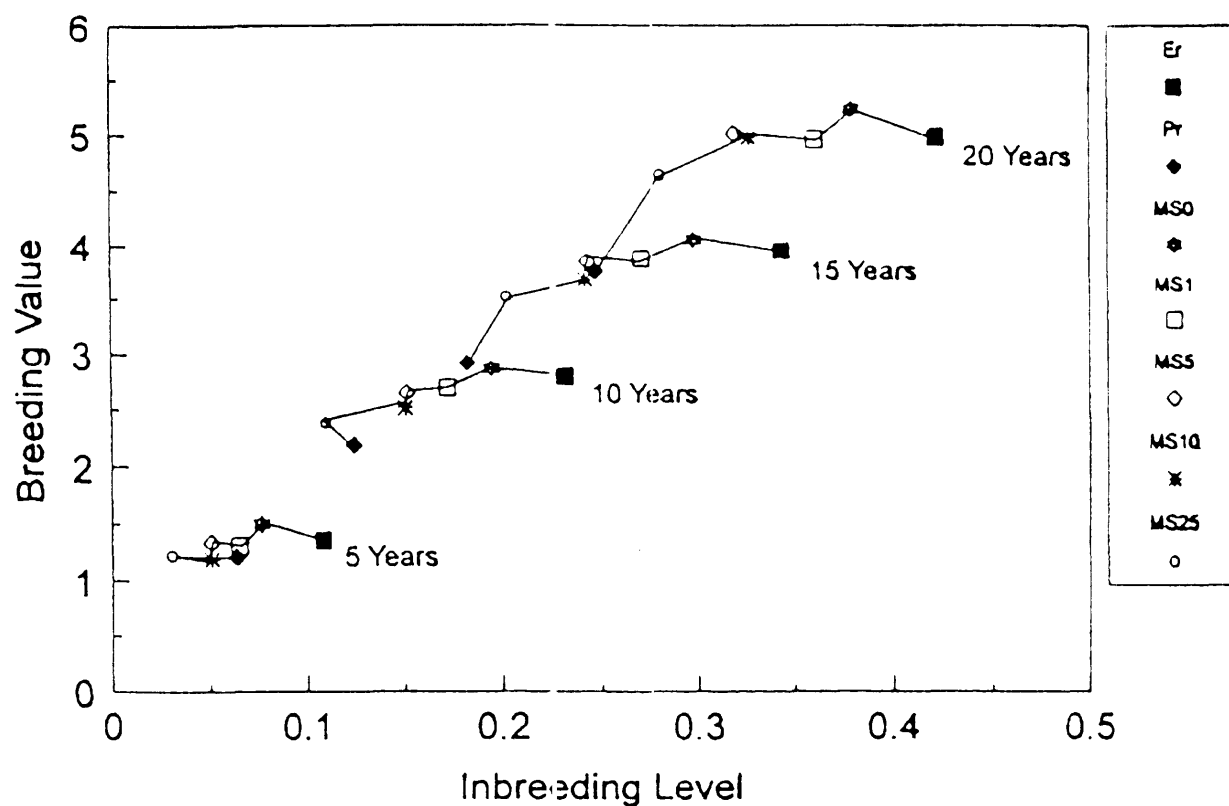


Figure 4.5. Simulated changes in mean inbreeding level and breeding value for different selection strategies, in the form of realised BV-F from iers after 5, 10, 1, 5 and 20 years of selection.

4.4 Discussion

The association between inbreeding and particular breeding plans has long been recognised (for example, Morley 1954), and a number of authors have recently examined ways of constraining increases in the level of inbreeding or the impact of modern selection methods on inbreeding (Toro & Perez-Enciso, 1990; Wray *et al.*, 1990; Quinton *et al.*, 1992). Dempfle (1990) recognised that some restrictions on selection strategies are required to maintain a reasonable effective population size, and suggested that there may not be much additional efficiency to be gained once such restrictions are satisfied.

The present study demonstrates a method for constraining inbreeding which allows inbreeding and rate of genetic gain to be considered jointly. It demonstrates the effectiveness of mate selection in achieving both a greater rate of gain and lower inbreeding compared with selection using BLUP and random mating. It shows that further sizeable reductions in inbreeding are also achievable while maintaining rates of genetic gain that are little different from those obtained under selection utilising BLUP and random mating.

The work is based on simulation of only a small sized population, and this imposes some limitations on interpretation. With larger populations, there will be lower levels of inbreeding due to higher associated effective population size. But with larger and more complex breeding structures the potential for usefully applying mate allocation and selection procedures can also be increased. In addition, the relatively low heritability used for our simulation is likely to have led to more marked differences among strategies than with a higher value, the benefit from use of information on relatives being greater at lower heritability.

The method presented here uses the frontier of genetic merit and inbreeding level which defines the most efficient portfolios of matings as a basis for choosing reasonable constraints to apply to rate of genetic gain and inbreeding. In this way, practical decisions are able to be made about 'acceptable' levels of lost genetic response and gain from reduced inbreeding. Further questions which might be addressed include ways of arriving at the optimal point on the frontier at which to operate and the circumstances which make definition of this point possible and desirable. These are questions warranting further study.

CHAPTER 5

The Comparison and Ranking of Selection Strategies

5.1 Introduction

Increasingly, the relationship between selection strategies and the associated levels of inbreeding is being recognised (Quinton, *et al.*, 1992; Wray & Thompson 1990). High levels of inbreeding have the potential to reduce the returns to producers from their current and future stock through loss in fertility, depressed production, reduction in genetic variance and genetic response (see, for example, Morley 1954, Quinton, *et al.* 1992). Hill (1994) noted that fitness problems in one form or another are an inevitable consequence of long term selection. Therefore, an important aspect of any selection strategy will be its capacity to address aspects such as the genetic progress derived from the program as well as the rate of inbreeding associated with this progress

Current work in this area suggests that expected genetic gain and the factors that impact on its achievement can be effectively addressed through selection strategies to

provide better long term outcomes, with Meuwissen and Woolliams (1994b) concluding that while the results of specific studies vary, the general returns are almost invariably the same, large reductions in risk are possible without decreasing genetic gain significantly. Such risk can refer to aspects such as the accuracy of estimated breeding values, the level of inbreeding associated with a breeding strategy, or the variation in returns.

The problem of comparing breeding schemes on the basis of expected genetic response has recently been highlighted by Quinton *et al.* (1992), who demonstrated that while strategies based on BLUP estimates do have higher expected levels of genetic response, the inclusion of a consideration of the associated levels of inbreeding changes the relative rankings of such strategies, and needs to be taken into account in the development of preferred management practices.

