RISK MANAGEMENT AND THE DEFINITION OF BREEDING OBJECTIVES

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SUMMARY
The risk of breeding schemes comprises the variance of the selection response and the inbreeding. Both are high in modern breeding schemes, and can be reduced by including them with a cost factor in the breeding objective. The cost factors of inbreeding and variance of the selection response are however difficult to derive, and a more practical solution may be to set a constraint on the inbreeding and/or the variance of the selection response. Including a cost factor in the breeding objective, can lead to large reductions of inbreeding and/or variance of response with little reduction in genetic gain. At the same rate of inbreeding, a constraint on breeding can result in a up to 60% higher selection response, than conventional selection for BLUP estimated breeding values. With overlapping generations an increase in response of 28% was found.
KEYWORDS: Breeding Schemes, Risk, Inbreeding, Long-term Selection Response

INTRODUCTION
During the last decade, selection for animal model Estimated Breeding Values (EBV) has become increasingly common. Theoretically, selection for EBV maximises the expected genetic level of the next generation of animals. However, it does not maximise the genetic level of the offspring of the next generation of animals, because their genetic variance may be reduced. Strict selection for EBV leads to the selection of just one sire and one dam, which reduces the scope for selection in their offspring, i.e., one full sib family, leads to high inbreeding, and a high risk of the breeding scheme. In almost all breeding schemes more than one sire and more than one dam are selected, which clearly shows that breeders do account for future possibilities of selection, inbreeding, and/or risk. The question arises whether simply selecting more parents for the same criterion, i.e. EBV, is an optimal strategy. It seems more optimal to account directly for risk, inbreeding and/or future selection response in the selection criterion.

This is especially important in modern breeding schemes, with selection for BLUP-EBV, that use all family information. Hence, the correlations between the EBV of relatives are increased, and the probability of co-selection of relatives is also increased, which results in inbreeding. Also, in modern schemes with short generation intervals, e.g. MOET nucleus schemes (Nicholas and Smith 1983), selection is for pedigree indices, which are identical for full sibs, and co-selection of sibs results, i.e., inbreeding is increased. Further, improved reproductive technologies, make selection of fewer dams and sires feasible, which again leads to small effective population sizes. All these aspects of modern breeding schemes that increase inbreeding also increase the variance of the selection response, because of the close relationship between these two parameters. In modern breeding schemes it seems pertinent that inbreeding and variance of the selection response are

controlled and, if necessary, reduced.

The aim of the present paper is to investigate alternative breeding goals that account for the risk of a breeding scheme. The components of risk are inbreeding (= drift variance) and variance of the selection response. The weight given to the inbreeding and variance of the selection response depends on the weight given to long term genetic gain, inbreeding depression, and risk of the breeding schemes. These weights are difficult to assess, but some attempts have been made and will be discussed. Alternatively, if weights are difficult to assess, but some notion of acceptable inbreeding and risk rates is present, inbreeding and variance of the selection response may be restricted to these acceptable values.

VARIANCE OF THE SELECTION RESPONSE AND INBREEDING
The variance of the selection response and the inbreeding rate are highly related, as the following approximation shows (Meuwissen and Woolliams 1994a):

$$V(\Delta G) = 2\Delta F \sigma_{a\infty}^2 (1 - r_\infty^2 k), \qquad\qquad [1]$$

where ΔG = annual genetic gain; ΔF = rate of inbreeding; $\sigma_{a\infty}^2$ (r_∞) = genetic variance (accuracy of selection) after variance reduction due to selection (Bulmer 1971); k = the relative phenotypic variance reduction after selection. Under truncation selection, $k = \bar{i}(\bar{i}-x)$, where $\bar{i}$ = intensity of selection; and x = the standardised truncation point. From Formula [1] follows that $V(\Delta G)$ can be decreased by increasing the accuracy of selection, while this increases ΔF somewhat (Wray and Thompson 1990). This seems the main difference between $V(\Delta G)$ and ΔF.

Nicholas (1989) argued that a constraint on the coefficient of variation of the response from 10 years of selection ($CV(\Delta G_{10})$) of .05 - .1 is a more stringent constraint than a constraint on ΔF of .5% per year. This may not be the case when generation intervals are very short and/or selection is very accurate (Meuwissen and Woolliams 1994a). The question is whether a constraint on $CV(\Delta G_{10})$ of, say, .05 is realistic. In a breeding scheme this implies that after 10 years of selection the response deviates probably less than $2*.05*\Delta G_{10}$ from the expected response. In a closed nucleus scheme, such a low coefficient of variation is probably desirable, because a large negative deviation from the expected response may lead to large reductions in sales of breeding stocks. In a more or less open breeding scheme, a negative deviation from the expected response can be compensated by the use of breeding animals from outside the nucleus. Hence, in an open scheme, more variance of the selection response can be accepted. In completely open schemes, such as the world wide selection of dairy cattle, a high $V(\Delta G)$ may be necessary to breed young bulls that are several genetic standard deviations above the current population mean.

