LIVESTOCK BREEDING SCHEMES: CHALLENGES AND OPPORTUNITIES

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SUMMARY

A selected number of elements of the optimization of livestock breeding programs has been discussed which are all related to the inaccuracies which are inevitably linked to breeding schemes. It is shown that pedigree registration errors can lead to a substantial reduction in genetic progress. Parentage testing might be used to reduce these errors and it also opens ways for more breeding schemes which make more efficient use of the female reproductive capacity. A marker assisted selection scheme is used to illustrate the impact of inaccurate estimates of genetic parameters. The aim of the paper has been to assist breeders in developing a rational breeding schemes which balances theoretical gains and practical restrictions.

Keywords selection, efficiency, pedigree recording, genetic markers

INTRODUCTION

The identification and optimum use of the superior animals has for a long time played, and will continue to play, a crucial role in livestock breeding schemes. Over time, large changes have occurred in the understanding of what is superior, the identification of superior animals and their use. In the past it was mainly the intuition of the breeder which determined what type of animal should be aimed for. Today the breeding organizations try to determine the best animal from an economic point of view, taking into account the future production and market circumstances. Intuition has not completely been replaced because future circumstances can not be predicted with certainty. Although it has not been documented in great detail, it seems safe to claim that in the past the main emphasis in the identification of superior animals was on the phenotypic expression of the animal itself and perhaps even stronger on the performance of the ancestors (Dempfle 1988). Currently, sophisticated statistical procedures are employed to make optimum use of the different pieces of information on the animal and relatives. The application of these methods is enable by extensive pedigree and performance recording schemes in livestock populations and due to the availability of powerful computers. Developments in reproduction technology, e.g. artificial insemination, multiple ovulation and embryo transfer, have greatly affected the use of superior animals.

Today's breeding schemes are very different in structure and size than those in place twenty years ago. Looking at developments in our understanding of genetic differences and developments in reproduction technologies, it is obvious that also within the next decade changes in breeding

schemes will take place. Apart from these changes due to adaptation of new technologies there is also scope for improvement by making better use of the currently available technologies.

In this paper a number of areas which might contribute to improvement of livestock breeding programs are described. These areas have in common that they are all related to (in)accuracies in information or parameters, it was not our intention to review all possible improvements of schemes. Further it is assumed that we know what animal is desired from an economic point of view.

COMBINATION OF TRAITS

In recent years, the number of traits incorporated in a breeding program has increased. The economic merit of an animal may depend on some of these traits, and others are incorporated to improve the accuracy of selection. Multiple trait methods for genetic evaluation are available and can be used to predict breeding values for the aggregated genotype (economic merit), for traits in the aggregate genotype, and for the recorded traits. The predicted breeding values for all recorded traits can be combined into a predicted breeding value for the aggregated genotype without loss of information (Schneeberger *et al.*, 1992). In practice, multiple trait methods are sometimes used for certain combinations of traits but hardly, if at all, for all traits. This can be explained by the large amount of data might make a multiple trait evaluation intractable and the difficulty to obtain reliable estimates of the genetic and environmental (co)variances of the involved traits, especially reliable estimates of genetic correlations between traits are often hard to obtain.

Uncertainty on the level of genetic correlations is used as an argument to use single trait methods instead of multiple trait methods for the prediction of breeding values. There are three disadvantages of using single trait methods for the prediction of breeding values. Firstly, ignoring information on other traits might lead to a lower accuracy of the predicted breeding value, depending on the genetic and environmental correlations as well as the amount of information on the trait of interest. Secondly, predicted breeding values might be biased due to the inability to account for selection on correlated traits. Finally, combining the single trait predictions of breeding values into a predicted breeding value for the aggregate genotype is no longer a trivial task, the weight for a trait depend on the economic value as well as the genetic correlation with other traits.

Application of the theoretically optimal method for prediction of breeding values might not be possible in practice. In current selection schemes, observations are often used to predict breeding values for traits in the aggregated genotype and these traits are combined using economic weights. The consequences of such a system and a multiple trait evaluation can be evaluated based on the relative selection response expected. The disadvantage of the frequently used system is when observations on a trait are used to predict the breeding value for one aggregate genotype trait the same information can not be used for the another. In order to solve this dilemma, other methods to deal with the multiple trait situation need to be considered.