In Chapter 4, stochastic simulations of a range of mating and selection strategies were undertaken. These strategies varied both in the selection criteria used (whether selection was based on the observed level, the phenotype, of the trait or on the estimated breeding value, the *ebv*) and on whether the steps of selection and mating were carried out sequentially (selection followed by random mating) or simultaneously (by mate selection, where the optimal combination of mates defines the selected mating stock). The defined mate selection strategies were differentiated by an acceptable maximum level of decrease in the expected response, with the selection objective directed to minimise inbreeding subject to the achievement of this minimum level of response.

From the time series information available from the above modelling it was demonstrated that for a small compromise in the expected level of genetic gain, considerable benefits through reduced levels of inbreeding were possible. However, this assessment does not allow a quantitative evaluation of the merit, or utility, of such

strategies. While the question of whether a degree of joint regulation can be achieved between genetic gain and inbreeding was satisfied, the further issue of which strategy was preferred was not definitively addressed. A similar concern was expressed by Quinton and Smith (1994) who, in considering a range of genetic evaluation-selection systems, looked to ascertain if there was a generally optimal system. Their approach used graphical methods to compare the cumulative genetic response and inbreeding for varying numbers of sires.

Leitch *et al.* (1994) provide another approach to the question of how to compare strategies recording both merit and inbreeding. They developed a ratio - the Relative Inbreeding to Response Ratio (RIRR):

$$RIRR = (\Delta F_i / \Delta F_j) / (\Delta R_i / \Delta R_j) \quad 5.1$$

where i and j refer to the strategy examined and used, respectively, and F and R refer to the rates of inbreeding and genetic response. While this measure facilitates the comparison of strategies in any year, the actual application of a mating strategy has impacts over a far longer time period. To accommodate this, RIRR could be aggregated over such periods, however, it would seem more effective to directly manage the use of all available information - namely the time series data for R and F , this requiring a more complex process than is provided either by the use of graphical approaches or through the RIRR.

Thus, while the assessment and comparison of schemes addressing a single objective, over time, or multiple objectives, at one time, can be relatively straightforward, comparisons are more involved where competing objectives (such as genetic progress and rate of inbreeding) are measured over a time period. The different sources of information available (including the costs and returns of implementing selection strategies) must be integrated to allow the complete picture to be considered.

In developing an approach through which the effectiveness of mating strategies can be compared, the needs must be identified. The information available on these strategies can usually be summarised either as benefits (for example, through increases in the expected level of response) or risks, or costs (the potential reduction in that response through, for example, inbreeding depression and reduced genetic variation).

By defining this problem of the benefits and costs of mating strategies as one of assessing alternative mechanisms for resource allocation, the available information can be used, through a benefit cost analysis, to quantitatively assess possible investment strategies (specifically, mating strategies). This perspective, of viewing animals as investment options, and breeding and selection as a resource allocation issue, is becoming increasingly common in animal breeding research with techniques such as Linear Programming (e.g. Jansen & Wilton, 1985; Kinghorn, 1987; Toro & Sillio, 1992) and Portfolio Analysis (e.g. Schneeberger, Freeman & Boehlje, 1982), being applied from this perspective. The application of benefit cost approaches is a useful extension to the current application of economic evaluation approaches in this area.

5.2 Method

Benefit Cost Analysis (BCA) is a procedure for comparing alternative courses of action by reference to the net social benefits that they produce (Department of Finance, 1991). While its application traditionally has been the selection between alternative activities measured on a financial basis, it potentially has a far wider application, providing a flexible approach to investigate variables over time. Goddard (1992) used this approach to consider the benefits and costs associated with the export of genetic material. In this thesis, the methodology is used to assess time series evaluations of competing selection strategies on the basis of the benefits (estimated genetic response) and costs (associated inbreeding).

The BCA approach operates through an integration of benefits and costs discounted across the time series to provide a single measure. Although a formal application of BCA is not appropriate to the comparison of selection strategies, the general approach does offer a mechanism through which the identified needs can be satisfied.

The genetic simulation model used to evaluate strategies for the joint regulation of genetic gain and inbreeding is detailed in Chapter 4, with the results (true breeding value and inbreeding level) summarised in Figures 4.2 and 4.3. The Benefit Cost Model, used to evaluate and rank the strategies analysed in this work, is detailed below.

5.2.1 The Benefit Cost Model

The aim of this model is to provide a mechanism through which the relative ranking of selection strategies, based on the output data from a simulation modelling study, can be achieved. Real estimates of either the total benefits and costs of such strategies is not an objective - thus, a quantitative analysis is described, based on the variable costs and benefits of the enterprise, with elements common to all strategies excluded.

5.2.1.1 The Decision Rule

The cost benefit approach is based on an identification and evaluation of the total costs and benefits associated with possible courses of action. Within the benefit cost framework there are a number of indicators, or decision rules, used for assessment where B are benefits (\$'s) and C the costs (\$'s) in year t , for interest rate, r , including.

(1) The Net Present Value

$$NPV = \sum_{t=1}^n \frac{(B_t - C_t)}{(1 + r)^t} \quad 5.2$$

(2) Benefit Cost Ratio

$$B / C = \frac{\text{Present Value}_{\text{BENEFITS}}}{\text{Present Value}_{\text{COSTS}}} \quad 5.3$$

The NPV is the benefit-cost rule recommended for public sector assessments (Department of Finance, 1991) with this assessment being equally appropriate for situations such as are considered here.

The Handbook of Cost Benefit Analysis (Department of Finance, 1991) cautions that care should be taken in the application of both the Benefit Cost Ratio (B/C) and the Internal Rate of Return (IRR), noting that *the benefit cost ratio is only as reliable as the net present value rule when ... project alternatives are not mutually exclusive.*

Gittinger (1972), in looking at the impact on B/C of different netting out conventions, noted that different conventions would change the resultant rankings of project. Similarly, where there is difficulty in accurately identifying and defining all benefits and costs, it is important that the sensitivity of the decision rule to the accuracy of such values is considered. In particular, the use of a decision rule applying a linear transformation of benefits and costs (the NPV rule) will be far more reliable than will one where a ratio of these values is applied.

Similar issues have been considered in the use of ratio approaches in other areas of animal breeding. McClintock and Cunningham (1974) used the discounted gene-flow method to evaluate the effects of varying cow replacement policies. They recognised that changes in the relative economic weights will alter the value of different items of information. Interestingly, Quinton et al. (1992), in looking for a means by which to combine the levels of inbreeding and genetic response in an effective index assessed the use of ratios or other alternatives and found ratios wanting.