THE RISK OF CHANGING MARKETS
In the above, risk was defined as the risk of not obtaining the predicted selection response. There is also the risk of changing future markets, such that the predicted response turns out to be not the

optimal response. If the uncertainty about the future market is large, it seems not reasonable to strive for very low $V(\Delta G)$. In this case, there are hopefully other schemes breeding for different markets from which breeding stocks can be used to correct for the difference between expected and realised future markets. Unfortunately, with the globalisation of the markets, schemes are becoming more alike and fewer schemes result. Some preliminary modelling of schemes for different breeding goals (results not shown) indicated that correlations between different breeding goals higher than .7 - .8 leads to one breeding scheme for all goals being optimal. Correlations lower than .7 - .8 leads to one scheme for every goal. World wide markets and environments differ considerably such that a large number of selection goals with correlations lower than .7 - .8 result. However, there is a strong tendency for the markets and environments to become more alike and one global breed takes over many local breeds. If the rule is used that the global breed has to be proven superior to the local breed for the local market and that it's apparent superiority is not due to heterosis, novelty, or other side effects, a lot of local breeds may survive in their local markets, e.g. with the aid of some foreign genes. This survival of many different schemes would reduce the risk of all breeding schemes. Smith (1985) argues that many selection lines should be kept to reduce the risk of the breeding schemes, but that may be too costly for some species and breeding companies.

REDUCING THE VARIANCE OF THE SELECTION RESPONSE
From the previous section, it seems that an objective measure for the constraint on $CV(\Delta G_{10})$ is difficult to obtain. Woolliams and Meuwissen (1993) putted a cost factor on the variance of response and used the following objective for the selection of the parents of the next generation:

$$\mathbf{c'\hat{u}} - k\ \mathbf{c'PEVc}, \qquad\qquad\qquad [2]$$

which is maximised for $\mathbf{c}$, where $\mathbf{c}$ = vector of contributions of selection candidates to the next generation of animals, i.e., $c_i > 0$ for selected animals, $\mathbf{\hat{u}}$ = vector of BLUP-EBV of the selection candidates, $\mathbf{PEV}$ = prediction error (co)variance matrix of $\mathbf{\hat{u}}$, and k = cost factor on the variance of the genetic level (= $\mathbf{c'PEVc}$). Note that $\mathbf{c'\hat{u}}$ is the mean genetic level of the next generation. The contributions, c_i, sum to .5 per sex, and an c_i value of .05 implies that $2*.05 = 10\%$ of the offspring have to come from parent i.

The cost factor, k, comprises: 1) loss due to uncertainty of the mean of the true breeding values of the selected group in planning and investment; 2) extra loss when $\mathbf{c'u}$ was overestimated by $\mathbf{c'\hat{u}}$ (costs from restoring and correcting genetic gains); 3) extra profit when $\mathbf{c'u}$ was underestimated by $\mathbf{c'\hat{u}}$. All three these effects are difficult to quantify. It is also possible to try several cost factors in a simulation and to study the variance vs. mean response curve. The latter may help to choose a cost factor. The variance of the selection response can be reduced substantially with little loss of the expected selection response by this selection rule (Woolliams and Meuwissen 1993).

Meuwissen and Woolliams (1994b) optimized the structure of open nucleus dairy cattle breeding schemes with constraints on the coefficient of variation of the response, $CV(\Delta G_{10})$, of .10 and .05.

They found that this reduction of the coefficient of variation of the response resulted in an increased number of sires and dams selected, longer generations intervals, especially in the sire path, where more progeny tested bulls were selected, and a more open nucleus, i.e., more nucleus dams came from commercial herds.

