

# Maximizing the Response of Selection with a Predefined Rate of Inbreeding<sup>1</sup>

T.H.E. Meuwissen

DLO-Institute of Animal Science and Health, Box 65, 8200 AB Lelystad, The Netherlands

**ABSTRACT:** A method was derived that maximizes the genetic level of selected animals while constraining their average coancestry to a predefined value. The average coancestry of the selected parents equals the inbreeding level in the next generation, so that rates of inbreeding were controlled. When this method was applied for several generations of selection, stable rates of genetic gain were attained, which indicates that the method could control the short- and long-term effects of selection on inbreeding. At equal rates of inbreeding, genetic gains were 21 to 60% greater than that with selection for BLUP-EBV, because of increased selection differentials. The difference was larger when the desirable rate of inbreeding

was smallest. Selection with a constraint on inbreeding required only EBV of, and relationships between, the selection candidates and is therefore easy to apply in practice. The optimal solution is expressed in genetic contributions of selection candidates to the next generation, which is equivalent to numbers of offspring per candidate. These optimal numbers of offspring may be difficult to attain because of female reproductive limitations. The optimal method could be adapted to situations with additional reproductive constraints. The method can also be used to constrain the variance of response by restricting the average prediction error variance of the selected animals.

Key Words: Selection Methods, Inbreeding, Genetic Gain

J. Anim. Sci. 1997. 75:934-940

## Introduction

Selection schemes are usually designed to maximize genetic gain with no or an implicit limitation of rates of inbreeding. Some authors have designed selection methods that reduce rates of inbreeding. Grundy and Hill (1993) and Verrier et al. (1993) reduced the weight of the family mean in their selection index relative to that in BLUP EBV, which reduced the probability of coselection of relatives and thus reduced inbreeding. Brisbane and Gibson (1994) and Wray and Goddard (1994) selected animals while putting a cost on the average relationship of the selected animals. There is no guarantee that these methods yield maximum genetic gains at some level of inbreeding. Further, the actual rate of inbreeding is not known before the breeding scheme commences.

Goddard and Howarth (1994) advocated the use of dynamic selection rules in contrast to static designs of optimal breeding schemes. Dynamic rules optimize the selection of the actual available candidates and thus

take advantage of opportunities that were not foreseen when the breeding program was planned. My article presents a dynamic selection rule that maximizes the genetic level of the selected parents while restricting their average relationship and hence the future coefficient of inbreeding. I assumed that acceptable rates of inbreeding were approximately known (e.g., from Meuwissen and Woolliams, 1994a). Breeding schemes were simulated to test whether the intended rate of inbreeding was achieved and to compare rates of gain to that with BLUP selection. Mating was at random for all the breeding schemes considered.

## Methods

*Optimal Genetic Contributions to the Next Generation.* Within every round of selection, we want to maximize the genetic level of the next generation of animals  $G_{t+1}$ :

$$G_{t+1} = \mathbf{c}_t' \mathbf{EBV}_t \quad [1]$$

where  $\mathbf{EBV}_t$  = vector of BLUP estimated breeding values of the candidates for selection in generation  $t$  and  $\mathbf{c}_t$  = vector of genetic contributions of the selection candidates to generation  $t+1$ . The problem is to find an

<sup>1</sup>Financial support of Holland Genetics is gratefully acknowledged.

Received February 12, 1996.

Accepted September 19, 1996.

optimum  $\mathbf{c}_t$ . The genetic contributions of all males sum to 1/2, and likewise for all female candidates:

$$\mathbf{Q}'\mathbf{c}_t = 1/2, \quad [2]$$

where  $\mathbf{Q}$  = known incidence matrix for sex (the first column yields ones for males and zeros for females, and the second column yields ones for females and zeros for males); and  $\frac{1}{2}$  = a vector of halves of order 2.

Further, we restrict the average coancestry between selected animals, because the increase in coancestry equals the future increase in inbreeding:

$$\bar{C}_{t+1} = \mathbf{c}_t'\mathbf{A}_t\mathbf{c}_t/2, \quad [3]$$

where  $\mathbf{A}_t$  = the matrix of additive genetic relationships among selection candidates in generation  $t$ , which equals twice the matrix of coefficients of coancestry. Constraint [3] replaces the constraint  $\bar{C}_{t+1} \geq \mathbf{c}_t'\mathbf{A}_t\mathbf{c}_t/2$ , because objective [1] is linear, such that the optimum is always at the boundary of the space  $\bar{C}_{t+1} \geq \mathbf{c}_t'\mathbf{A}_t\mathbf{c}_t/2$ , (i.e., where constraint [3] holds). When generation 0 is noninbred ( $F_0 = 0$ ), we may set  $\bar{C}_{t+1}$  equal to  $\Delta F(t+1)$ , where  $\Delta F$  is the desired rate of inbreeding.

