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The use of mathematical programming to control inbreeding in selection schemes

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Introduction

Selection on the best estimate of the breeding value of individuals should, in large populations, provide the maximal response in breeding value. However, many breeders deal with the selection of small numbers of animals from relatively small populations and therefore there is a trend for inbreeding to rise because of genetic drift. Moreover, as the evaluation of candidates is traditionally based on methodologies including information from relatives [selection indices, best linear unbiased predictor (BLUP)] more individuals are selected from the best families and so closely related individuals will generate most of the offspring. This effect is more important for traits with low heritability as phenotype gives little information on the breeding value of the individuals and more weight is given to relatives' data.

The need for controlling inbreeding refers not only to a better use of the genetic variability available and to a reduced inbreeding depression in the selected trait, but also to a reduced depression of fitness-related traits, which may be the most serious drawback at present due to the increase in inbreeding in domestic populations (MEUWISSEN and WOOLLIAMS 1994).

In recent years considerable work has been carried out on the design of strategies to maintain genetic diversity in selection programmes. These strategies are aimed at simultaneously optimizing genetic gain and inbreeding, either by reducing the rate of inbreeding (or variance of response) while keeping genetic gains at a predetermined level, or by increasing selection response under a restriction on inbreeding (or on variance of response). Following TORO and PÉREZ-ENCISO (1990) the different strategies can be classified according to the factor on which they act: (i) the selection criterion used; (ii) the mating system imposed; (iii) the number of selected individuals and their contribution to the next generation.

The first group of strategies proposes the use of a suboptimal selection criterion that reduces the weight given to family information or the use of an upward-biased heritability in BLUP evaluation (TORO and PÉREZ-ENCISO 1990; see GRUNDY et al. 1998a for the latest development of this idea). The second group of strategies proposes action on the mating system including factorial mating designs, minimum co-ancestry mating (using linear programming) or compensatory mating (see review by CABALLERO et al. 1996).

The third group of strategies includes the ones considered in the present work. The first possibility is to modify the contribution of the selected individuals of generation t to the selected individuals of generation $t + 1$, by practising some form of within-family selection with respect to BLUP values. Two strategies of this type were considered: modified within-family selection (MWFS) and restricted co-ancestry selection (RCS). The second possibility is to modify the contribution of the selected individuals of generation t to the evaluated individuals of generation $t + 1$ (instead of to the selected individuals) by a strategy called *weighted selection* (TORO and NIETO 1984). Three strategies were considered in this case: weighted selection (WS), restricted co-ancestry weighted selection (RCWS) and pair weigh-

ted selection (PWS). More specifically, the aim of the present paper is to show how these five strategies can be implemented using mathematical programming techniques. A small example comparing all of these strategies with standard truncation selection (TS) is also given for illustration.

Methods

Strategies analysed

(a) Truncation selection

As a reference case, traditional truncation selection (TS) was practised by ranking the individuals of each sex by their expected breeding values (EBV) and then taking the best s sires and the best d dams. Each selected male of generation t was mated to d/s females and each selected female contributed $N/2d$ sons and $N/2d$ daughters (being N the total number of evaluated individuals, half of each sex, in any generation) to the individuals to be evaluated in generation $t + 1$.

(b) Modified within-family selection

Classical within-family selection is known to result in the lowest variance of family size whereas with family selection the variance of family size will be maximum. However, as pointed out by TORO and PÉREZ-ENCISO (1990), there is a wide range of intermediate selection methods, which differ in the magnitude of the variance of family sizes. If, for example, only full-sib families were considered, then all possible distributions of family sizes are equivalent to all possible forms of arranging marbles (the selected individuals) among boxes (families), each of fixed capacity (maximum family size). With different number of selected sires (s) and dams (d) the effective population size (N_e) of all possible distributions of family sizes will be given by the HILL (1979) formula

$$\frac{1}{N_e} = \frac{1}{16s} \left(\frac{1}{\mu_{ss}} + \frac{1}{\mu_{sd}} + \frac{S_{ss}^2}{\mu_{ss}^2} + \frac{2S_{ss,sd}}{\mu_{ss}\mu_{sd}} + \frac{S_{sd}^2}{\mu_{sd}^2} \right) + \frac{1}{16d} \left(\frac{1}{\mu_{dd}} + \frac{1}{\mu_{ds}} + \frac{S_{dd}^2}{\mu_{dd}^2} + \frac{2S_{dd,ds}}{\mu_{dd}\mu_{ds}} + \frac{S_{ds}^2}{\mu_{ds}^2} \right) \quad (1)$$

where μ_{ss} , μ_{sd} , μ_{dd} , μ_{ds} are the average number of males produced by each selected sire, the average number of females from each selected sire, the average number of females from each selected dam and the average number of males from each selected dam, respectively. The terms S_{ss}^2 , $S_{ss,sd}$, S_{sd}^2 , S_{dd}^2 , $S_{dd,ds}$, S_{ds}^2 are the corresponding variances and covariances.