5.2.1.2 Identification of Benefits and Costs

The main benefit associated with the strategies under consideration is the overall level of production. The main cost is the degree to which this production is diminished, due to inbreeding depression. In addition, there will be some increased cost associated with mate selection strategies due to slightly higher management costs.

In a benefit cost analysis it is standard practice to identify **all costs** associated with a scheme. However, as discussed above, the costs relating, for example, to the maintenance of stock, will be common across all strategies, and therefore will not impact on their relative ratings.

Similarly, many of the benefits associated with production will be common to all strategies, and so will not be included in the analysis. In addition to the additional effort required in estimating common costs and benefits is the potential impact of the inaccuracies of such estimates. The inclusion of such information would reduce the accuracy of the analysis by introducing information of variable reliability which is not required for the achievement of the objective of the analysis - the ranking of strategies.

The evaluation of NPV arises from the basic genetic model with the phenotype a combination of genetic and environmental contributions and inbreeding leading to a depression in the expected performance level, providing a mechanism to evaluate a measure of the performance of a scheme taking into account the likely benefits (expected response) and costs (associated inbreeding), with each BCA. The set of simulations undertaken allow a consideration of the outcomes of breeding schemes based on a possible level of inbreeding depression.

$$NPV_{b,S,r} = \sum_{i=1}^{20} \frac{(E_{i,b,S,r} + G_{i,b,S,r}) * (1 - b * F_{i,b,S,r}^*)}{(1 + r)^i} \quad 5.4$$

where:

S is the mating strategy under assessment (E_r, P_r, MS_0 to MS_{25})

E_i representing the environmental impact, in selecting from a $N(0,4)$ distribution

G_i the genetic contribution, selected from a $N(\bar{g}_{i-1}, \sigma_{g_{i-1}}^2)$ distribution, where

\bar{g}_{i-1} is the mean genetic contribution in year i and $\sigma_{g_{i-1}}^2$ its variance

b is the weighting placed on the impact of inbreeding

F_i^* the associated inbreeding impact, selected from an $N(\bar{F}_{i-1} * b, \sigma_{f_{i-1}}^2 * b)$

where \bar{F}_{i-1} is the mean inbreeding level and $\sigma_{f_{i-1}}^2$ its variance (so correlating higher merit with higher inbreeding)

r interest rate

Seven levels of b , the weighting on inbreeding depression, were used, varying between 0 and 10% (in steps of 2), and 20%. Falconer (1981) tabulated examples of inbreeding depression, detailing levels between 0.6% (of the non-inbred mean per ten percent increase of the inbreeding coefficient) for mice bodyweight to 7.2% for litter size in mice.

Two specifications of the model were used:

A) *Basic Specification* : A basic Benefit - Cost specification, with E selected from a Normal distribution $E \sim N(0,4)$, and G and F selected from a Normal distribution with mean and variance taken from Tables 4.1 and 4.2.

B) *Additional Cost of Management*: For all mate selection strategies, an additional management cost of 5% of productivity was incorporated.

The @RISK software for Excel (Palisade, 1992), was used to select values for the stochastic elements used in the model specified below, with input data from Tables 4.1 and 4.2. Two hundred and fifty replications of each variation of the model were carried out, with the mean NPV and the Standard Error reported in Tables 5.1 to 5.4. While NPVs are reported, it should be noted that these do not reflect actual values associated with the application of strategies, but provide relative ratings of such strategies.

5.3 Results

The results from the simulations are presented in Tables 5.1 to 5.4. Figures 5.1 to 5.4 show these results and facilitate the comparison of the strategies under variation in interest rate, impact of inbreeding and effect of additional management cost. Of particular interest is the relative rankings between mate selection strategies - these assessing different mixes of benefits and costs.

Two levels of interest rate, r , were considered in this analysis, and while there is a significant difference between the absolute value of strategies (the NPV) under these levels, the impact on the rankings is not significant - these maintaining a similar pattern for both levels. The main impact of r is on the scale of the relationship, with the results for $r=.1$ showing a narrower range than for $r=.06$ - this same pattern occurring in both Models considered.

For Model A MS_0 is clearly superior to E_r with P_r ranked below all the mate selection strategies (for b in the range 0 to 10%). Turning to the impact of additional management costs, the main difference between Models is that the relative benefit of mate selection options are somewhat eroded compared to alternatives. Unlike in Model A, the returns in Model B associated with E_r and MS_0 are very similar at the