The optimal  $\mathbf{c}_{t+1}$  that maximizes  $G_{t+1}$  under constraints [2] and [3] is obtained by introducing LaGrangian multipliers, similar to the approach of Wray and Goddard (1994), who applied this method within their algorithm to obtain optimal contributions of selected animals. We would like to maximize  $H_t$  for  $\mathbf{c}_t$ ,  $\lambda_0$ , and  $\lambda$ , with

$$H_t = \mathbf{c}_t'\mathbf{EBV}_t - \lambda_0(\mathbf{c}_t'\mathbf{A}_t\mathbf{c}_t - 2\bar{C}_{t+1}) - (\mathbf{c}_t'\mathbf{Q} - 1/2')\lambda, \quad [4]$$

where  $\lambda_0$  and  $\lambda$  are LaGrangian multipliers ( $\lambda$  = a vector of two LaGrangian multipliers).

Equating the first derivative of  $H_t$  with respect to  $\mathbf{c}_t$  to zero yields

$$\mathbf{EBV}_t - 2\lambda_0\mathbf{A}_t\mathbf{c}_t - \mathbf{Q}\lambda = 0.$$

Solving for  $\mathbf{c}_t$  yields

$$\mathbf{c}_t = \mathbf{A}_t^{-1}(\mathbf{EBV}_t - \mathbf{Q}\lambda)/2\lambda_0. \quad [5]$$

From the constraint  $\mathbf{Q}'\mathbf{c}_t = 1/2$  follows an equation for  $\lambda$ :

$$\mathbf{Q}'\mathbf{A}_t^{-1}\mathbf{Q}\lambda = \mathbf{Q}'\mathbf{A}_t^{-1}\mathbf{EBV}_t - 1\lambda_0, \quad [6]$$

and from the constraint  $\mathbf{c}_t'\mathbf{A}_t\mathbf{c}_t/2 = \bar{C}_{t+1}$  follows

$$8\bar{C}_{t+1}\lambda_0^2 = (\mathbf{EBV}_t - \mathbf{Q}\lambda)'\mathbf{A}_t^{-1}(\mathbf{EBV}_t - \mathbf{Q}\lambda).$$

Solving this equation and [6] for  $\lambda_0$  yields

$$\lambda_0^2 = \frac{\mathbf{EBV}_t'(\mathbf{A}_t^{-1} - \mathbf{A}_t^{-1}\mathbf{Q}(\mathbf{Q}'\mathbf{A}_t^{-1}\mathbf{Q})^{-1}\mathbf{Q}'\mathbf{A}_t^{-1})\mathbf{EBV}_t}{8\bar{C}_{t+1} - \mathbf{1}'(\mathbf{Q}'\mathbf{A}_t^{-1}\mathbf{Q})^{-1}\mathbf{1}}. \quad [7]$$

A negative right hand side of equation [7] implies that the constraint  $\mathbf{c}_t'\mathbf{A}_t\mathbf{c}_t/2 = \bar{C}_{t+1}$  cannot be met. The minimum average relationship that can be achieved is  $1/4\mathbf{1}'(\mathbf{Q}'\mathbf{A}_t^{-1}\mathbf{Q})^{-1}\mathbf{1}$ , which is readily obtained by minimizing  $\mathbf{c}_t'\mathbf{A}_t\mathbf{c}_t$  under the constraint  $\mathbf{Q}'\mathbf{c}_t = 1/2$ .

The value for  $\lambda_0$  from equation [7] is used in [6] to obtain  $\lambda$ . Now equation [5] yields the optimal  $\mathbf{c}_t$ . This  $\mathbf{c}_t$  may contain negative values for some animals with poor EBV. Negative values of  $\mathbf{c}_t$  are easily constrained to zero by eliminating those animals from the optimization process. The elimination of animals with negative  $\mathbf{c}_t$  is repeated, one at a time, until all elements of  $\mathbf{c}_t$  are positive. This will yield an optimal  $\mathbf{c}_t$  within the solution space  $\mathbf{c}_t \geq 0$ , as the following will show.