For a long time, production accumulated over 305 days of lactation has been the selection criteria for milk production in dairy cows. Test day models, which use the actual milk production recorded on different days during the lactation, have recently been suggested to achieve a better adjustment of breeding values for fixed effects and to account for differences in the number test day records per animal (Van der Werf *et al.*, 1997). In addition, these methods allow for genetic variation in the shape of the lactation curve. Breeding values for milk production at a (number of) specified day(s) or period(s) of lactation can be predicted which enables a more tailored selection. Similar methods can be used for the evaluation of body weight or feed intake measured on growing pigs or chicken. This enables a better use of information collected during different periods and would enable prediction of breeding values for different end weights.

For many years, people have shown that the genetic correlation between performance in different parts of the production period (lactation, growth) is not equal to one. This fact has been ignored for a long period because adequate methods to account for this were lacking until recently. Covariance functions (or variations thereof) to describe covariances between traits measured at different times have opened the way to handle information on a larger number of observations for a trait on an animal. It only seems to be a further, but not essentially different, extension to apply these techniques for the simultaneous analysis of different traits, such as body weight and feed intake. This opens new ways for the definition of traits of interest as well as for a reduction of the number of traits in the aggregate genotype.

ACTIVE BREEDING POPULATION
In most breeding programs BLUP (Best Linear Unbiased Prediction) of breeding values are used to identify breeding animals. The predicted breeding values of animals of different ages and tiers in the breeding schemes can be compared directly, because the BLUP procedure takes account of genetic trend. The genetic level of the next generation can be maximized by selecting animals with the highest predicted breeding values as parents, irrespective of their age, tier or the accuracy of the predicted breeding value (James 1987; Meuwissen 1989). This procedure optimizes selected proportions from different tiers and age groups provided that there are sufficient genetic ties between different groups of animals and that breeding values are unbiased. These characteristics have facilitated selection of animals across herds and tiers within a breeding scheme. Furthermore, advances in computing algorithms and computer hardware have facilitated the use of BLUP methods on large populations. In dairy cattle breeding, national data bases containing milk production records and pedigree registration are already used for a long time to predict breeding values. Pig and poultry breeding companies have only recently started to use information from outside the nucleus.

Several studies have clearly demonstrated that genetic response can be increased by the use of more information from relatives and/or information from (crossbred) animals outside of the nucleus. In all these studies it was assumed there were no errors in pedigree registration or performance recording of animals. Little information is available on the impact of pedigree errors on genetic

Table 1. Genetic progress after 5 generations of selection with no pedigree errors (Max response) and reduction in response (%) due to 15% pedigree errors (sire and dam) for sex limited and unlimited trait with h^2 of 0.1 or 0.4 (average over 50 replicates) [A]

h^2	phenotypes on	Max. Response (σ_p)	Reduction (%)
0.1	males+females	1.05	8.9
0.1	females	0.87	13.4
0.4	males+females	2.98	3.0
0.4	females	2.32	10.6

[A] Discrete generations were used, in each generation 16 sires were selected, each sire was mated to 16 dams, each dam was used for a single mating and produced 4 female and 1 male offspring, phenotypes were recorded on all (female) animals prior to selection, selection was based on animal model breeding values.

progress. Van Vleck (1970) derived that when p is the fraction of cows whose sire is correctly identified, the heritability estimated from a paternal half sib analysis would be p^2 of the actual heritability. Long et al. (1990) demonstrated that up to 20% of pedigree errors, selection based on BLUP breeding values would still result in a higher response than mass selection or selection based on an index combining phenotypes on the individual and full- and half-sib averages. To quantify the effects of pedigree errors on genetic progress, a closed pig breeding nucleus was studied using stochastic simulation. A sex unlimited and a sex-limited trait measured on females with a h^2 of 0.1 or 0.4 was used. The reduction in genetic response to 5 generations of selection are given in Table 1. The mean predicted breeding value after 5 generations of selection was used as evaluation criteria. The same reductions in response were found when looking at the true breeding value or the mean phenotype after 5 generations. When 15% of the animals were assigned to a wrong sire and dam, the genetic response was reduced by 3 to 13.4%. A larger reduction in response was found when the trait was recorded on females only and/or the trait had a lower heritability. This can be explained by the larger impact of pedigree information on the predicted breeding values in both cases. The genetic gain per generation was evaluated as well. No effect was found for the first generation which was to be expected because simulation was started from an unrelated base population. The proportional reduction in the second generation due to pedigree errors was clearly larger than that after 5 generations. For the sex unlimited trait with h^2 of 0.1, nearly 50% of the absolute reduction in response occurred at the second generation. The smaller loss in the subsequent generations can be explained by the smaller reduction in genetic variance as a result of the less accurate selection in case of pedigree errors. In the simulation study, the true heritability was used in all alternatives for the prediction of breeding values. As shown by Van Vleck (1971), the heritability estimate in a population with pedigree errors will be biased downwards. Using a lower

heritability in prediction of breeding values will reduce genetic progress and it will also increase the impact of pedigree errors.