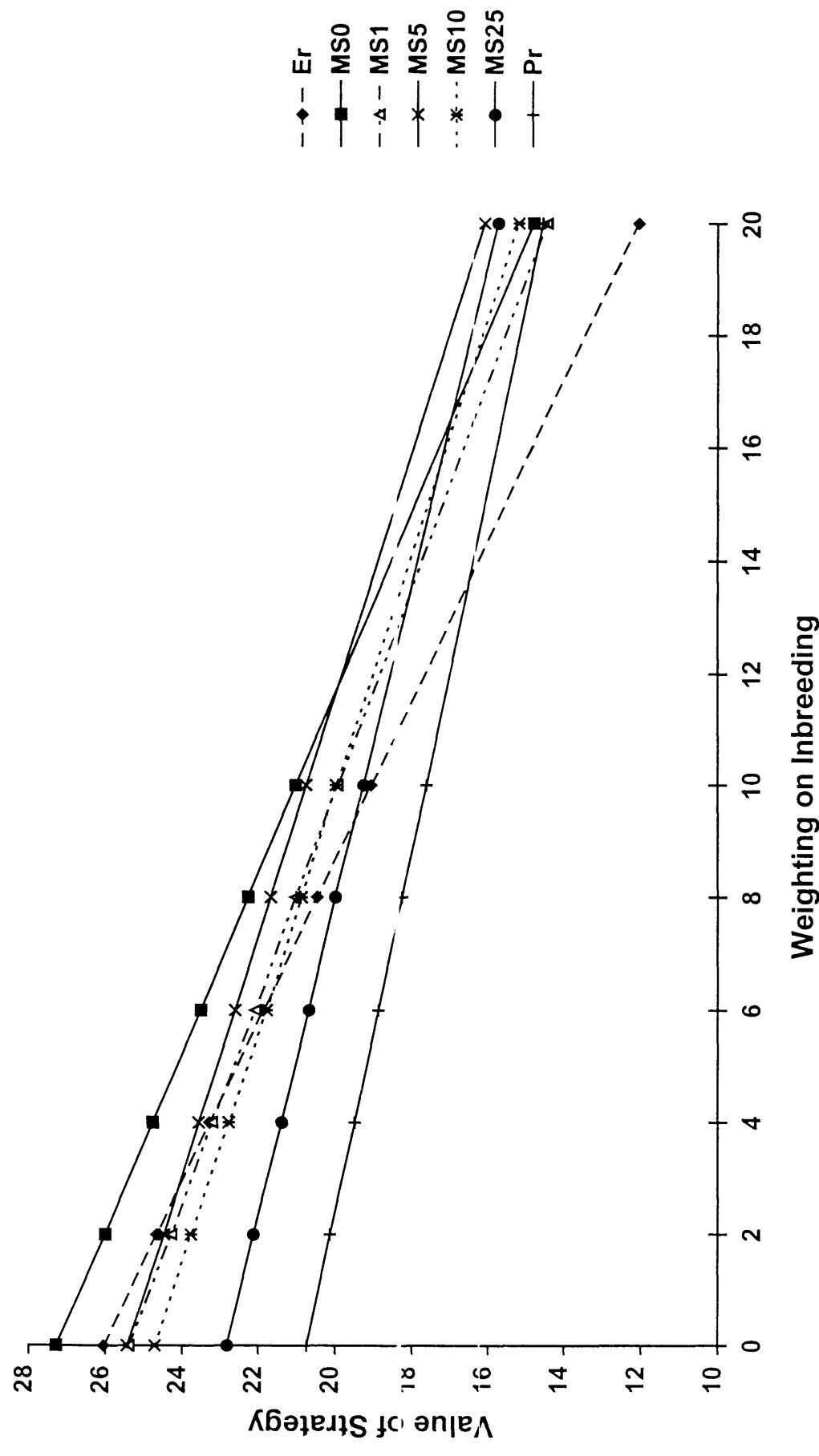


Figure 5.1 The change in value (ranking) of selection strategies for varying levels of b , the weight of inbreeding, where $r = .06$, Model A.

Table 5.2 The NPV (standard error) of selection strategies for Model A for varying weights on inbreeding, b , and for an interest rate, r .10.

Selection Strategy	Weighting on Inbreeding % decrease in production per 10 % increase in F						
	0	2	4	6	8	10	20
E_r	16.96 (0.55)	16.11 (0.53)	15.28 (0.53)	14.41 (0.49)	13.55 (0.52)	12.71 (0.46)	8.52 (0.42)
MS_0	17.75 (0.55)	16.98 (0.52)	16.27 (0.57)	15.55 (0.54)	14.75 (0.51)	14.04 (0.50)	10.31 (0.46)
MS_1	16.39 (0.54)	15.73 (0.53)	15.11 (0.51)	14.45 (0.51)	13.80 (0.50)	13.17 (0.52)	9.91 (0.50)
MS_5	16.36 (0.54)	15.86 (0.51)	15.29 (0.51)	14.78 (0.53)	14.17 (0.53)	13.64 (0.51)	10.90 (0.47)
MS_{10}	15.95 (0.51)	15.38 (0.54)	14.82 (0.53)	14.24 (0.55)	13.76 (0.50)	13.14 (0.52)	10.35 (0.45)
MS_{25}	14.64 (0.55)	14.25 (0.61)	13.84 (0.51)	13.41 (0.51)	13.00 (0.52)	12.56 (0.52)	10.53 (0.51)
P_r	13.63 (0.58)	13.23 (0.54)	12.87 (0.56)	12.48 (0.50)	12.13 (0.52)	11.75 (0.56)	9.86 (0.48)