Because the objective  $\mathbf{c}_t'\mathbf{EBV}_t$  is linear, the optimal  $\mathbf{c}_t(\text{max})$  is at the boundary of the ellipsoid solution space  $\mathbf{c}_t'\mathbf{A}_t\mathbf{c}_t = 2\bar{C}_{t+1}$ , with  $\mathbf{c}_t(\text{max})'\mathbf{EBV}_t = G_{\text{max}}$  and, say,  $c_{ti(\text{max})} < 0$ , where  $c_{ti(\text{max})}$  =  $i^{\text{th}}$  element of  $\mathbf{c}_t(\text{max})$ . If we let the value of  $\mathbf{c}_t'\mathbf{EBV}_t$  decrease somewhat to  $G_{\text{sub}} < G_{\text{max}}$ , the solution space for  $c_{ti}$  increases from the point  $c_{ti(\text{max})}$  to the small interval  $c_{ti(\text{max})} \pm \delta$ , because the boundaries are the solution to the quadratic equation that results from substituting  $\mathbf{c}_t'\mathbf{EBV}_t = G_{\text{sub}}$  and all possible  $c_{tj}$ ,  $j \neq i$  in  $\mathbf{c}_t'\mathbf{A}_t\mathbf{c}_t = 2\bar{C}_{t+1}$ . When  $G_{\text{sub}}$  decreases further, the size of the interval  $c_{ti(\text{max})} \pm \delta$  increases and, when  $\delta = c_{ti(\text{max})}$ , will include 0, which is a permissible solution for  $c_{ti}$  and yields highest  $G_{\text{sub}}$ . Because the optimal permissible is  $c_{ti} = 0$ , this solution could also be obtained by directly constraining the negative  $c_{ti}$  solution to zero.

*Limitations of Reproductive Techniques.* Optimal genetic contributions of sires can be achieved in practice, when each sire can inseminate the required number of dams. If only a limited number of dams can be inseminated by one sire, an additional constraint can be applied for each sire that exceeds the biologically maximum contribution (i.e.,  $\mathbf{c}_t \leq \mathbf{c}_{\text{max}}$ , where  $\mathbf{c}_{\text{max}}$  = the biologically maximum contribution of a sire). The contributions of the sires that exceed  $\mathbf{c}_{\text{max}}$  are set equal to  $\mathbf{c}_{\text{max}}$ , and the remaining contributions are optimized as in the Appendix. This yields optimal results under the restriction  $\mathbf{c}_t \leq \mathbf{c}_{\text{max}}$  because of arguments analogous to those for the  $\mathbf{c}_t > 0$  restriction.

Achieving the optimal genetic contributions of females will require high female reproductive rates, which may be possible in poultry, pigs, or in cattle by the use of Ova Pick Up (Kruip et al., 1994). For instance, when the number of sires selected exceeds the number of dams, the optimal solution requires the mating of one dam to several sires. Such flexible female reproductive techniques may not be available and often a predefined number of dams is selected, say  $n_d$ , with equal genetic contributions per dam. In this situation, we may simply select the  $n_d$  dams with the highest optimal contributions.

Also, it may be practical or desirable to have equal numbers of offspring per selected sire and(or) per

selected dam. In this case, the contributions of animals  $i$  with small  $c_{mi}$  are set to zero until the remaining animals (i.e., the selected animals) fulfill the constraint  $\mathbf{c}_t' \mathbf{A}_t \mathbf{c}_t \leq 2\bar{c}_{t+1}$  when their contributions are set to equal values, where  $c_{mi}$  = optimal contribution of animal  $i$  without the equal contribution constraint. Because of the similarity between this approach and the implementation of the  $\mathbf{c}_t > \mathbf{0}$  constraint, it is expected that this solution will be close to optimal.

When the contributions of the dams are modified due to reproductive limitations, the contributions of the sires may be reoptimized conditional on the suboptimal contributions of the dams (see Appendix). The method in the Appendix can also be used to reoptimize the contributions of the dams, when the contributions of the sires have been modified.

**Simulation.** Closed nucleus programs were simulated from generation 1 (the base generation) until generation 10. In the base generation, all animals were unrelated and genotypes,  $g_i$ , were from the distribution  $N(0, .25)$ . Independent environmental effects,  $e_i$ , were obtained from the distribution  $N(0, .75)$ , which implies a heritability of .25. Phenotypes were obtained from  $p_i = g_i + e_i$  (i.e., no fixed effects were simulated). In later generations,  $g_i$  was simulated from  $N(1/2g_s + 1/2g_d, .125)$ , which ignores the effect of inbreeding on the within-family variance. The latter implies that an equilibrium genetic variance will be achieved after some initial decrease of genetic variances because of the Bulmer (1981) effect. Thus, equilibrium genetic gains are expected to be obtained except when it becomes increasingly difficult during the course of selection to select animals that satisfy the average relationship constraint.

Every generation, 50 male and 50 female selection candidates were born. A sire and dam for each candidate were chosen at random with probabilities that correspond to the genetic contributions that were obtained from the previously described algorithm. In the case of BLUP selection, the best  $n_s$  sires and best  $n_d$  dams were selected based on EBV and had contributions of  $1/2n_s$  and  $1/2n_d$ , whereas the other animals had zero contributions. It may be noted that the predefined genetic contributions are expected contributions; the actual contributions will vary due to sampling according to the multinomial distribution with a fixed total number of offspring.

