Chapter 5

General Discussion

5.1 Selection Criteria

Simulation results presented in Chapters 3 and 4 showed that response to selection was improved relative to mass or index selection alternatives using BLUP estimated breeding value (EBV) as the selection criterion. Improved response was the result of higher accuracy of selection, as illustrated in single trait studies by Figure 3.2. However, inbreeding under EBV selection was also higher relative to selection on individual performance measures. Use of family information in the prediction of EBVs increases covariances between relatives for the selection criterion, thereby resulting in increased selection between families and subsequently higher inbreeding. Relative response and rates of inbreeding under EBV selection are dependent on trait characteristics.

Increases in response and inbreeding under EBV selection were somewhat higher for lowly heritable ($h^2 = 0.1$) and/or sex limited traits (NBA). For these types of traits, use of additional family information makes significant contributions to both accuracy of selection and the covariances between relatives. However, the sex-limited nature of NBA reduced the amount of additional information contributing to EBVs for this trait. In comparison, substantial amounts of performance data accumulated for ADG and BF. This resulted in larger increases in inbreeding under EBV selection for ADG relative to NBA, although selection bias resulting from scale effects offset changes in response and inbreeding for BF from this cause. The relative performance of selection alternatives for traits with differing characteristics were consistent with results from other studies (Belonsky and Kennedy, 1988; Quinton et al. 1992; Roehe et al., 1992; Sorensen, 1988; Wray, 1989). However, results for BF were sometimes difficult to interpret due to the presence of a simulated scale effect.

5.2 Positive Assortative Mating

Positive assortative mating was shown to further improve response to selection where heritability of performance measures was moderate to high, and/or where BLUP EBV was the criterion for selection. This observation was consistent with theory and results from other simulation studies (Shepherd and Kinghorn, 1994; Smith and Hammond, 1987a; Tallis, 1989). Relative performance of assortative mating was lower where selection was based on individual performance or where the selection criterion described aggregate merit. Lower accuracy of selection hindered the ability of assortative mating to alter variation amongst the progeny through reduced correlations between mates in true breeding value. Further, assortative pairing of mates for aggregate merit was not as efficient for increasing variation with respect to component traits. Thus, improvements in aggregate merit under assortative mating were lower relative to its impact under single trait selection.

Where assortative mating was effective for improving response to selection, elevated rates of inbreeding relative to random mating also resulted. Assortative mating increases the effectiveness of selection between families through generating increased between family variation, thereby increasing the effect of selection on inbreeding. Further, pairing of like mates increases the probability of pairing related individuals, acting to increase progeny inbreeding coefficients. Moreover, assortative mating improved accuracy of selection relative to random mating using BLUP as a result of reduced prediction error variances (see Table 4.10). This result was consistent with the work of Wood et al. (1991a). Under EBV selection, inbreeding was substantially increased under assortative relative to random mating. This result was less apparent under BLUP index selection for an aggregate genotype, for the reasons noted above. However, high inbreeding under assortative mating reduces the desirability of using this mating system to improve response to selection in practice.

5.3 Controlling Inbreeding

High rates of inbreeding under BLUP EBV selection will reduce the potential for response through the detrimental effects of inbreeding on variance loss, and inbreeding depression. Quinton et al. (1992) showed that response under more intensive selection on individual performance was superior to EBV selection when selection alternatives were compared at the same low (desirable) levels of inbreeding. Given elevated rates of inbreeding, a similar conclusion would be expected for breeding programs combining EBV selection with assortative mating. Thus, the conflicting issues of response and inbreeding need to be addressed for breeders who operate within a closed herd framework.

Typically, concerns about inbreeding have been dealt with by altering selection and/or mating decisions to reduce rates of inbreeding. However, the challenge to lower inbreeding without reducing response over the desired time frame may not have been met with methods commonly used to control inbreeding. Methods which reduce the direct effects of selection on inbreeding include increasing the proportion of individuals selected (Robertson, 1970), increasing generation intervals (De Roo, 1988b), within family selection (Dempfle, 1975), reducing variation in family size through constraining selection decisions (Toro and Pérez-Enciso, 1990), and lowering accuracy of selection (Grundy et al., 1994; Toro and Pérez-Enciso, 1990). Post-selection, avoiding matings between close relatives and/or use of structured avoidance mating systems (De Rochambeau and Chevalet, 1982; Kimura and Crow, 1963; Wright, 1921) will also act to reduce inbreeding in the short term. However, these methods are usually accompanied by reduced response to selection (De Roo, 1988b; De Vries, 1989; Toro and Pérez-Enciso, 1990).

Hill (1985a) noted that altering family structures to control inbreeding may reduce response as a result of lower selection differentials. Methods which simultaneously act to maintain selection differentials tend not to have detrimental effects on response, although actual response outcomes are difficult to predict (Grundy et al., 1994; Klieve et al., 1993; Toro and Nieto, 1984; Toro and Pérez-Enciso, 1990). Most studies have examined methods to control inbreeding while maintaining response in the short term using rigid population structures. Studies in this thesis were aimed at examining the performance of a simple mate selection approach for joint control of response and inbreeding while allowing for constraints common to breeding populations. Results presented in Chapters 3 and 4 illustrate that it is possible to favourably alter the balance between inbreeding and response using mate selection in this scenario.

