

# DYNAMIC SELECTION PROCEDURES FOR CONSTRAINED INBREEDING AND THEIR CONSEQUENCES FOR PEDIGREE DEVELOPMENT

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## SUMMARY

A novel selection algorithm for maximising genetic response while constraining the rate of inbreeding is presented. This method uses an augmented numerator relationship matrix and represents an improvement on previous procedures where the constraint is applied to an increase in the inbreeding coefficient. It is shown that the proposed method controls inbreeding by maintaining the squared genetic contributions at a constant value. The regression of the long-term contributions on the assigned mating proportions was close to one and the ratio of the sum of squared contributions to the sum of squared mating proportions was greater than one, even when the heritability was one. It was concluded that the known ideal solution to maximise genetic gain under constrained inbreeding is in general unattainable, at least from using this approach.

**Keywords:** inbreeding, response, genetic contributions.

## INTRODUCTION

Wray and Thompson (1990) described the relationship between long-term genetic contributions and the asymptotic rate of inbreeding and this work was extended by Woolliams and Thompson (1994) to predict genetic response in terms of genetic contributions and to describe the ideal solution to maximise gain with constrained inbreeding. Meuwissen (1997) developed an algorithm for obtaining optimum selection decisions for maximising genetic gain while constraining the rate of inbreeding using the numerator relationship matrix ( $\mathbf{A}$ ). This paper has two objectives: firstly to improve existing methods by introducing modifications by using an augmented matrix ( $\mathbf{A}^*$ ) and associated constraint in order to better control the rate of inbreeding; and secondly, to examine the relationship of the mating proportions in dynamic selection procedures with long-term contributions.

## METHODS

Stochastic computer simulations were used to model selection schemes with discrete generations evaluated over 20 generations. The trait of selection was assumed to be of known heritability and the genetic evaluation used was BLUP. A dynamic selection procedure was employed following the selection algorithm presented by Meuwissen (1997). The number of sires and dams were optimised each generation of selection in order to maximise the predicted rate of gain subject to a constraint on the rate of inbreeding. The number of offspring born per generation was 100 (50 males and 50 females).

The selection algorithm identifies an optimum mating proportion for each individual ( $\mathbf{x}$ ), where  $x_i=0$  implies that the individual is not required for breeding. For each generation the sum of all mating proportions over both sexes is one. Matings were allocated by rounding to the nearest integer the required number of offspring and then allocating a mate at random to produce a single offspring per mating.

This scheme was run with the standard  $\mathbf{A}$  matrix (Meuwissen, 1997) and also with an augmented matrix  $\mathbf{A}^*$ . The augmented matrix for individuals in the cohort (t+1) was calculated as

$$\mathbf{A}_{(t+1)}^* = \mathbf{Z}_{(t)} \mathbf{A}_{(t)}^* \mathbf{Z}_{(t)}^T + \mathbf{D}_{(t+1)}$$

where  $\mathbf{D}_{(t+1)}$  is diagonal with elements equal to  $1/2$ . This differs from  $\mathbf{A}$  where the diagonal terms are further scaled by  $(1-\bar{F})$ , where  $\bar{F}$  is the average inbreeding of the parents (Thompson, 1977).  $\mathbf{Z}_{(t)}$  is the matrix identifying parents of cohort (t+1) whose elements are either 1/2 (parents) or 0 (otherwise).

The constraint that controls  $\Delta F$  in the algorithm of Meuwissen is related to  $\mathbf{x}^T \mathbf{A} \mathbf{x} / 2$  and this is constrained to be  $t\Delta F$ , which increments by  $\Delta F$  per generation. When  $\mathbf{A}^*$  is substituted for  $\mathbf{A}$  the annual increment in the constraint ( $\Delta C$ ) is set to  $\Delta F(1-3\Delta F+12(\Delta F)^2)$ ; this is  $\approx \Delta F$  for small values but is marginally greater for larger  $\Delta F$ , due to second order effects.

The total number of parents each generation was recorded along with the 'effective' number of each sex ( $N$ ) derived from  $4\mathbf{x}^T \mathbf{x}$ . For each replicate using  $\mathbf{A}^*$ , the long-term contributions ( $\mathbf{r}$ ) were calculated for individuals in generation 15, defined as the proportion of genes in generation 20 that derived from that ancestor. The regression of  $r_i$  on  $x_i$  was calculated for each replicate using only those individuals for which  $x_i > 0$ . In addition,  $\mathbf{r}^T \mathbf{r}$ ,  $\mathbf{x}^T \mathbf{x}$  and their ratio were calculated for ancestors in generation 15.

The schemes were run for a range of  $h^2$  (0.01, 0.25 and 0.99) and constraints on  $\Delta F$  (0.006, 0.025 and 0.050).

## RESULTS

**Comparison of using  $\mathbf{A}$  or  $\mathbf{A}^*$ .** Rates of inbreeding and response are reported in Table 1 for  $h^2=0.25$  and desired  $\Delta F=0.025$ .  $\Delta F$  and  $\mathbf{r}^T \mathbf{r}$  are maintained at their predefined levels throughout the period of selection with  $\mathbf{A}^*$  and the modified constraint but not with the standard  $\mathbf{A}$ . The numbers selected are also constant with  $\mathbf{A}^*$  but they decline over time when  $\mathbf{A}$  is used, resulting in a steady increase in  $\Delta F$ . Despite the breaking of the constraint for  $\Delta F$  using  $\mathbf{A}$ , there is little difference in  $\Delta G$  achieved.