## Results

**Optimal Contributions.** Table 1 shows the results when the average coefficient of coancestry of the parents of generation  $t$  is limited to  $(t-1)\Delta F$  for  $t=2, \dots, 10$ , where  $\Delta F = .025$  per generation. The average coancestry constraint was achieved in all generations and without reduction of rates of genetic gain in later

Table 1. The average coancestry of the parents of generation  $t$ , the inbreeding in generation  $t$ , and the genetic gain from generation  $t-1$  to  $t$ , when the average coancestry was limited to .025 ( $t-1$ ) and genetic contributions were optimized within each generation for both sexes<sup>a</sup>

Generation (t)	Coancestry parents	Inbreeding	Genetic gain
2	.025	0	.380
3	.050	.029	.322
4	.075	.052	.293
5	.100	.076	.318
6	.125	.100	.287
7	.150	.127	.303
8	.175	.150	.301
9	.200	.175	.311
10	.225	.202	.315

<sup>a</sup>Average of 100 replicated simulations of the breeding scheme. The standard errors of the inbreeding and genetic gain were approximately .0011 and .011, respectively. The coancestry did not vary, because it was constrained.

generations. The initial reduction in genetic gain is due to reduced genetic variances because of selection (Bulmer, 1981). During later generations, rates of genetic gain seem to increase slightly. Although this increase is small relative to the standard error, and thus not statistically significant, an explanation may be that the inbreeding constraint becomes less stringent. The absolute increase in inbreeding is .025 per generation, and this implies initially a rate of inbreeding of .025 and later in generation 10 of .0303 ( $= .025/(1-F_9)$ , with  $F_9 = .175$ ).

The rate of inbreeding followed approximately the average coancestry of the parents with a lag of one generation (Table 1). The average coancestry coefficient included the coancestry of an animal with itself. This coancestry within animals will not result in inbreeding in the offspring of the selected parents because there was no selfing. However, in the next generation, the coancestry of the parent with itself is translated into breeding when the genes from the same animal can meet due to the matings of sibs. Hence, the inbreeding levels lag one generation compared with the average coancestry levels.

**Best Linear Unbiased Prediction Selection.** Figure 1 compares rates of gain and inbreeding of the optimal selection methods to rates obtained from selection on BLUP-EBV (BLUP selection). With BLUP selection, the rate of inbreeding depends mainly on the number of sires and dams selected, which was varied in Figure 1. Figure 1 also shows the results of schemes that optimize the selection of sires and dams but with equal contributions of the selected sires and the selected dams, as described in Methods. The optimized numbers of sires and dams selected were close to the numbers based on Wright's (1931) inbreeding formula for random mating:  $\Delta F = 1/8n_s + 1/8n_d$ , where  $n_s$

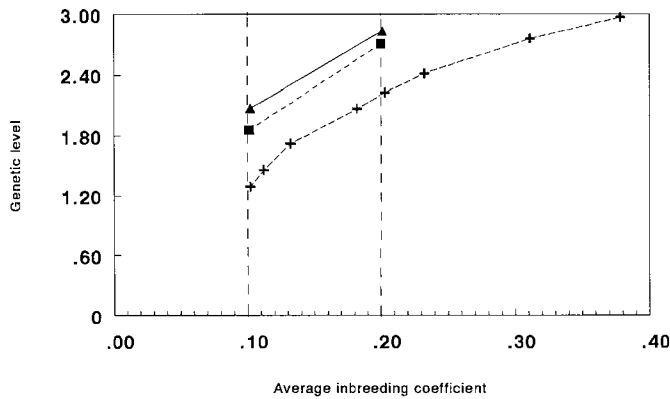


Figure 1. Genetic and inbreeding levels in generation 10 with inbreeding levels constrained to .1 and .2 and with optimal genetic contributions (▲), optimal selection of sires and dams but with equal contributions of selected sires and selected dams (■), and BLUP selection with selection of (from left to right) 32, 30, 26, 20, 18, 16, 12, and 10 sires and equal numbers of dams (+).

( $n_d$ ) = the number of sires (dams) selected (Table 2). In later generations, the number of selected animals decreased, because the rate of inbreeding increased from .025 and .0125 to .0303 and .0137, respectively (see previous section).

When 18 sires and 18 dams were selected, BLUP selection achieved inbreeding and genetic levels of .203 and 2.224, respectively, in generation 10 (Figure 1). At the same level of inbreeding, the genetic levels of schemes with optimal genetic contributions and optimal sire and dam selection (with equal contributions) were 27 and 21% higher, respectively. When the required inbreeding level in generation 10 was .1, genetic levels of these optimized schemes were 60 and 44% higher, respectively, than that of BLUP selection where 32 sires and 32 dams had to be selected to reach this level of inbreeding. Hence, the superiority of the optimal contribution methods increases when smaller rates of inbreeding are required.