TORO and PÉREZ-ENCISO (1990) show that, compared with optimal unrestricted selection, some of the distributions of family sizes would lead to an important reduction of inbreeding together with only a small reduction of response.

(c) Restricted co-ancestry selection

MWFS strategy assumes that families are unrelated and that the only possible genetic relationship among individuals is to be unrelated, full-sibs or half-sibs, and also ignores the possibility that some of the individuals could be inbred. A natural extension of the method would be to estimate effective population size as $1/(2\Delta\bar{f})$ where $\Delta\bar{f}$ is the rate of increase of the average co-ancestry between the selected individuals calculated as

$$\bar{f} = \frac{1}{4}\bar{f}_s + \frac{1}{2}\bar{f}_{s,d} + \frac{1}{4}\bar{f}_d \quad (2)$$

with \bar{f}_s , $\bar{f}_{s,d}$ and \bar{f}_d being the mean co-ancestry between sires, between sires and dams and between dams. So the largest effective population size will be attained by minimizing \bar{f} in the selected individuals.

This strategy was proposed by BRISBANE and GIBSON (1995a, b) in the context of animal breeding and by LACY (1994) and BALLOU and LACY (1995) in the context of conservation programmes.

(d) *Weighted selection*

In the previous strategies action is directed to modifying the family distribution of selected individuals but, afterwards, the contribution of the selected individuals of generation t to the individuals to be evaluated in generation $t + 1$ is fixed. If this is not the case and it is possible to modify the contribution of the selected individuals to the individuals to be evaluated in generation $t + 1$, a new strategy, called weighted selection (TORO and NIETO 1984; LINDGREN 1991), can be implemented. With unequal contributions a larger number of individuals may be selected, but with each individual making a contribution to the next generation that is proportional to its breeding value in such a way that the selection differential is maintained but the expected inbreeding is minimized. The advantages of weighted selection have been previously shown both in simulation (TORO et al. 1988) and in experiments with *Drosophila* (NIETO et al. 1986).

(e) *Pair weighted selection*

As an extension of the scheme presented in section (d) the following strategy (TORO et al. 1988) could be implemented. If the pairs of sire and dam that will be mate are previously decided, specific contributions for each couple can be found, by mathematical programming, as to maximize the effective population size.

(f) *Restricted co-ancestry weighted selection*

A limitation of weighted selection, as originally proposed, is that it does not take into account the fact that, after the first generation, the selected animals became genetically related. WRAY and GODDARD (1994) and MEUWISSEN (1997) proposed to take account of co-ancestry among selected individuals weighted by their contribution to the population to be evaluated in the next generation. MEUWISSEN (1997) proposed breeding programmes based on the maximization of the function:

$$H_t = c'_t EBV_t - \lambda_0 (c'_t A_t c_t - 2\bar{C}_{t+1}) - (c'_t Q - 1/2) \lambda \quad (3)$$

In this expression c_t is the vector of individuals' contributions, EBV_t the estimated breeding values from a BLUP evaluation, A_t the additive relationship matrix, Q a two column matrix with zeros and ones to denote the sex of the individual, $1/2$ a vector of halves to denote that males contribution is the same as females contribution so the following equation holds

$$Q' c_t = 1/2 \quad (4)$$

and \bar{C}_{t+1} is the inbreeding level allowed in the next generation, which is related to the A matrix (and so with parents' co-ancestry) by the expression

$$\bar{C}_{t+1} = \frac{c'_t A_t c_t}{2} \quad (5)$$

Once this level is established λ_0 (representing the importance of inbreeding control) can be calculated by derivation (further explanations in MEUWISSEN 1997 and GRUNDY et al. 1998b).

Implementation by mathematical optimization

The compromise solution between the two opposed parameters of selection, response and inbreeding (or N_e), can be accomplished using different approaches: maximizing response with a restriction on the maximum allowed level of inbreeding in next generation, minimizing inbreeding imposing a minimum level of response or including both terms into the objective function. To test if the same solutions are obtained through the three approaches all of them have been applied in some of the studied cases.