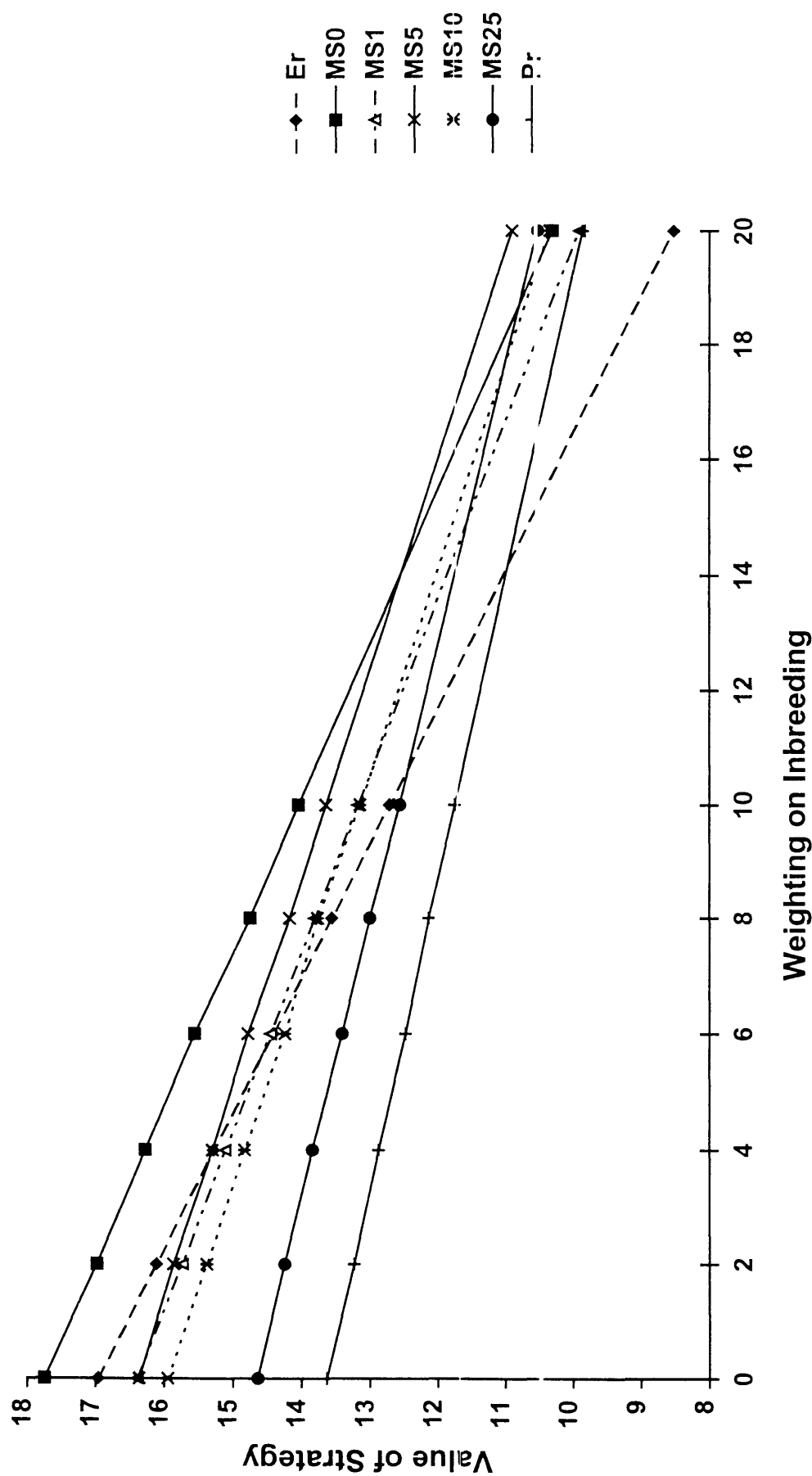


Figure 5.2 The change in value (ranking) of selection strategies for varying levels of b , the weight of inbreeding, where $r = .10$, Model A.

Table 5.3 The NPV (standard error) of selection strategies for Model B for varying weights on inbreeding, b , and interest rate r .06.

Selection Strategy	Weighting on Inbreeding % decrease in production per 10 % increase in F						
	0	2	4	6	8	10	20
E_r	26.04 (0.71)	24.66 (0.64)	23.28 (0.64)	21.82 (0.64)	20.47 (0.62)	19.06 (0.57)	12.00 (0.53)
MS_0	25.93 (0.63)	24.73 (0.61)	23.56 (0.58)	22.38 (0.60)	21.11 (0.59)	19.98 (0.62)	14.04 (0.52)
MS_1	24.14 (0.63)	23.09 (0.67)	22.05 (0.66)	21.01 (0.62)	19.99 (0.57)	18.90 (0.56)	13.73 (0.49)
MS_5	24.15 (0.66)	23.27 (0.64)	22.38 (0.59)	21.50 (0.60)	20.60 (0.57)	19.70 (0.58)	15.27 (0.58)
MS_{10}	23.41 (0.63)	22.54 (0.61)	21.63 (0.67)	20.76 (0.61)	19.83 (0.60)	18.94 (0.62)	14.44 (0.53)
MS_{25}	21.71 (0.68)	21.02 (0.63)	20.34 (0.64)	19.69 (0.62)	18.98 (0.59)	18.31 (0.58)	14.93 (0.57)
P_r	20.73 (0.67)	20.12 (0.64)	19.48 (0.64)	18.88 (0.63)	18.24 (0.63)	17.64 (0.64)	14.53 (0.57)

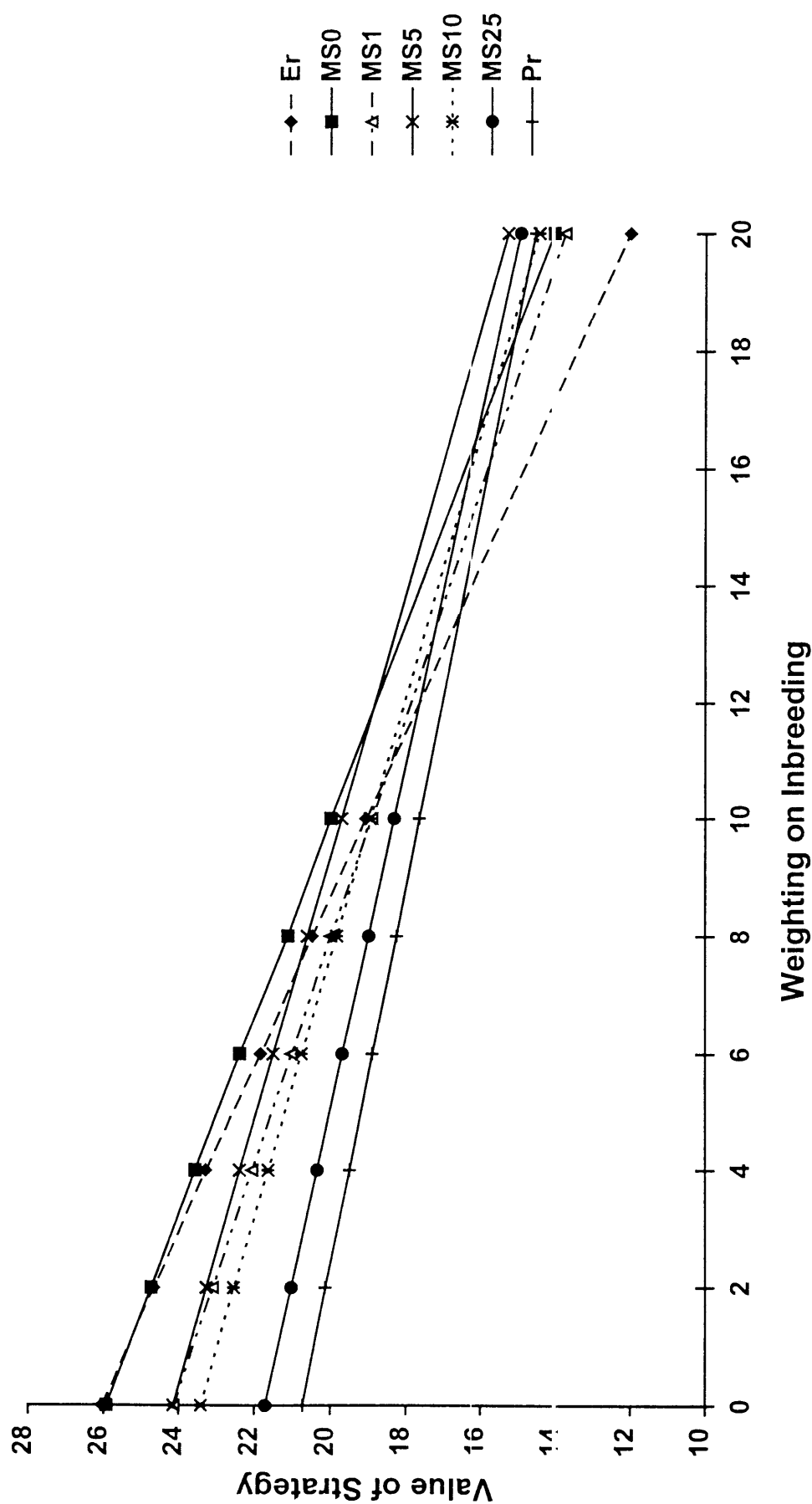


Figure 5.3 The change in value (ranking) of selection strategies for varying levels of b , the weight of inbreeding, where $r = .06$, Model B.