## Discussion

Wray and Goddard (1994) and Brisbane and Gibson (1994) described a method that reduced inbreeding by maximizing the objective

$$c_t'EBV_t - k \quad c_t'A_t c_t,$$

where  $k$  = a cost factor. They used optimization algorithms that did not guarantee to find the optimum  $c_t$ , but the optimum solution for the cost factor method is found by replacing  $\lambda_0$  with  $k$  in equations [5] and [6]. Wray and Goddard (1994) find optimum  $c_t$ , within the group of animals that is selected by their optimization algorithm. The cost factor  $k$  is usually unknown, although Wray and Goddard (1994) calcu-

lated a cost factor based on inbreeding depression, variance reductions due to inbreeding, and a time horizon. However, inbreeding also increases the risk of a breeding scheme, i.e., the probability that deleterious genes drift to high frequency, and the breeding goal is dominated by production traits that show little inbreeding depression. The latter results in  $k$ -factors that allow moderate to high rates of inbreeding, and reproductive traits will suffer from substantial inbreeding depression, which will eventually increase their weight in the breeding goal, but by then a lot of positive reproduction genes might have been lost due to inbreeding. The presumption made here was that practical breeders do approximately know which rates of inbreeding are acceptable, but they do not have a feel for cost factors and thus are willing to accept only cost factors that result in acceptable rates of inbreeding. Hence, the cost factor  $\lambda_0$  is calculated from the acceptable rate of inbreeding by equation [7].

If acceptable rates of inbreeding are unknown, it is also possible to generate a response surface of inbreeding against selection response by simulating schemes with different constraints on the rate of inbreeding such as Figure 1, but with more levels of the constraint. Based on this response surface, a small rate of inbreeding may be chosen that still yields a high selection response, whereas a further decrease of the inbreeding rate would yield a substantial reduction of the selection response. A similar approach was taken by Brisbane and Gibson (1994) to find their  $k$ -factor. A drawback of this approach is that simulation of the breeding scheme is needed to find the response curve, and every change of the breeding scheme would require new simulations to assess this curve.

The present method of selection achieves, on average, a predefined rate of inbreeding. Realized rates of inbreeding fluctuate around this desired rate. This is because the realized contributions of the parents fluctuate around the optimal contributions due to variances of family sizes. However, because the average relationships among the selected parents did not vary around their predefined levels, the standard deviation of the inbreeding level at generation 10 was much lower than with BLUP selection (.013 vs. .028, respectively, when the level of inbreeding was .2).

The present method constrained the average coancestry of the selected parents instead of the average inbreeding coefficient of their offspring. In the latter case, only one sire and one dam would have been selected from the unrelated base population yielding full sib offspring with a coefficient of inbreeding of 0. When parents are selected from this generation of full siblings, only full sibs can be selected as parents and the rate of inbreeding cannot be lower than .25. This shows that a direct constraint on inbreeding cannot effectively control rates of inbreeding. When the coancestry was constrained, it did not become increasingly difficult to achieve the predefined rate of

inbreeding during the course of selection; the rates of gain did not decrease (Table 1) and numbers of animals selected did not increase (Table 2), which suggests that previous selections affect future inbreeding only by affecting the present coancestry.

This implies that nonrandom mating cannot control inbreeding, because the relationships between the selected parents will in later generations be converted into inbreeding. Nonrandom mating can postpone the time until the close relationships are converted into inbreeding, but cannot prevent it. However, nonrandom mating, in which the selected animals with many coselected relatives are mated to those with few coselected relatives, reduces the cumulative effect of multiple generations of selection on inbreeding by reducing the variance of the long-term genetic contributions (Santiago and Caballero, 1994). The effect of reducing the coselection of relatives (e.g., by the present method) and compensatory mating on inbreeding is additive (Grundy et al., 1994); hence, both BLUP selection and the present method can equally benefit from it.

Wray and Thompson (1990) showed that rates of inbreeding can be predicted from the sum of squares of the long-term contributions:  $\Delta F = 1/4SSC_{t(\infty)} = 1/4\sum_{i \in t} c_{i(\infty)}^2$ , where  $c_{i(T)}$  = contribution of ancestor  $i$  to the descendants in generation  $T$ ; and summation is over all ancestors in generation  $t$ . Figure 2 compares the effects of optimal selection with constrained inbreeding and BLUP selection on  $SSC_{t(10)}$ . When going from generation 9 to 1 (i.e., from young to old ancestors of generation 10), the  $SSC_{t(10)}$  increases steadily with BLUP selection. Hence, BLUP selection affects the contributions of old ancestors, which contributes to inbreeding. When inbreeding is constrained and when going from generations 9 to 1,  $SSC_{t(10)}$  increases only for the first two generations (from 9 to 7) and stabilizes or decreases for old ancestors. This shows that the constrained selection achieves the genetic