(a) Truncation selection

No special algorithms are required except one to sort individuals by their estimated breeding values.

(b) Modified within-family selection

Effective population size (N_e) as a function of family sizes is indicated in eqn (1). Operating in this formula the following expression can be reached

$$\frac{1}{N_e} = \frac{1}{16s^2} \left(\frac{s}{\mu_{ss}} + \frac{s}{\mu_{sd}} - 4s + \frac{\sum_{i=1}^s x_{ss,i}^2}{\mu_{ss}^2} + \frac{2 \sum_{i=1}^s x_{ss,i} x_{sd,i}}{\mu_{ss} \mu_{sd}} + \frac{\sum_{i=1}^s x_{sd,i}^2}{\mu_{sd}^2} \right) + \frac{1}{16d^2} \left(\frac{d}{\mu_{dd}} + \frac{d}{\mu_{ds}} - 4d + \frac{\sum_{i=1}^d x_{dd,i}^2}{\mu_{dd}^2} + \frac{2 \sum_{i=1}^d x_{dd,i} x_{ds,i}}{\mu_{dd} \mu_{ds}} + \frac{\sum_{i=1}^d x_{ds,i}^2}{\mu_{ds}^2} \right) \quad (6)$$

where $x_{ss,i}$ and $x_{sd,i}$ are, respectively, the number of males and females produced by sire i and $x_{ds,i}$ and $x_{dd,i}$ the same for dams. The above expression depends on the sums of the squared number of sires and dams selected from each male and female family and the products of such quantities. Minimizing the variable part of this formula will maximize N_e .

The natural way to optimize within-family selection would be by building a quadratic program to maximize N_e with a restriction about the minimum expected response to achieve. Being \overline{EBV}_{t+1} the minimum expected mean EBV of next generation (assuming additivity), that restriction would have the following expression

$$\sum_{i=1}^d (x_{ds,i} + x_{dd,i}) \cdot \bar{m}_{x_{ds,i}, x_{dd,i}} \geq \overline{EBV}_{t+1} \quad (7)$$

where $\bar{m}_{x_{ds,i}, x_{dd,i}}$ is the average of the EBVs of the best $x_{ds,i}$ males and the best $x_{dd,i}$ females selected from the i th female family weighted by the mating ratio. Usually less sires than dams are selected and thus the weight on sires will be d/s and the sum of weights through all selected individuals equals $2d$. But $\bar{m}_{x_{ds,i}, x_{dd,i}}$ changes as decision variables change and therefore mathematical programming is not possible.

To avoid this problem another strategy can be applied. Let x_{ijk} be a dichotomic variable (0, 1) which takes the value 1 if, in female family i , j sires and k dams have been selected and it takes value 0 otherwise; y_{ijk} indicates the same for male families. To reach a structure similar to truncation selection a limit in the number of males to choose from every sire family ss is to be imposed; the same for females from sire families (sd), males from dam families (ds) and females from dam families (dd). This way the final linear program will look like this

minimize

$$\frac{1}{16s^2} \left[\sum_{i=1}^s \sum_{j=0}^{ss} \sum_{k=0}^{sd} y_{ijk} \left(\frac{j^2}{\mu_{ss}^2} + \frac{2jk}{\mu_{ss}\mu_{sd}} + \frac{k^2}{\mu_{sd}^2} \right) \right] + \frac{1}{16d^2} \left[\sum_{i=1}^d \sum_{j=0}^{ds} \sum_{k=0}^{dd} x_{ijk} \left(\frac{j^2}{\mu_{ds}^2} + \frac{2jk}{\mu_{dd}\mu_{ds}} + \frac{k^2}{\mu_{dd}^2} \right) \right]$$

such that

$$\sum_{i=1}^d \sum_{j=0}^{ds} \sum_{k=0}^{dd} x_{ijk} \cdot \bar{m}_{ijk} \geq \overline{EBV}_{t+1} \tag{8}$$

$$\begin{array}{l} \text{UNIX1} \\ \vdots \\ \text{UNIX}d \end{array} \left\{ \begin{array}{l} \sum_{j=0}^{ds} \sum_{k=0}^{dd} x_{1jk} = 1 \\ \vdots \\ \sum_{j=0}^{ds} \sum_{k=0}^{dd} x_{djk} = 1 \end{array} \right. \quad \begin{array}{l} \text{UNIY1} \\ \vdots \\ \text{UNIY}s \end{array} \left\{ \begin{array}{l} \sum_{j=0}^{ss} \sum_{k=0}^{sd} y_{1jk} = 1 \\ \vdots \\ \sum_{j=0}^{ss} \sum_{k=0}^{sd} y_{sjk} = 1 \end{array} \right.$$