Table 5.4 The NPV (standard error) of selection strategies for Model B for varying weights on inbreeding, b , and interest rate, r . 10.

Selection Strategy	Weighting on Inbreeding % decrease in production per 10 % increase in F						
	0	2	4	6	8	10	20
E_r	16.97 (0.56)	16.12 (0.54)	15.23 (0.52)	14.43 (0.51)	13.60 (0.45)	12.74 (0.51)	8.52 (0.42)
MS_0	16.84 (0.52)	16.16 (0.54)	15.45 (0.52)	14.76 (0.49)	14.03 (0.47)	13.35 (0.46)	9.815 (0.46)
MS_1	15.56 (0.53)	14.95 (0.53)	14.23 (0.52)	13.72 (0.55)	13.10 (0.49)	12.49 (0.46)	9.43 (0.41)
MS_5	15.56 (0.54)	15.03 (0.49)	14.51 (0.52)	14.00 (0.55)	13.49 (0.49)	12.95 (0.46)	10.36 (0.41)
MS_{10}	15.13 (0.51)	14.58 (0.50)	14.06 (0.49)	13.53 (0.51)	13.02 (0.50)	12.49 (0.46)	9.831 (0.45)
MS_{25}	13.92 (0.49)	13.54 (0.52)	13.13 (0.49)	12.73 (0.54)	12.35 (0.50)	11.96 (0.46)	10.00 (0.48)
P_r	13.63 (0.52)	13.25 (0.52)	12.87 (0.54)	12.49 (0.51)	12.12 (0.57)	11.73 (0.50)	9.85 (0.49)

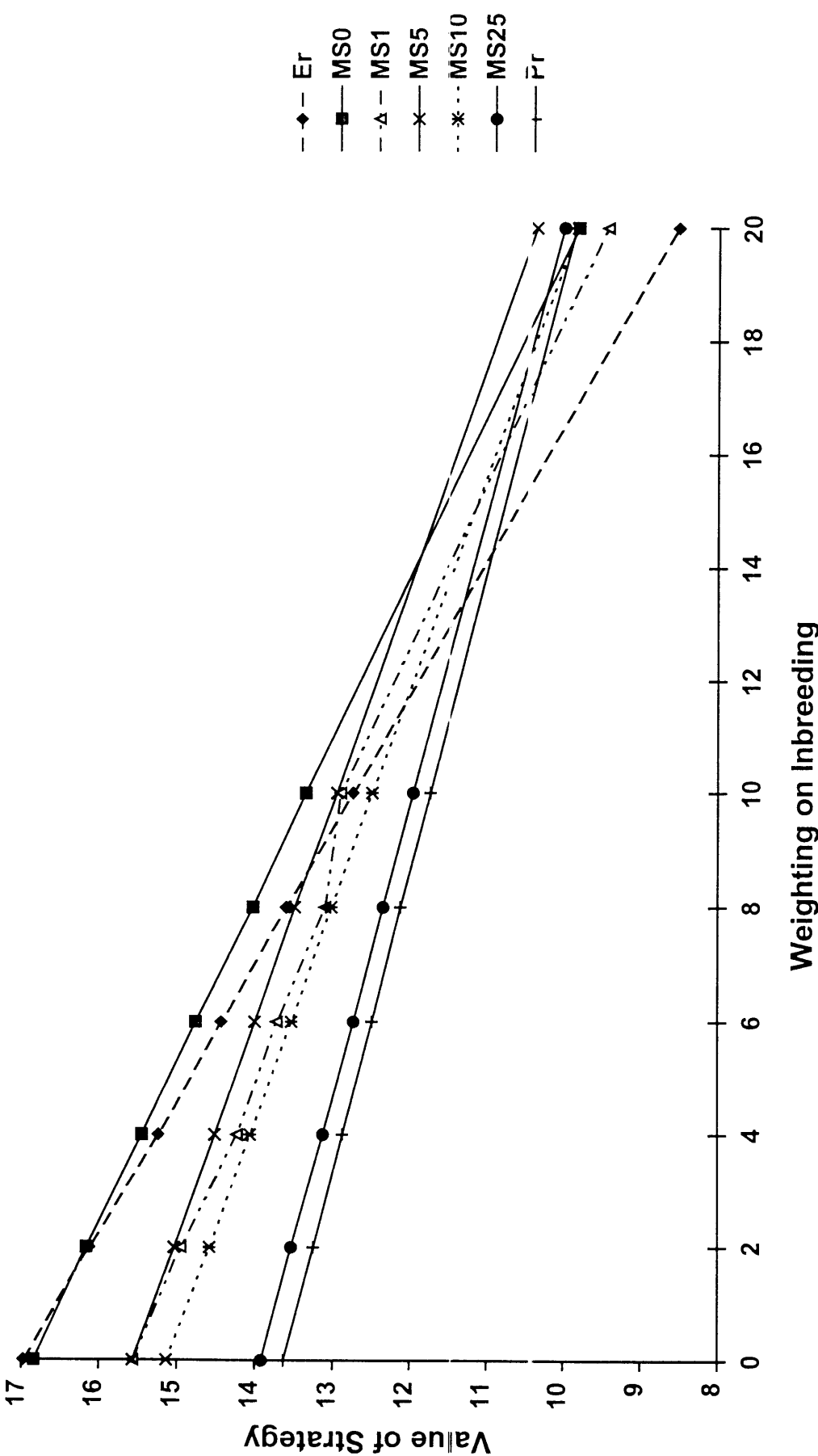


Figure 5.4 The change in value (ranking) of selection strategies for varying levels of b , the weight of inbreeding, where $r = .10$, Model B

5.4 Discussion

Recent research has focussed on ways to obtain maximum genetic response and simultaneously limit inbreeding (e.g. Leitch *et al.*, 1994). This move reflects the recognition of need associated with a move from theoretical refinements in the prediction of elements of merit, for example, to the application of breeding strategies to satisfy the observed objectives of decision makers.

This chapter looks to the resolution of two issues - the former determining the validity of the latter. Firstly, can BCA provide an effective approach through which information such as that generated in Chapter 4, be used to analyse and compare mating strategies ? And, given that it can, what conclusions can be made on the information under consideration ?

Does BCA offer an approach through which the effective integration of time series assessment information can provide ranking of alternative strategies ?