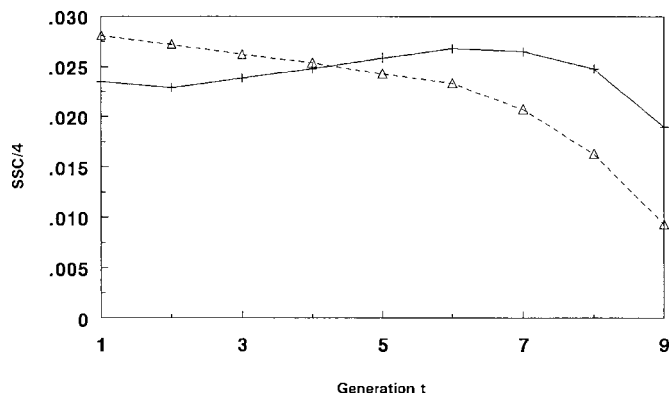


Figure 2. Sum of squared contributions (SSC) of ancestors in generation  $t$  to descendants in generation 10 with BLUP selection of 18 sires and 18 dams, which yielded an inbreeding coefficient of .2 in generation 10 ( $\Delta$ ) and optimized parental contributions with the inbreeding constrained to .2 in generation 10 (+).

gain by changing the contributions of young ancestors rather than those of old ancestors. Contributions of old ancestors are hardly changed and do not contribute to rates of inbreeding. This agrees with Woolliams and Thompson (1994), who concluded that the changes in genetic contributions of old ancestors added much more to the rate of inbreeding than to the genetic gain and should be avoided when rates of inbreeding are to be reduced. Thus, at equal rates of inbreeding, selection differentials are higher when the contributions of the selection differentials are optimized compared with when BLUP selection is applied.

Generations were assumed discrete here, but in practice they overlap. Overlapping generations are not a problem for the presented algorithm; it will limit the

Table 2. Optimal numbers of parents selected when the number of offspring per sire and per dam are equal. For comparison, the numbers according to Wright's (1931) random mating formula are given

Generation	$\Delta F_{init} = .025^a$		$\Delta F_{init} = .0125^a$	
	Sires	Dams	Sires	Dams
2	10	10	21	20
3	10	10	19	19
4	10	10	18	19
5	9	9	18	18
6	9	9	18	17
7	9	9	17	17
8	8	8	17	17
9	8	8	16	17
10	8	8	17	16
Wright's formula	10	10	20	20 <sup>b</sup>

<sup>a</sup> $\Delta F_{init}$  = the initial rates of inbreeding; in later generations  $\Delta F$  increased to .0303 and .0137, respectively.

<sup>b</sup>Wright's formula is  $\Delta F = 1/8n_s + 1/8n_d$ , where the numbers of males ( $n_s$ ) and females ( $n_d$ ) are assumed equal.

average coancestry of the animals selected across the generations to the desired level. However, the algorithm will not be optimal because it neglects the relationships between the animals born in year  $t$  and those born in year  $t - 1$ , which will serve together as selection candidates in the future. In practice, it seems unlikely that the average relationship between the animals born in year  $t$  and year  $t - 1$  is larger than that among the animals born in year  $t$ , such that selection across age classes is not hampered by high average relationships between animals from age class  $t$  and class  $t - 1$ . If the relationships between age classes turn out to be extremely large, an additional constraint could be applied that constrains the average coancestry between the selected parents for the offspring in year  $t$  and the animals born in year  $t - 1$  to equal that among the animals born in year  $t - 1$ .

Extension of the method to multitrait breeding goals is straightforward by setting  $EBV = \Sigma v_i \text{ebv}_i$ , where  $\text{ebv}_i$  = the vector of estimated breeding values for the  $i^{\text{th}}$  breeding goal trait and  $v_i$  is its economic value. Note that  $\text{ebv}_i$  may also reflect breeding values for maternal effects if they are included in the breeding goal. Inbreeding depression was not considered here, because the constraint on the inbreeding implicitly determines how much inbreeding depression is accepted in the breeding scheme, and the BLUP breeding value estimation should correct for it, just as it should correct for any fixed effects that are present in practice but not simulated here.

Woolliams and Meuwissen (1993) used a cost factor method to reduce the variance of the selection response. The present method can also be used to constrain the variance of the response by replacing  $A_t/2$  with  $PEV_t$  in equations [5], [6], and [7], where  $PEV_t$  = the prediction error (co)variance matrix of  $EBV_t$ . The  $\lambda_0$  from Equation [7] will yield the cost factor for Woolliams and Meuwissen's method to obtain a predefined variance of the selection response. The latter would provide a dynamic selection rule as an alternative to the static optimal designs of Meuwissen and Woolliams (1994b).