REDUCING INBREEDING
Wray and Goddard (1994) and Brisbane and Gibson (1994) reduced inbreeding by putting a cost factor on the average relationship of the selected animals:

$$\mathbf{c'\hat{u}} - \tfrac{1}{2}k\ \mathbf{c'Ac}, \qquad\qquad\qquad [3]$$

where A = the additive relationship matrix. Both papers developed a similar algorithm to maximise the objective [3]. The factor ½ is because the rate of inbreeding equals half the rate of increase of the average relationships. The cost factor k was defined by Wray and Goddard (1994) as:

$$k = \Delta G(t-1)/2 + D,$$

where t = the time horizon, and D = inbreeding depression of the breeding goal. The term $\Delta G(t-1)/2$ represents the average reduction of the genetic gain because of the variance reduction due to inbreeding up to generation t, i.e., in generation 1 genetic gain was reduced by $0*\Delta F$, in generation 2 by ΔF, in generation 3 by $2\Delta F$, etc. If the inbreeding depression of the breeding goal is small, k is largely determined by the time horizon, t, which is not easy to determine in a breeding scheme. Furthermore, this expression for k ignores the effect of inbreeding on the risk of the breeding scheme and the inbreeding depression on traits not included in the breeding goal. Inbreeding depression mainly affects fertility and fitness traits, which are often not included in the breeding goal.

In a simulation study, Brisbane and Gibson (1994) varied k in the objective [3] and investigated the selection response vs. inbreeding curve. The curve looked like a typical diminishing returns curve, i.e., at high ΔF and ΔG (modern scheme), large additional ΔF was required to achieve little extra selection response. Hence, in a modern breeding scheme with high ΔF and ΔG, large reductions in inbreeding can be achieved with little reduction of the selection response.

A CONSTRAINT ON INBREEDING
The costs of inbreeding are difficult to quantify, and if one of the cost aspects of inbreeding is neglected, a breeding scheme with a too high rate of inbreeding results. However, most breeders will have an opinion on how much inbreeding is acceptable in a breeding scheme. For instance, the rate of inbreeding of a new breeding strategy may not be a lot larger than that of the conventional strategy, because otherwise genetic defects, that were kept at low frequency by natural selection in the large conventional population, will drift to high frequency when inbreeding and genetic drift are markedly increased.

It seems more practical to put a constraint on the rate of inbreeding than to accurately assess the costs of inbreeding. Meuwissen (1997) maximised the genetic gain while constraining the inbreeding, i.e.,

$$\text{Max}_{(\text{for } \mathbf{c})} \ G = \mathbf{c'\hat{u}},$$

while $\mathbf{c'Q} = [\frac{1}{2} \ \frac{1}{2}]$, and $C = \mathbf{c'Ac}/2$,

where G = average genetic merit of the parents, which equals that of their offspring, C = the desired average coancestry of the selected parents ($\approx$ the average inbreeding coefficient of their offspring), $\mathbf{Q}$ = (n*2)-incidence matrix for the sex of the candidates (n = the number of candidates). The constraint $\mathbf{c'Q} = [\frac{1}{2} \ \frac{1}{2}]$ ensures that the contributions of the sires and that of the dams sum to $\frac{1}{2}$. The optimal solution of this optimization problem is obtained from the Lagrangian multiplier method, and is:

$$\mathbf{c} = \mathbf{A^{-1}}(\mathbf{\hat{u}} - \mathbf{Q}\lambda)/2\lambda_0,$$

with $\lambda = (\mathbf{Q'A^{-1}Q})^{-1}(\mathbf{Q'A^{-1}\hat{u}} - \mathbf{1}\lambda_0)$, and

$$\lambda_0 = [\mathbf{\hat{u}'}(\mathbf{A^{-1}} - \mathbf{A^{-1}Q}(\mathbf{Q'A^{-1}Q})^{-1}\mathbf{Q'A^{-1}})\mathbf{\hat{u}}] \ / \ [8C - \mathbf{1'}(\mathbf{Q'A^{-1}Q})^{-1}\mathbf{1}],$$

where $\mathbf{1}$ = (2*1)-vector of ones. When the rate of inbreeding is to be restricted to ΔF, the desired value of C is approximately equal to the current average coancestry plus ΔF. This algorithm can also be used to put a constraint on the variance of the selection response by replacing $\mathbf{A}$ by the **PEV**-matrix.

The method may yield some $c_i < 0$. Meuwissen (1997) showed that an optimum solution can be obtained by deleting the candidate with the smallest negative c_i from the list of candidates, and re-calculating $\mathbf{c}$ until all $c_i \geq 0$. The algorithm becomes much faster when all negative c_i are at once deleted from the list of candidates, which probably yields a close to optimal solution.

If this method is repeatedly applied from one generation to the next, the vector of optimal genetic contributions, $\mathbf{c}$, maximizes the genetic level within each generation and thus maximizes the selection response across generations. Simulation showed that the realized inbreeding coefficient did actually increase by ΔF per generation and genetic gains stabilised (Meuwissen 1997). At equal rates of inbreeding, these optimal contributions yielded 30 - 60% more selection response than conventional selection for BLUP-EBV.