In the identification of the optimal strategy for the breeding management, many of the potential limitations in the BCA approach do not present major constraints. Many of the costs associated with animal production will, under any strategy, be common, and so, as fixed costs, can be excluded from the analysis - avoiding complex estimation and the associated error. Similarly, social benefits are not relevant to this analysis, except perhaps through some marginally greater maintenance of biodiversity associated with the avoidance of inbreeding - as with other difficulties associated with estimation, this aspect is not considered in the current analysis.

In addition to the specific results from this analysis assisting in the evaluation, it is apparent that this approach has providing one means of jointly considering the available information of such selection schemes. This provides a capacity to consider

such resource allocation options from an objective perspective addressing both the costs and returns associated with the adoption of such a strategy.

The evaluation undertaken here provides a comparison of the relative benefits of different selection and mating strategies. In looking at these results, It is possible to identify an optimum strategy for particular settings, but more importantly, to assess the overall impact of such settings on different strategies.

CHAPTER 6

General Discussion

6.1 Introduction

The basic issue addressed in this thesis is that of increasing the overall response to selection, and the achievement of the objectives of given selection programs.

The selection process, impacting on the population structure through differential opportunities for inclusion in succeeding generations, carries with it both the benefits of the increased representation of desirable traits for future populations, and the disadvantages associated with non-random selection. As stated by Robertson (1977) *you can't have your cake and eat it too*.

However, even given such problems, selection is still the most viable means through which progress can be made. Thus, while the associated difficulties arising from increased efficiency and intensity of selection are increasingly recognised, it is generally found that these are outweighed by the benefits.

What is becoming apparent is that while there are some disadvantages associated with efficient selection processes, there also are mechanisms through which the negative impacts of such selection can be more effectively managed. For example, while increased inbreeding compared to that associated with random selection may be an inevitable consequence of intensive selection, this impact does not have to be accepted at the maximum level.

With the refinement of Mixed Model methodology, there is a move from a concentration on effective estimation and prediction to the expansion of the selection objective to recognise the need to address risk in the management of animal breeding - reflecting a move from *an optimal solution in a simplified world to a satisfactory solution for a more real world* (Simons, 1979).

6.2 The Selection Process

6.2.1 Objectives

Quinton *et al.* (1992) stressed that comparisons between the outcomes under selection from BLUP and random selection should be made in the light of **all** impacts. From their analysis they showed that *phenotypic selection can give higher rates of response than BLUP over a range in time for low to moderate rates of inbreeding*. Similarly, in reviewing the literature on this area they noted that gains by BLUP may be reduced if:

- parameters are not well estimated (from Sales and Hill, 1976);
- if there are pedigree errors (Long, *et al.* 1990); or if
- there are time delays in obtaining BLUP evaluations (Smith and Burnside, 1990).

The first point to address is what *actually* are the objectives of those using animal breeding techniques. The main area normally evaluated by research, an increase in the expected genetic merit, is obviously important, since it indicates expected performance in progeny. However, before this performance occurs an animal breeder must also manage:

- the difference between predicted and true genetic merit (accuracy);
- the difference between expected genetic merit and phenotype, including environmental components and inbreeding depression;
- impacts of the costs involved in reaching selection decisions; and
- other personal preferences.

And while it may not be viable to effectively manage all these, their identification highlights the complexity of defining and achieving the true selection objective.

Even the apparently simple assumption of profit maximisation fails to truly capture the objectives of producers, with additional risk preference and lifestyle considerations needing to be recognised in modeling producer behaviour. As discussed above, and as is strongly recognised through growing use of risk utility functions, *the rational decision maker is not interested in maximising the absolute gain from a decision but in maximising its utility* (Bernoulli, 1738, quoted in Wyler, Hagger & Stranzinger, 1994).

So what do more realistic expressions of the objectives involve ?

Generally, these might be expressed, as above, in a simple single objective form. However, even in looking at simple selection theory, we are really dealing with

multiple, competing, and not entirely consistent, objectives (without considering the specific risk preference of any decision maker), for example:

- *estimated response* - is desirable in increased quantities;
- *high variance in this response* - this can be beneficial, through the impact this variance can have on response;
- *low variance in this response* - this can be beneficial through the knowledge on outcomes; and
- *strong linkage between estimated and actual response* - implying minimal bias from, for example, inbreeding depression, reducing achieved response.

Where can effort be optimally directed to achieve increased desirable genetic change ?

We know that expected response, R , can be defined as:

$$R = ih^2\sigma_p \quad 6.1$$

or, where $h = \sigma_A/\sigma_p$,

$$R = ih\sigma_A \quad 6.2$$

Here, R is a function of the selection intensity, i , the heritability h^2 , and the phenotypic and additive genetic variance (σ_p^2 and σ_A^2 , respectively). While there is some choice over which variables can be targeted in maximising R , a significant opportunity to achieve this objective will occur through a targeting of variance.

Selection intensity can be manipulated quite dramatically, significantly impacting on the resultant response, for example through the application of artificial insemination. However, as this will also impact on the population structure and so the profitability of the enterprise, it may not be a realistic option for achieving change.

With some rearranging, R_y , the response per year, can be expressed as:

$$R_y = i r_{AC} \sigma_A / L \quad 6.3$$

where r_{AC} is the accuracy of selection, which equals h under mass selection.

The measure impacting on R over which we have the greatest control, r_{AC} , is also a function of the amount of variation in the population. This highlights the consequence that various forms of variation have on the impact of the selection process.

The additive genetic variance is of prime interest here as this can enhance the response that can be achieved. Related to this is the error variation of estimated breeding values associated with the accuracy of estimation of genetic parameters, r_{AA} :

$$SE_{\hat{A}} = (1 - r^2) \sigma_A^2 \quad 6.4$$

where the greater the accuracy the more precise the estimation. While such precision is highly desirable, avoiding the downside risk of selecting poor animals, it also reduces the capacity to capture superior animals of unproven merit.

6.2.2 Management of Impacts

Consideration of alternative strategies generally assume that these alternatives will involve a cost over standard selection practices - for example, a decline in expected response. While this *cost* will be seen in the evaluation of the immediate selection period, it may not be translated to the longer term evaluation - some selection strategies demonstrating the capacity to enhance performance in the longer term.