### Implications

A dynamic selection rule was presented that yielded 21 to 60% greater selection response than best linear unbiased prediction selection at the same rate of inbreeding, which is due to increased selection differentials. The rule is easy to implement in any breeding scheme. Reproductive limitations may require some modification of the optimal solution.

### Literature Cited

- Brisbane, J. R., and J. P. Gibson. 1994. Balancing selection response and rate of inbreeding by including genetic relationships in selection decisions. 5th World Congr. Genet. Appl. Livest. Prod. (Guelph) 19:135.
- Bulmer, M. G. 1981. The mathematical theory of quantitative genetics. Clarendon Press, Oxford, U.K..
- Goddard, M. E., and J. M. Howarth. 1994. Dynamic selection rules and selection of males to progeny test. 5th World Congr. Genet. Appl. Livest. Prod. (Guelph) 19:306.
- Grundy, B., A. Caballero, E. Santiago, and W. G. Hill. 1994. A note on using biased parameter values and non-random mating to reduce rates of inbreeding in selection programmes. Anim. Prod. 39:463.
- Grundy, B., and W. G. Hill. 1993. A method for reducing inbreeding with best linear unbiased prediction. Anim. Prod. 56:427.
- Kruip, Th.A.M., R. Boni, Y. A. Wurth, M.W.M. Roelofsen, and M. C. Pieterse. 1994. Potential use of Ovum Pick-Up for embryo-production and breeding in cattle. Theriogenology 42:675.
- Meuwissen, T.H.E., and J. A. Woolliams. 1994a. Effective sizes of livestock populations to prevent a decline in fitness. Theor. Appl. Genet. 89:1019.
- Meuwissen, T.H.E., and J. A. Woolliams. 1994b. Maximizing genetic response in breeding schemes of dairy cattle with constraints on variance of response. J. Dairy Sci. 77:1905.
- Santiago, E., and A. Caballero. 1994. Effective size of populations under selection. Genetics 139:1013.
- Verrier, E., J. J. Colleau, and J. L. Foulley. 1993. Long-term effects of selection based on the animal model BLUP in a finite population. Theor. Appl. Genet. 87:446.
- Woolliams, J. A., and T.H.E. Meuwissen. 1993. Decision rules and variance of response in breeding schemes. Anim. Prod. 56:179.
- Woolliams, J. A., and R. Thompson. 1994. A theory of genetic contributions. 5th World Congr. Genet. Appl. Livest. Prod. (Guelph) 19:127.
- Wray, N. R., and M. E. Goddard. 1994. Increasing long term response to selection. Genet. Sel. Evol. 26:431.
- Wray, N. R., and R. Thompson. 1990. Prediction of rates of inbreeding in selected populations. Genet. Res. 55:41.
- Wright, S. 1931. Evolution in Mendelian populations. Genetics 16:97.

### Appendix: Optimal Contributions of Selection Candidates Conditional on the Fixed Contributions of Other Candidates

Often reproductive techniques will limit the contributions of some candidates (e.g., dams). This may result in some fixed contributions. For example, if the optimal contribution of an animal is higher than its biologic maximum, the contribution of this animal will be fixed to the biologically maximum contribution. Also, it may be that  $n_d$  dams are selected with equal contributions and that the contributions of the males need to be optimized. The question is what is the optimal contribution of the remaining candidates, which will be called class 1 candidates in the following. The candidates with fixed contributions will be termed class 2.

In this case, we would like to maximize:

$$H = c_1'EBV_1 - \lambda_0(c_1'A_{11}c_1 + 2c_1'A_{12}c_2 - K) - (c_1'Q_1 - s')\lambda,$$

where  $c_1$  = genetic contributions of class 1 candidates that are to be optimized,  $c_2$  = known vector of

contributions of class 2 candidates,  $\mathbf{EBV}_1$  = vector of EBV of class 1 candidates,  $\mathbf{A}_{xy}$  = part of additive relationship matrix pertaining to the candidates of classes x and y,  $K = 2\bar{C} - \mathbf{c}_2'\mathbf{A}_{22}\mathbf{c}_2$ ,  $\bar{C}$  = the required average coefficient of coancestry,  $\mathbf{s} = \mathbf{1}/2 - \mathbf{Q}_2'\mathbf{c}_2$ ;  $\mathbf{Q}_x$  = known incidence matrix for the sex of class x candidates (contains two columns of 0 and 1 figures), and  $\lambda_0$  and  $\lambda$  are unknown Lagrangian multipliers. Equating the derivative of H with respect to  $\mathbf{c}_1$  to zero yields

$$\mathbf{EBV}_1 - 2\lambda_0(\mathbf{A}_{11}\mathbf{c}_1 + \mathbf{A}_{12}\mathbf{c}_2) - \mathbf{Q}_1\lambda = 0.$$