**Relationship of  $\mathbf{r}$  with  $\mathbf{x}$ .** The regression of the long-term contributions in generation 15 on the original mating proportions are reported in Table 2 for three values of desired  $\Delta F$  and a

range of heritabilities. With a heritability close to unity the regression of  $r_i$  on  $x_i$  is approximately 1 for the values chosen. As heritability decreases so the regression coefficients became smaller.

**Table 1.** Rates of genetic gain ( $\Delta G$ , phenotypic standard deviation units) from generation  $t-1$  to  $t$ , rates of inbreeding ( $\Delta F$ ), sum of squared contributions and the effective numbers of parents of each sex ( $N$ ) at generation  $t$  when using the standard A or the augmented A in the objective function. The increment in the average coancestry was constrained to 0.025 per generation.

t	Standard A				Augmented A			
	$\Delta G$	$\Delta F$	$r^T r / 4$	N	$\Delta G$	$\Delta F$	$r^T r / 4$	N
1	0	0	0.023	10.1	0	0	0.021	10.9
4	0.322	0.025	0.025	8.8	0.303	0.023	0.023	9.7
8	0.293	0.027	0.028	7.8	0.293	0.026	0.023	9.6
12	0.274	0.034	0.032	7.5	0.256	0.025	0.023	9.6
16	0.266	0.038	0.037	6.9	0.255	0.024	0.023	9.9
20	0.223	0.040	-	5.9	0.221	0.025	-	9.6

Average of 100 replicates, standard errors were 0.011 for  $\Delta G$ , 0.001 for  $\Delta F$  and 0.2 for N.

**Table 2.** The regression coefficient of long term contributions on mating proportions for three values of the desired  $\Delta F$  and a range of heritabilities ( $h^2$ ).

$h^2$	$\Delta F$		
	0.05	0.025	0.00625
0.01	0.93	0.96	0.98
0.25	0.94	0.97	0.98
0.99	1.05	1.04	1.02

Average over 100 replicates, standard errors ranged between 0.01 and 0.05.

**Relationship of  $r^T r$  with  $x^T x$ .** The ratio of  $r^T r$  to  $x^T x$  is presented in Table 3. The ratio varies with the heritability and  $\Delta F$ . As heritability tends to 1, and as the restriction on  $\Delta F$  becomes more severe, the ratio tends to 1.

## DISCUSSION

**Augmentation of A.** Rates of inbreeding are determined by controlling the convergence of the contributions of ancestors before fixation. Therefore each generation or cohort is as important as the next, since each serves as a base for controlling inbreeding in the course of its own convergence. In the standard A, the weighting of cohorts is unequal since the contributions of later cohorts are down-weighted by  $(1 - \bar{F})$ . As a result, in the absence of continuous modification to the increment applied to the constraint, the  $r^T r$  of later cohorts are

allowed to inflate, thereby increasing  $\Delta F$  (as observed in Meuwissen, 1997). Removal of  $(1 - \bar{F})$  in  $\mathbf{A}^*$  completely removes this problem.

**Table 3. The rate of inbreeding ( $\Delta F$ ) and, the sum of squared contributions and their ratio to the sum of squared mating proportions for a range of heritabilities.**

$\Delta F$	$\mathbf{r}^T \mathbf{r} / 4$	$h^2$		
		0.01 $\mathbf{r}^T \mathbf{r} / \mathbf{x}^T \mathbf{x}$	0.25 $\mathbf{r}^T \mathbf{r} / \mathbf{x}^T \mathbf{x}$	0.99 $\mathbf{r}^T \mathbf{r} / \mathbf{x}^T \mathbf{x}$
0.0063	0.0063	1.41	1.35	1.19
0.0250	0.0233	1.89	1.72	1.27
0.0500	0.0440	2.33	1.92	1.30

Average of a 100 replicates, standard errors were less than 0.0002 for  $\mathbf{r}^T \mathbf{r} / 4$ .

**Relationship of  $\mathbf{r}^T \mathbf{r}$  with  $\mathbf{x}^T \mathbf{x}$ .** The results of Woolliams and Thompson (1994) give the form of the ideal solution to maximising genetic gain with constrained inbreeding rates. However they speculated that this ideal was perhaps only achievable when  $h^2=1$ , since in that case it might be feasible to achieve the ideal genetic contributions (in relation to the Mendelian sampling term) in a single step for each cohort in turn. In this situation  $\mathbf{x}=\mathbf{r}$  and then  $\mathbf{x}^T \mathbf{x}=\mathbf{r}^T \mathbf{r}$ . If it required several steps then it seemed unlikely to be achievable since the simultaneous optimisation of several cohorts seemed a less tractable problem. The results of this study show that using the current approach, this ideal appears unattainable, except in the special case of the extreme lower bound for  $\Delta F$  in a population (0.0025 in this example) in which each parent is required to be replaced by two offspring (results not shown). The results shown by Meuwissen (1997) tend to obscure this point, since the apparent close relationship between  $\mathbf{x}^T \mathbf{x}$  and  $\mathbf{r}^T \mathbf{r}$  arises from the bias produced by using  $\mathbf{A}$  and, consequently, failing to constrain  $\Delta F$  to be constant over multiple generations.

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