With regard to accuracy, the perspective over the last decade has changed considerably, with an increasing recognition that the rational decision maker should not necessarily prefer high accuracy (e.g. compare Freer & Sunstrom with Klieve *et al.*, 1993 or Woolliams and Meuwissen, 1993). The results from Chapter 3 provide some support from a single generation assessment, showing that minimal, if any, decrease in response can occur where there is some imposed preference for low accuracy. When the criterion is extended to utility, there was an indication that some preference for lesser accuracy may show a benefit. Adding to this conclusion is the impact that inbreeding can have on the net economic response, including the cost of potentially lost animals - further enhancing the possible benefits in moving away from a preference for maximising accuracy.

Consideration over a longer time period further strengthens the support for the view that the optimal selection practice on one objective (maximising simply estimated genetic merit, excluding inbreeding effects) may well be suboptimal where other real objectives are included. As shown in Chapter 4, mate selection approaches can be used to mediate between the multiple objectives of risks and returns. This has been shown by a range of recent research (e.g. Quinton *et al.*, 1992; Brisbane & Gibson, 1994; Kinghorn & Shepherd, 1994; Meuwissen & Woolliams, 1994).

One significant impact of mate selection may come through its ability to increase genetic variation. Where the mate selection objective focuses on matings which result in a reduced level of inbreeding, an increase in the overall variation can result. It is interesting to compare the outcomes of the strategies considered in Chapter 4, where it can be noted that MS_0 (effectively a mate allocation option) has a greater rate of improvement in response than does E_r (random mating based on BLUP *ebvs*). In each selection process, the matings made under MS_0 must have *no greater* level of inbreeding than under E_r . In fact, at every selection event there may be a slightly greater level of variation in the population under MS_0 than E_r , leading to an gradual increase in the potential response. Kinghorn and Shepherd (1994), in developing information rich mating strategies, identify possible benefits from mating allocations

that capture the benefits from higher levels of variance over those that depend on maximising parental *ebvs* above.

The analysis of Woolliams and Mouwissen (1993) identified one of the major issues contributing to this trend. Basically, where there is a choice between a high and low accuracy animal with comparable *ebvs* (A and B respectively), there are two facets to the higher associated variance:

- **upside benefit** - thus, the chance that the true merit of B is above that of A; and
- **downside risk** - thus a greater chance of B having merit well below that of A.

While most decision rules assume that risks will outweigh benefits, in one decision rule (80% rewarding uncertainty in prediction), it was identified that rewards from the underestimation of merit outweighed the losses from such errors - thus the upside benefit was greater than the downside risk. The results from their study showed an increase in the expected genetic progress associated with rewarding uncertainty in prediction, and, more interestingly, a dramatic increase in the variance of this increase. The latter point highlights the increased potential for benefits in future generations.

Basically, the approaches discussed above provide mechanisms through which the negative impacts of intensive selection processes can be mediated to optimally effect response. This is achieved through recognising and addressing the multiple objectives identified above, by:

- targeting genetic response, but recognising that it must be expressed, not predicted; and
- harnessing the benefits of increased variation while managing the cost of reduced predictability by other mechanisms (price and preference benefits).

In this discussion, the focus on variation and on the associated strategies currently being developed to manage inbreeding, suggest that inbreeding is the principal target for the reduction of impacts. While this obviously is one factor which strategies must address, it is critical that the real, underlying problem, being addressed is identified - ensuring that the most efficient and effective strategies are developed and implemented.

6.3 Is Inbreeding the Problem ?

While inbreeding depression, and associated decreases in variation, are highly recognisable negative impacts associated with selection, it is important to consider if inbreeding itself is the problem. Alternatively, do the problems of inbreeding, arise from a more basic issue. The results of Chapter 4, while targeting the issue of jointly regulating inbreeding and response, provide some insights, as does the discussion of accuracy in Chapter 3.

Work looking at accuracy (e.g. Klieve *et al.*, 1993; Woolliams and Meuwissen, 1993) has demonstrated the feasibility of placing the emphasis on variability rather than on certainty. The long held assumption that high accuracy is preferred arises from the use of limited information. Relationships are included in the mixed model equations leading to a misbalance, with differential accuracies for individuals holding different levels of pedigree information. Thus, while the different levels of relationships between individuals are used to estimate genetic merit, they perhaps are not as fully utilised as is possible - a reliance on *ebvs* implying that limited information is information on merely average merit.

By incorporating the level of accuracy as a risk factor in the decision process, this risk can be captured, and managed. This represents a move from working at the norm, the *ebv*, to managing the variation either side - thus the risk. The capacity to capture the

upside benefit associated with low accuracy animals offers considerable benefits, and, as discussed above, there is considerable evidence that this can outweigh the downside risk that the true merit is low (e.g. Klieve *et al.*, 1993; Woolliams and Meuwissen, 1993).

Brisbane and Gibson (1994, also Wray and Goddard, 1994) adopted a different approach to this problem, identifying the benefits from the inclusion of information on relationships in addition to the use of BLUP *ebvs*. They found that this would be likely to lead to an approach that would outperform other strategies being proposed to reduce inbreeding (e.g. Grundy and Hill, 1993). Even more recently, Wray and Goddard (1994) using a stochastic simulation model, showed that the selection strategy which selected a variable number of sires, allocated a variable proportion of matings and exploited random annual variations in breeding stock was successful in maximising the response to selection.

While these approaches offer reasonable methods to manage inbreeding, they also provide support for the view of inbreeding and accuracy as secondary factors, arising from the high levels of relationships, or networks, in breeding herds. The mate selection algorithm detailed in Chapter 4 focused on the management of inbreeding. However, as discussed in Chapter 4 (Equation 4.10):

$$\text{Minimize } \sum_{i=1}^{noF} \sum_{j=1}^{noM} x_{i,j} * F_{i,j} + x_{i,j} * R_{i,j} \quad 6.1$$

(where $R_{i,j}$ is a measure of the information, through relationship, available on a potential offspring from parents i and j) this approach can also be more directly focused on relationships, providing a longer term targeting of the impacts seen, for example, through inbreeding.

6.4 Conclusion

Increasingly, research is supporting the view that selection strategies designed to address longer term population impacts are competitive with those maximising immediate expected genetic response. The benefits from the longer term framework including benefits from increased variation (Kinghorn & Shepherd, 1994), reduced inbreeding (e.g. Brisbane & Gibson, 1994; Klieve *et al.*, 1994; Meuwissen & Woolliams, 1994) and improved costs (Klieve *et al.*, 1993).

Further work that specifically addresses the capacity to manage relationships is likely to lead to a more direct, and thus effective, management of this problem. Thus, rather than managing inbreeding as it arises, it is important to adopt a longer time frame in developing a rationale for long term selection through the management of risks.

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