Parentage testing can be applied to detect errors in the sire or dam identification. Three scenarios using parentage testing have been evaluated for a sex-unlimited trait with h^2 of 0.1. In the first scenario, the parentage of all potential sires was tested and only the best sires with correct pedigree were used. In the second scenario both sires and dams were subject to parentage testing and excluded from breeding when an error was detected. These two scenarios hardly improved the genetic response, i.e. the reduction in genetic response due to pedigree errors was nearly as big as without parentage testing. This reflects that animals with the highest predicted breeding values have smaller probability of having an incorrect pedigree. In the simulation study, on average for 10% of the selected sires the parents were misidentified whereas the level of misidentification in the population was 15% on average. This demonstrates that the degree of pedigree errors in a population should not be based on errors detected in animals which are selected as parents for the next generation. In the last scenario, all animals were parentage tested and animals with incorrect pedigrees were excluded as parent and their phenotypes were not used in estimation of breeding values. The genetic response after 5 generations was $0.97\sigma_p$ which means that only 26% of the reduction in genetic response could be retrieved with this parentage testing scheme. Maximum genetic response is reduced because elimination of animals with pedigree errors reduces the population size by 15%.

Breeding values of dairy bulls are largely based on the progeny testing results. When a fraction of the daughters is incorrectly assigned to a sire, the breeding value will be calculated less accurately. If the error fraction is equal in all sires, consequences can be derived as if breeding values were estimated with a reduced heritability. This implies that predicted breeding values of sires with a given number of offspring would be closer to zero. However, the fraction of incorrectly assigned offspring will randomly vary between sires. When a fraction p of offspring are incorrectly assigned to the sire, the standard error on the fraction misidentified in N progeny equals $\sqrt{\{p(1-p)/N\}}$. For p of 5%, the standard error only reduces from 3.1% to 1.5% by increasing N from 50 to 200. As a consequence, pedigree errors will affect the ranking of bulls after progeny testing. Eliminating the consequence of pedigree errors would require progeny group sizes which are far outside the range which is optimum for genetic gain. Correlations between progeny means of sires in different countries will also depend on the accuracy of pedigree recording in both countries. In deriving the expected genetic correlation it is important again to account for the random fluctuations in fraction of pedigree errors between sires. Genetic correlations between countries as obtained by MACE are a function of the accuracy of pedigree registration in both countries and the genotype-environment interaction.

In our calculations animals were excluded from breeding when an pedigree error was detected. Alternatively, parentage testing should not only aim at detection of errors but also attempt to correct errors in order to avoid elimination of animals. There are even cases in which it is advantageous to use mixed semen and to determine the sire after parentage testing based on information from

genetic markers. Van der Beek (1996) described the potential advantages of such a scheme in poultry. A major constraint in current poultry breeding schemes is that hens are mated to one cock. This constraint can be lifted if genetic markers are used for parentage testing of offspring. As a result, a factorial mating design can be implemented which leads to a higher selection response without increasing the rate of inbreeding than a hierarchical design (Woolliams 1989; Ruane 1991; De Boer and Van Arendonk 1994). Assigning the correct sire of an individual based on information on genetic markers requires that the group of potential sires is known and not too large. When the markers used for parentage control can also be used for marker assisted selection, the genetic response can be increased even further. The procedure described by Van der Beek (1996) can also be applied in situations where the number of offspring of a female after a single mating is large, e.g. in pig breeding and definitely in fish breeding. With the use of mixed semen of boars, all animals in a litter can be used as candidates for selection without increasing the rate of inbreeding. *In vitro* production of embryos may also offer the potential for increasing the number of offspring available per cow. In a number of studies (Woolliams and Wilmut 1989; Kinghorn et al. 1991; De Boer and Van Arendonk 1994) the benefits of the production of a large number of gametes per female have been evaluated. A complete factorial scheme with more sires than dams resulted in the highest genetic response adjusted for the effect of inbreeding. These studies clearly demonstrated that the genetic gain and the rate of inbreeding in a population depend on the reproduction rate of males and females as well as the opportunities to achieve a factorial mating scheme. Parentage testing may play an important role in achieving factorial mating schemes.