$$\text{TOTXM} \quad \sum_{i=1}^d \sum_{j=0}^{ds} \sum_{k=0}^{dd} x_{ijk} \cdot j = s \quad \text{TOTYM} \quad \sum_{i=1}^s \sum_{j=0}^{ss} \sum_{k=0}^{sd} y_{ijk} \cdot j = s$$

$$\text{TOTXF} \quad \sum_{i=1}^d \sum_{j=0}^{ds} \sum_{k=0}^{dd} x_{ijk} \cdot k = d \quad \text{TOTYF} \quad \sum_{i=1}^s \sum_{j=0}^{ss} \sum_{k=0}^{sd} y_{ijk} \cdot k = d$$

$$\begin{array}{l} \text{IGM1} \\ \vdots \\ \text{IGMs} \end{array} \left\{ \begin{array}{l} \sum_{j=0}^{ss} \sum_{k=0}^{sd} y_{1jk} \cdot j - \sum_{i=1}^{d/s} \sum_{j=0}^{ds} \sum_{k=0}^{dd} x_{ijk} \cdot j = 0 \\ \vdots \\ \sum_{j=0}^{ss} \sum_{k=0}^{sd} y_{sjk} \cdot j - \sum_{i=d+1-d/s}^d \sum_{j=0}^{ds} \sum_{k=0}^{dd} x_{ijk} \cdot j = 0 \end{array} \right.$$

$$\begin{array}{l} \text{IGF1} \\ \vdots \\ \text{IGFs} \end{array} \left\{ \begin{array}{l} \sum_{j=0}^{ss} \sum_{k=0}^{sd} y_{1jk} \cdot k - \sum_{i=1}^{d/s} \sum_{j=0}^{ds} \sum_{k=0}^{dd} x_{ijk} \cdot k = 0 \\ \vdots \\ \sum_{j=0}^{ss} \sum_{k=0}^{sd} y_{sjk} \cdot k - \sum_{i=d+1-d/s}^d \sum_{j=0}^{ds} \sum_{k=0}^{dd} x_{ijk} \cdot k = 0 \end{array} \right.$$

$$\begin{array}{llll} 0 \leq x_{ijk} \leq 1 & i = 1, \dots, d & j = 0, \dots, ds & k = 0, \dots, dd \\ x_{ijk} \text{ integer} & i = 1, \dots, d & j = 0, \dots, ds & k = 0, \dots, dd \\ 0 \leq y_{ijk} \leq 1 & i = 1, \dots, s & j = 0, \dots, ss & k = 0, \dots, sd \\ y_{ijk} \text{ integer} & i = 1, \dots, s & j = 0, \dots, ss & k = 0, \dots, sd \end{array}$$

In this form \bar{m}_{ijk} does not depend on the value of the decision variable and is equal to the weighted average of EBVs of the best k females and j males of the i th female family. Restrictions labelled UNIXx control that just one solution per family is found and the ones called TOTxx ensure a total of s males and d females to be selected. The last two groups of

restrictions (IGMx and IGFx) make a male family contribute the same individuals as the d/s associated female families.

(c) *Restricted co-ancestry selection*

To maximize the response limiting the overall co-ancestry of the selected individuals (including reciprocals and self-co-ancestries) a quadratic scheme would be ideal. Let the first $N/2$ individuals be the evaluated sires and the rest the evaluated dams, s the number of sires to select, d the number of dams to select, x_i a variable to denote if individual i is selected (1) or not (0) and EBV_i the EBV of that individual. Therefore the program would be

minimize

$$\frac{1}{4} \sum_{i=1}^{N/2} \sum_{j=1}^{N/2} \frac{x_i x_j f_{ij}}{s^2} + \frac{1}{2} \sum_{i=1}^{N/2} \sum_{j=N/2+1}^N \frac{x_i x_j f_{ij}}{s \cdot d} + \frac{1}{4} \sum_{i=N/2+1}^N \sum_{j=N/2+1}^N \frac{x_i x_j f_{ij}}{d^2}$$

such that

$$\frac{d/s}{2d} \sum_{i=1}^{N/2} EBV_i x_i + \frac{1}{2d} \sum_{i=N/2+1}^N EBV_i x_i \geq \overline{EBV}_{t+1} \quad (9)$$