OVERLAPPING GENERATIONS
The previous sections deal with discrete generations. When generations overlap, a sire (or a dam) has to be penalised for his use during previous years, because his current offspring will become selection candidates together with his previous offspring. For simplicity, it will be assumed here

that a selection round takes one year. The increase of the average relationships in the population has to be controlled from one year to the next. But, old animals with no real probability of selection, do not seem relevant to current selection decisions and thus should be excluded from the population. M.E. Goddard (pers. comm.) suggested to constitute the population by weighing the animals by the summed contribution that their age class is still expected to have (based on the current distribution of the parents over the age classes). Next year's population consists then of already born animals, with fixed average relationships, and new born animals, whose relationships depend on the current selection decisions. The optimization problem becomes now:

$$\text{Max}_{(\text{for } c_1)} \ G = c_1' \hat{u},$$

while $c_1'Q = [s \ s]$, and $C = (c_1'Ac_1 + 2c_1A_{12}c_2 + c_2A_{22}c_2)/2$,

where c_1 = contributions of selection candidates to next years population by having offspring; c_2 = the known contribution from the already alive animals to next years population by ageing:

$$c_{2i} = (\Sigma_{k>j} C_k)/(L \ n), \text{ (animal i is from age-sex class j)}$$

with C_k = the total contribution of age-sex class k to the offspring ($\Sigma_{k>j}$ denotes summation over all age classes older than j of the same sex); n = the number of animals per age-sex class; L = the average generation interval (which can be shown to equal the sum of the future contributions of all sex-age classes), s = the sum of the future contributions of age class 0, which equals per sex: $1/2L$; A_{12} = relationship matrix between the selection candidates and the population; A_{22} = relationship matrix among the animals of the population (diagonals are 0). Note that the sum of all c_{1i} plus all c_{2i} is one. The Appendix of Meuwissen (1997) shows how to optimise the contributions, c_1, when some contributions are fixed, i.e., c_2. Grundy et al. (1997) use a (slightly) different method based on lifetime breeding profiles, which was able to control the rate of inbreeding. Their paper did not compare the genetic gains of this method to that with BLUP selection.

A preliminary simulation study of a closed MOET nucleus dairy cattle scheme was conducted to test the present method. Male and female reproductive rates were assumed unrestrictive, and 256 new born animals entered the nucleus per year. Inbreeding was restricted to .5% per year, which was achieved with BLUP selection by selecting 64 sires and 64 dams. Table 1 shows that, with the inbreeding constraint method the inbreeding level of the animals born in year 20 was slightly higher than .1, which is because the average inbreeding of the whole population was restricted and a somewhat higher inbreeding of the animals born in year 20 was thus allowed. The genetic level is 28% higher with the inbreeding constraint method than with BLUP selection. Part of this difference will be due to the more optimal numbers of sires and dams selected. The more accurate EBVs of cows (bulls were not progeny tested) favoured more intense selection of dams than of sires (De Boer et al. 1994). Note however that when 24 sires and 5 dams were selected based on

BLUP-EBV, a too high rate of inbreeding resulted. This clearly shows where the extra genetic gain comes from: the inbreeding constraint method yields a higher selection differential at the same rate of inbreeding. The increase in genetic gain in Table 1 is lower than that for discrete generations, hence, the overlapping generations method may need some further improvements.

In Table 1, the distribution of the parents over the sex-age classes, C_k, of the previous year were used to optimize c_1. This may result in some sub-optimality of the solutions c_1, because after a year of long generation intervals, extremely short generation intervals can be allowed, which may then result into difficulties to achieve the constraint in the next year. The method may be improved by using the current solution, c_1, to determine the distribution of the parents over the sex-age classes, but this requires iteration, because c_1 depends on C_k, and thus requires more computing time.

Table 1. Genetic gain (G; σ_p units) and inbreeding (F) in dairy MOET scheme after 20 years of BLUP selection or optimal selection with a constraint on inbreeding. Inbreeding was constrained to .1 at year 20, h^2 =.3, repeatability of lactation records was .5, and the annual survival rate of animals was .7 (10 replicated simulations).

Selection	G	F	No of selected sires	dams
BLUP	2.01	.10	64	64
constraint on F	2.58	.11	24	5

CONCLUSIONS
The components of the risk of a breeding scheme are: inbreeding (drift variance); and variance of the selection response. The risk of a breeding scheme can be markedly reduced by putting a cost factor on inbreeding and/or the variance of the selection response with little loss of genetic gain. The costs of risk are however difficult to assess and it may be more practical to put a constraint on the variance of the selection response and/or inbreeding. Such methods can yield substantially higher selection differentials at the same rate of inbreeding than conventional selection for BLUP-EBV.

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