MARKER ASSISTED SELECTION

Recently a number of studies have reported results from quantitative trait locus (QTL) experiments (e.g. Georges *et al.* 1995; Anderson *et al.* 1994). It is well documented that QTL effects might be overestimated in experiments with low power (Wang 1995; Georges *et al.* 1995) and that it is hard to get an accurate estimate of QTL position. For a breeding organization it is, therefore, important to have insight into effects of inaccuracies in parameter estimates on the expected response. Spelman and Van Arendonk (1997) conducted a stochastic simulation study to ascertain how sensitive genetic response resulting from marker assisted selection is to incorrect estimates of variance explained by the QTL and QTL location. With correct parameter estimates, overall genetic superiority of MAS over the control was 7% after 1 generation of MAS and 5% after 7 generations of MAS for a QTL explaining 5% of the phenotypic variance (Table 2). The effect of over-estimating the variance explained by the 5% QTL was evaluated with assumed variance of 10% and 15%. Greater genetic response at the QTL was observed with the over-estimated variance, but at the expense of lower polygenic response (Table 2). The genetic advantage over the situation without MAS in generation 1 for the 10% assumption is 0.016, i.e. 75% of that achieved with QTL variance correctly estimated at 5%.

After a number of generations additional information will have been collected in the course of the MAS breeding scheme which will allow re-estimation of QTL parameters. The scenario of correctly re-estimating QTL variance after three generations of MAS and then utilizing this in the breeding

value prediction procedure was evaluated by Spelman and Van Arendonk (1997). In the first three generations a variance of 15% was for a QTL explaining 5%. This resulted in half the genetic loss at generation seven compared to an incorrect estimate for all generations. This scenario is likely to be indicative of MAS in practice. The effect of incorrect QTL location estimate was a reduction in genetic gain compared to the scenario when location was correct. The loss at the QTL became more predominant as the true QTL location was further away from the postulated position (Spelman and Van Arendonk 1997). Genetic loss due to incorrect location was more pronounced than that experienced by QTL variance error.

Table 2 Effect on superiority of MAS over non-MAS breeding program using correctly estimated and over-estimated QTL variance (+5 or +10%) for a trait with heritability (polygenes and QTL) of 35% and QTL explaining 5% of phenotypic variance (from Spelman and Van Arendonk 1997)[A,B]

	Generation 1			Generation 7		
	QTL	Overall (σ_p)	Overall (%)	QTL	Overall (σ_p)	Overall (%)
Correct	0.048	0.021	+7%	0.197	0.097	+5%
+5%	0.062	0.016	+5.3%	0.203	0.074	+3.8%
+10%	0.070	0.010	+3.3%	0.202	0.050	+2.6%

[A] Superiority of MAS over the control is: genetic gain (QTL or total) from generation 0 to generation x for MAS minus genetic gain over the same time for the control

[B] Closed nucleus breeding scheme with 64 sires, 256 dams and 512 male and 512 female offspring per generation, single female sex limited trait with heritability (polygenic and QTL) of 35% and QTL explaining 5% of phenotypic variance in base population, selection based on BLUP breeding values calculated using the method of Meuwissen and Goddard (1996)

LONG TERM GENETIC RESPONSE

Most evaluations of alternative breeding programs methods are used which aim at maximizing response in the next generation, e.g. use of BLUP in stochastic simulation studies or selection index based deterministic studies. Truncation selection of animals on BLUP breeding values maximizes the genetic level of individuals in the next generation but does not lead to the highest response on the longer term (Dempfle, 1990). Longer term response requires a lower rate of inbreeding which can be achieved by increasing the emphasis on within family deviations. A major theoretical advance in the simultaneous deterministic prediction of long term genetic gain and inbreeding was made by Wray and Woolliams (1990) and Woolliams and Thompson (1994). The method is based on prediction of contributions of animals to future generations, as a function of the selective

advantage of the animal. Using this approach, Villaneuva and Woolliams (1997) found that with restriction on inbreeding and a longer time horizon, index weights in the optimum index closely resembled phenotypic selection. This procedure is currently being developed and is expected to provide general procedure for selecting individuals to maximize genetic progress whilst restricting rate of inbreeding.

CONCLUDING REMARK
In the design and implementation of breeding schemes uncertainty about genetic parameters and practical limitations are inevitable. In this paper we have dealt with some of these issues which will assist the breeders in developing a rational breeding schemes which balances theoretical gains and practical restrictions.

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