$$\sum_{i=1}^{N/2} x_i = s$$

$$\sum_{i=N/2+1}^N x_i = d$$

$$0 \leq x_i \leq 1 \quad i = 1, \dots, N$$

$$x_i \text{ integer} \quad i = 1, \dots, N$$

Integer quadratic programming is not common in commercial computer programs, but there is an easy way of transforming the problem into an integer linear program. As there are only two possibilities for an individual (to be chosen or not), $N \times N$ auxiliary z_{ij} (0, 1) variables (one for each pair of evaluated individuals, including an individual with itself) can be added. $z_{ij} = 1$ if individuals i and j have been both selected and so their co-ancestry has to be taken into account and $z_{ij} = 0$ if one or both of them are unselected. The matrix of auxiliary variables is symmetric so advantage of it can be taken to simplify the problem. With the required constraints the linear program looks like this

minimize

$$\frac{1}{4s^2} \sum_{i=1}^{N/2} \left(z_{ii} f_{ii} + 2 \sum_{j=i+1}^{N/2} z_{ij} f_{ij} \right) + \frac{1}{2s \cdot d} \sum_{i=1}^{N/2} \sum_{j=N/2+1}^N z_{ij} f_{ij} + \frac{1}{4d^2} \sum_{i=N/2+1}^N \left(z_{ii} f_{ii} + 2 \sum_{j=i+1}^{N/2} z_{ij} f_{ij} \right)$$

such that

$$\frac{d/s}{2d} \sum_{i=1}^{N/2} EBV_i x_i + \frac{1}{2d} \sum_{i=N/2+1}^N EBV_i x_i \geq \overline{EBV}_{t+1}$$

$$\sum_{i=1}^{N/2} x_i = s$$

$$\sum_{i=N/2+1}^N x_i = d$$

$$\sum_{i=1}^N \left(z_{ii} + 2 \sum_{j=i+1}^N z_{ij} \right) = (s + d)^2 \tag{10}$$

$$\left. \begin{array}{l} \text{COANC1} \\ \vdots \\ \text{COANCEN} \end{array} \right\} \begin{cases} \sum_{i=1}^1 z_{i1} + \sum_{i=2}^N z_{1i} - (s + d)x_1 = 0 \\ \sum_{i=1}^2 z_{i2} + \sum_{i=3}^N z_{2i} - (s + d)x_2 = 0 \\ \vdots \\ \sum_{i=1}^N z_{iN} - (s + d)x_N = 0 \end{cases}$$

$$\begin{array}{lll} 0 \leq z_{ij} \leq 1 & i = 1, \dots, N & j = 1, \dots, N \\ z_{ij} \text{ integer} & i = 1, \dots, N & j = 1, \dots, N \\ 0 \leq x_i \leq 1 & i = 1, \dots, N & \\ x_i \text{ integer} & i = 1, \dots, N & \end{array}$$

Restrictions in brackets (COANCx) are needed to ensure that no co-ancestries, for a nonselected individual, or co-ancestry with all (s + d) selected individuals, for a selected one, are to be taken into account.

If an approach combining response and inbreeding in the objective function, multiplying the latter by a negative factor, is desired, with the same restrictions explained above, the objective function would look like the following

maximize

$$\begin{aligned} \frac{d/s}{2d} \sum_{i=1}^{N/2} EBV_i x_i + \frac{1}{2d} \sum_{i=N/2+1}^N EBV_i x_i - \lambda \left[\frac{1}{4s^2} \sum_{i=1}^{N/2} \left(z_{ii} f_{ii} + 2 \sum_{j=i+1}^{N/2} z_{ij} f_{ij} \right) + \right. \\ \left. + \frac{1}{2s \cdot d} \sum_{i=1}^{N/2} \sum_{j=N/2+1}^N z_{ij} f_{ij} + \frac{1}{4d^2} \sum_{i=N/2+1}^N \left(z_{ii} f_{ii} + 2 \sum_{j=i+1}^{N/2} z_{ij} f_{ij} \right) \right] \tag{11} \end{aligned}$$

As indicated previously, if families are assumed to be unrelated and only full-and half-sib co-ancestries within families are considered and co-ancestry of an individual with itself is not taken into account, the scheme is equivalent to the one controlling the family size variance explained in section (b).