Solving for  $\mathbf{c}_1$  yields

$$\mathbf{c}_1 = \mathbf{A}_{11}^{-1}(\mathbf{EBV}_1 - 2\lambda_0\mathbf{A}_{12}\mathbf{c}_2 - \mathbf{Q}_1\lambda)/2\lambda_0. \quad [\text{A1}]$$

From the constraint  $\mathbf{Q}_1'\mathbf{c}_1 = \mathbf{s}$  follows equations for  $\lambda$ :

$$\begin{aligned} \mathbf{Q}_1'\mathbf{A}_{11}^{-1}\mathbf{Q}_1\lambda &= \mathbf{Q}_1'\mathbf{A}_{11}^{-1}(\mathbf{EBV}_1 - 2\lambda_0\mathbf{A}_{12}\mathbf{c}_2) \\ &\quad - 2\lambda_0\mathbf{s}, \end{aligned} \quad [\text{A2}]$$

which yields only one equation for  $\lambda$  when the class 1 candidates are all of the same sex (e.g., all males; the value for females in  $\lambda$  is then equal to 0).

From the constraint  $\mathbf{c}_1'\mathbf{A}_{11}\mathbf{c}_{11} + 2\mathbf{c}_1'\mathbf{A}_{12}\mathbf{c}_2 = K$  follows

$$\begin{aligned} \lambda_0^2 &= 1/4 \mathbf{EBV}_1' \mathbf{P} \mathbf{EBV}_1 / [K + \mathbf{c}_2' \mathbf{A}_{21} \mathbf{P} \mathbf{A}_{12} \mathbf{c}_2 \\ &\quad - \mathbf{s}'(\mathbf{Q}_1' \mathbf{A}_{11}^{-1} \mathbf{Q}_1)^{-1} \mathbf{s} - 2\mathbf{s}'(\mathbf{Q}_1' \mathbf{A}_{11}^{-1} \mathbf{Q}_1)^{-1} \mathbf{Q}_1' \mathbf{A}_{11}^{-1} \mathbf{A}_{12} \mathbf{c}_2], \end{aligned} \quad [\text{A3}]$$

where  $\mathbf{P} = \mathbf{A}_{11}^{-1} - \mathbf{A}_{11}^{-1}\mathbf{Q}_1(\mathbf{Q}_1'\mathbf{A}_{11}^{-1}\mathbf{Q}_1)^{-1}\mathbf{Q}_1'\mathbf{A}_{11}^{-1}$ . The solution of  $\lambda_0$  from [A3] is substituted in [A2] to obtain  $\lambda$ , and  $\lambda_0$  and  $\lambda$  are substituted in [A1] to obtain the optimal  $\mathbf{c}_1$ . If some elements of  $\mathbf{c}_1$  are negative, those contributions are constrained to zero by deleting those candidates from the optimization, and formulas [A3], [A2], and [A1] are applied again.

In the case where the contributions of the males (class 1) are to be optimized and those of the females are known (class 2), equations [A1], [A2], and [A3] reduce to [A4], [A5], and [A6], respectively, which are

$$\mathbf{c}_1 = \mathbf{A}_{11}^{-1}\mathbf{EBV}_1 - 2\lambda_0\mathbf{A}_{12}\mathbf{c}_2 - \lambda\mathbf{1}/2\lambda_0, \quad [\text{A4}]$$

with  $\lambda$  being scalar and

$$\begin{aligned} \lambda &= [\mathbf{1}'\mathbf{A}_{11}^{-1}(\mathbf{EBV}_1 - 2\lambda_0\mathbf{A}_{12}\mathbf{c}_2) \\ &\quad - \lambda_0]/\mathbf{1}'\mathbf{A}_{11}^{-1}\mathbf{1}. \end{aligned} \quad [\text{A5}]$$

$$\begin{aligned} \lambda_0^2 &= 1/4[\mathbf{EBV}_1'\mathbf{A}_{11}^{-1}\mathbf{EBV}_1 \\ &\quad - (\mathbf{EBV}_1'\mathbf{A}_{11}^{-1}\mathbf{1})^2/\mathbf{1}'\mathbf{A}_{11}^{-1}\mathbf{1}] / \\ &\quad \{2\bar{C} - \mathbf{c}_2'(\mathbf{A}_{22} - \mathbf{A}_{21}\mathbf{A}_{11}^{-1}\mathbf{A}_{12})\mathbf{c}_2 \\ &\quad - [\mathbf{1}'\mathbf{A}_{11}^{-1}\mathbf{A}_{12}\mathbf{c}_2 + 1/2]^2/\mathbf{1}'\mathbf{A}_{11}^{-1}\mathbf{1}\}. \end{aligned} \quad [\text{A6}]$$