5.4 Performance Under Mate Selection

As with assortative mating, mate selection options were most effective for further improving response to selection when initial accuracy of selection was high. More accurate evaluation allows genetic differences between boars to be correctly identified and used for the purposes of mate selection. Moreover, information on known additive relationships could be better balanced with accurate information relating to genetic merit in the formulation of paired merit under mate selection. Both single and multiple trait studies illustrated that the highest response was generally achieved under mate selection options which jointly considered genetic merit and inbreeding for the selection of mating pairs. For these alternatives selection differentials were maintained by greater use of superior boars, but matings were chosen between less related individuals, thereby reducing inbreeding. Where prospective inbreeding was not considered, elevated rates of inbreeding resulted (eg. **A** and **MS1**). Conversely, avoidance of matings between relatives without simultaneously considering differences in genetic merit of selected individuals resulted in significantly lower response to selection (eg. **MS5**).

Overall, the relative superiority in response for each non-random mating alternative was not consistent for the different traits evaluated. Thus, the most appropriate emphasis to place on information relating to inbreeding for improving response under mate selection was not identified by this study. However, similar levels of response to selection under **A** and **MS1-MS4** were apparent for each of the selection criteria evaluated, although average inbreeding under these mating alternatives differed by up to 20% where an EBV was the criterion for selection. This translates to approximately 2% per generation differences in rates of inbreeding at comparable or improved levels of response. Hence, the balance between response and inbreeding was considerably more favourable for **MS2-MS4** relative to **A**. Relative to random mating, slightly higher selection intensities and less balanced use of boars generally disadvantaged mate selection algorithms developed with regards to inbreeding, although response was substantially improved.

Consistent with single trait results, multiple trait studies illustrated that relative response in individual traits contributing to aggregate merit differed according to selection criterion and mating scheme under the same breeding objective. Relative improvements in response of individual traits under EBV selection differs according to trait characteristics (Roehe et al., 1992; Sorensen, 1988). Individual traits also respond differently under alternative mating options, as discussed in Chapter 4. Overall, assortative mating and mate selection options were less effective for altering response in aggregate merit relative to their impact under single trait selection. Index values for aggregate merit may mask differences between merit of individuals for component traits, thereby decreasing the ability to use differences between individuals at mating for improving response in individual traits, and thus aggregate merit overall. In addition, greater constraints on boar usage in this study will have contributed to this result.

Regardless of the selection criterion, appropriate scaling allowed differences between boars in their additive relationships with available mates to be used for selecting between mating pairs under mate selection. Thus, mate selection algorithms using information on inbreeding were consistently effective for reducing inbreeding relative to **MS1**. In addition, mate selection alternatives ranked identically in terms of resultant inbreeding for each selection alternative.

5.5 Implications for Breeders

Results presented in previous Chapters have shown that mate selection algorithms combining information on genetic merit and prospective inbreeding are appropriate for manipulating the balance between response to selection and inbreeding in a dynamic breeding population. This type of approach is preferable to mating systems which improve response while ignoring relationships between mates, as these are likely to result in elevated rates of inbreeding (eg. assortative mating). Further, choosing matings which minimise progeny inbreeding following selection decisions is shown to result in suboptimal response, which should also be avoided in practice.

In the presence of an independent selection step, inbreeding was shown to be more readily influenced by subsequent choice of mating system than response. This phenomenon is advantageous in that it provides breeders with the opportunity to favourably alter levels of inbreeding while retaining the advantages of improved response, particularly when using more accurate genetic evaluation procedures such as BLUP. A further implication of this observation is that response per unit inbreeding is not a good variable for comparing breeding strategies. This ratio would place too little emphasis on improvements in response, which contribute to substantial profits at the industry level.

Ideally, mate selection should be applied amongst all candidates for selection as discussed in Chapter 2.5.2, removing the independent selection stage allowed in these studies. However, several practical constraints reduce the viability of this approach, including computational feasibility, and the cost and logistics of extending performance testing to all possible candidates. In contrast, implementation of the mate selection approach outlined in previous chapters is feasible. However, further research into how much emphasis should be placed on controlling inbreeding is required. This would allow the most appropriate scaling of merit, and weighting of information on inbreeding, to be included in the mate selection formulation.

Finally, mate selection rules must be continually applied to maintain their impact on inbreeding. This is because each optimum solution under mate selection is based on current information, and does not consider the impact of previous solutions, or future implications of the current solution. Thus, mate selection provides a generalised strategy to address the problem of inbreeding. Subsequently, the relative advantages of mate selection for maintaining high response while reducing inbreeding may need to be re-evaluated over different time horizons, and where the breeding population is not closed.

5.6 Conclusions

Studies in this thesis provided evidence that the relatively simple approach of adjusting predicted merit for additive relationships can be used to alter the balance between response to selection and inbreeding under mate selection in dynamic breeding populations. The relative efficiency of this approach for improving response while constraining inbreeding was influenced by accuracy of selection and other characteristics of the selection criterion. The most appropriate weight to place on information relating to inbreeding was not quantified by this study. This is an area requiring further research.

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