(d) Weighted selection

If a variable contribution of the selected males and females of generation *t* to the evaluated individuals at generation *t* + 1 is considered the parameter calculated from using eqn (7) is not *N_s*, as the number of selected individuals is not fixed and therefore the number of evaluated individuals is to be used in the formula denoted as *M_e*. Considering that all individuals evaluated at generation *t* could potentially contribute *x_i* sons and *y_i* daughters to the evaluated individuals of the next generation, all the means that appear in eqn (7) will be equal to one. Selection will be implicitly incorporated because some or most of the contributions will be zero. If the number of evaluated males and females is the same, squares and cross products can be expressed with a binomial and minimizing *M_e* will be equivalent to minimizing $\sum_{i=1}^N (x_i + y_i)^2$ where *x_i* is the number of sons individual *i* contributes to the next

generation and y_i the same for daughters. Therefore the program, with EBV_i meaning as above, would be

minimize

$$\sum_{i=1}^N (x_i + y_i)^2$$

such that

$$\sum_{i=1}^N (x_i + y_i) \cdot EBV_i \geq 2N \cdot \overline{EBV}_{t+1}$$

$$\text{SUMT} \quad \sum_{i=1}^N (x_i + y_i) = 2N$$

$$\text{SUMM} \quad \sum_{i=1}^{N/2} (x_i + y_i) = N$$

$$\text{SUMO} \quad \sum_{i=1}^N x_i = N$$

$$\text{SUMOM} \quad \sum_{i=1}^{N/2} x_i = \frac{N}{2} \quad (12)$$

$$\begin{aligned} 0 \leq x_i \leq ss & \quad i = 1, \dots, N/2 \\ 0 \leq x_i \leq ds & \quad i = (N/2) + 1, \dots, N \\ x_i \text{ integer} & \quad i = 1, \dots, N \\ 0 \leq y_i \leq sd & \quad i = 1, \dots, N/2 \\ 0 \leq y_i \leq dd & \quad i = (N/2) + 1, \dots, N \\ y_i \text{ integer} & \quad i = 1, \dots, N \end{aligned}$$

N is the total number of evaluated individuals in generation t where the first $N/2$ are sires and the rest are dams as in the previous scheme. The bounds on the decision variables allow a male to leave a maximum of ss sons and sd daughters and a female to leave no more than ds and dd individuals of each sex.

To avoid quadratic programming a similar approach as the one in previous sections could be used. Let x_{ijk} be a variable equal to 1 if individual i will contribute j sons and k daughters to the evaluated individuals of the next generation and 0 otherwise. The linear program is shown below

minimize

$$\sum_{i=1}^{N/2} \sum_{j=0}^{ss} \sum_{k=0}^{sd} x_{ijk} (j+k)^2 + \sum_{i=N/2+1}^N \sum_{j=0}^{ds} \sum_{k=0}^{dd} x_{ijk} (j+k)^2$$

such that

$$\sum_{i=1}^{N/2} \sum_{j=0}^{ss} \sum_{k=0}^{sd} x_{ijk} (j+k) \cdot EBV_i + \sum_{i=N/2+1}^N \sum_{j=0}^{ds} \sum_{k=0}^{dd} x_{ijk} (j+k) \cdot EBV_i \geq 2N \cdot \overline{EBV}_{t+1}$$

$$\text{SUMT} \quad \sum_{i=1}^{N/2} \sum_{j=0}^{ss} \sum_{k=0}^{sd} x_{ijk} (j+k) + \sum_{i=N/2+1}^N \sum_{j=0}^{ds} \sum_{k=0}^{dd} x_{ijk} (j+k) = 2N$$

$$\text{SUMM} \quad \sum_{i=1}^{N/2} \sum_{j=0}^{ss} \sum_{k=0}^{sd} x_{ijk} (j+k) = N$$

$$\text{SUMO} \quad \sum_{i=1}^{N/2} \sum_{j=0}^{ss} \sum_{k=0}^{sd} x_{ijk} j + \sum_{i=N/2+1}^N \sum_{j=0}^{ds} \sum_{k=0}^{dd} x_{ijk} j = N$$

$$\text{SUMOM} \quad \sum_{i=1}^{N/2} \sum_{j=0}^{ss} \sum_{k=0}^{sd} x_{ijk} j = \frac{N}{2}$$

$$\text{UNIXn} \quad \left\{ \begin{array}{l} \sum_{j=0}^{ss} \sum_{k=0}^{sd} x_{1jk} = 1 \\ \vdots \\ \sum_{j=0}^{ss} \sum_{k=0}^{sd} x_{N/2jk} = 1 \end{array} \right. \quad \left\{ \begin{array}{l} \sum_{j=0}^{ds} \sum_{k=0}^{dd} x_{(N/2+1)jk} = 1 \\ \vdots \\ \sum_{j=0}^{ds} \sum_{k=0}^{dd} x_{Njk} + 1 \end{array} \right. \quad (13)$$

$$\begin{array}{llll} 0 \leq x_{ijk} \leq 1 & i = 1, \dots, N/2 & j = 0, \dots, ss & k = 0, \dots, sd \\ x_{ijk} \text{ integer} & i = 1, \dots, N/2 & j = 0, \dots, ss & k = 0, \dots, sd \end{array}$$

$$\begin{array}{llll} 0 \leq x_{ijk} \leq 1 & i = (N/2) + 1, \dots, N & j = 0, \dots, ds & k = 0, \dots, dd \\ x_{ijk} \text{ integer} & i = (N/2) + 1, \dots, N & j = 0, \dots, ds & k = 0, \dots, dd \end{array}$$

In the restriction controlling expected gain, EBV_i is the EBV of the individual i and $EB\bar{V}_{t+1}$ the expected level of the trait in next generation. SUMT makes the total number of offspring to be $2N$, SUMM the offspring from sires to be N , SUMO the males offspring to be N and SUMOM the males offspring from sires to be $N/2$. Restrictions labelled UNIXn control that just one solution per animal exists. Maximum contributions per selected male and female were the same as determined before.

(e) Pair weighted selection

To simulate this strategy the following procedure was used. Once sorted by their EBV the best s sires and the best d dams are taken as in truncation selection. Another s sires and d dams are selected too and mated within each of the defined groups. Two different schemes were simulated: to mate individuals at random or to perform mating with the minimum global co-ancestry (assignment problem solved with the *Hungarian algorithm*; DANTZIG 1963). Then the optimum contribution of each couple can be found through quadratic or linear programming. The scheme is somehow similar to section (b) using a parallel expression for the objective function with x 's referring to all dams considered and y 's to the sires involved in the mating. In the restriction on the minimum response to achieve the EBV of every possible parent appears, weighted by its contribution.

minimize

$$\frac{1}{16(2s)^2} \left[\sum_{i=1}^{2s} \sum_{j=0}^{ss} \sum_{k=0}^{sd} y_{ijk} \left(\frac{j^2}{\mu_{mm}^2} + \frac{2jk}{\mu_{mm}\mu_{mf}} + \frac{k^2}{\mu_{mf}^2} \right) \right] + \frac{1}{16(2d)^2} \left[\sum_{i=1}^{2d} \sum_{j=0}^{ds} \sum_{k=0}^{dd} x_{ijk} \left(\frac{j^2}{\mu_{ds}^2} + \frac{2jk}{\mu_{dd}\mu_{ds}} + \frac{k^2}{\mu_{dd}^2} \right) \right]$$

such that

$$\sum_{i=1}^{2d} \sum_{j=0}^{ds} \sum_{k=0}^{dd} x_{ijk} \cdot (j+k) \cdot EBV_i + \sum_{i=1}^{2s} \sum_{j=0}^{ss} \sum_{k=0}^{sd} y_{ijk} \cdot (j+k) \cdot EBV_i \geq 2N \cdot \overline{EBV}_{t+1}$$

$$\begin{array}{ll} \text{UNIX1} & \left\{ \begin{array}{l} \sum_{j=0}^{ds} \sum_{k=0}^{dd} x_{1jk} = 1 \\ \vdots \\ \sum_{j=0}^{ds} \sum_{k=0}^{dd} x_{(2d)jk} = 1 \end{array} \right. & \text{UNIY1} & \left\{ \begin{array}{l} \sum_{j=0}^{ss} \sum_{k=0}^{sd} y_{1jk} = 1 \\ \vdots \\ \sum_{j=0}^{ss} \sum_{k=0}^{sd} y_{(2s)jk} = 1 \end{array} \right. & (14) \\ \vdots & & \vdots & \\ \text{UNIX}(2d) & & \text{UNIY}(2s) & \\ \text{TOTYM} & \sum_{i=1}^{2d} \sum_{j=0}^{ds} \sum_{k=0}^{dd} x_{ijk} \cdot j = \frac{N}{2} & \text{TOTYM} & \sum_{i=1}^{2s} \sum_{j=0}^{ss} \sum_{k=0}^{sd} y_{ijk} \cdot j = \frac{N}{2} \\ \text{TOTXF} & \sum_{i=1}^{2d} \sum_{j=0}^{ds} \sum_{k=0}^{dd} x_{ijk} \cdot k = \frac{N}{2} & \text{TOTYF} & \sum_{i=1}^{2s} \sum_{j=0}^{ss} \sum_{k=0}^{sd} y_{ijk} \cdot k = \frac{N}{2} \end{array}$$

$$\begin{array}{l} \text{IGM1} \\ \vdots \\ \text{IGM}(2s) \end{array} \left\{ \begin{array}{l} \sum_{j=0}^{ss} \sum_{k=0}^{sd} y_{1jk} \cdot j - \sum_{i=1}^{d/s} \sum_{j=0}^{ds} \sum_{k=0}^{dd} x_{ijk} \cdot j = 0 \\ \vdots \\ \sum_{j=0}^{ss} \sum_{k=0}^{sd} y_{(2s)jk} \cdot j - \sum_{i=2d+1-d/s}^{2d} \sum_{j=0}^{ds} \sum_{k=0}^{dd} x_{ijk} \cdot j = 0 \end{array} \right.$$

$$\begin{array}{l} \text{IGF1} \\ \vdots \\ \text{IGF}(2s) \end{array} \left\{ \begin{array}{l} \sum_{j=0}^{ss} \sum_{k=0}^{sd} y_{1jk} \cdot k - \sum_{i=1}^{d/s} \sum_{j=0}^{ds} \sum_{k=0}^{dd} x_{ijk} \cdot k = 0 \\ \vdots \\ \sum_{j=0}^{ss} \sum_{k=0}^{sd} y_{8jk} \cdot k - \sum_{i=2d+1-d/s}^{2d} \sum_{j=0}^{ds} \sum_{k=0}^{dd} x_{ijk} \cdot k = 0 \end{array} \right.$$

$$\begin{array}{llll} 0 \leq x_{ijk} \leq 1 & i = 1, \dots, 2d & j = 0, \dots, ds & k = 0, \dots, dd \\ x_{ijk} \text{ integer} & i = 1, \dots, 2d & j = 0, \dots, ds & k = 0, \dots, dd \\ 0 \leq y_{ijk} \leq 1 & i = 1, \dots, 2s & j = 0, \dots, ss & k = 0, \dots, sd \\ y_{ijk} \text{ integer} & i = 1, \dots, 2s & j = 0, \dots, ss & k = 0, \dots, sd \end{array}$$

The highest possible contributions for an individual are the same as in the other schemes (*sd* males and *dd* females for couple, the same restrictions used for dams in other designs). IGxx restrictions ensure the desired structure of mating is to be maintained and UNIXx unique solution per individual. Interpretation of symbols is similar to previous sections.

(f) *Restricted co-ancestry weighted selection*

If the possibility of animals being related is included in the analysis simultaneous control of response and inbreeding could be made by minimizing the mean co-ancestry of individuals weighted by their contributions (x_i sons and y_i daughters) with restriction on the expected gain.

minimize

$$\sum_{i=1}^N \sum_{j=1}^N \frac{f_{ij}(x_i + y_i)(x_j + y_j)}{(2N)^2}$$

such that

$$\begin{aligned} \sum_{i=1}^N (x_i + y_i) \cdot EBV_i &\geq \overline{EBV}_{t+1} \\ \sum_{i=1}^N (x_i + y_i) &= 2N \\ \sum_{i=1}^{N/2} (x_i + y_i) - \sum_{i=N/2+1}^N (x_i + y_i) &= 0 \end{aligned} \tag{15}$$

$$\begin{aligned} 0 \leq x_i & \quad i = 1, \dots, N \\ x_i \text{ integer} & \quad i = 1, \dots, N \\ 0 \leq y_i & \quad i = 1, \dots, N \\ y_i \text{ integer} & \quad i = 1, \dots, N \end{aligned}$$

Although it is possible to construct a linear version of the problem it needs the inclusion of a huge number of artificial variables so the problem becomes impractical even for small populations such as the one used in this work. Therefore, besides quadratic programming, the *simulated annealing algorithm* (PRESS et al. 1989) was implemented to optimize the contributions.

The simulated annealing is a minimization process that uses the following procedure. (i) Start with a random feasible solution. (ii) An alternative solution is generated by a random small change; if the new solution is better than the previous solution the new solution is accepted; if worse, the solution will be accepted with a probability of $\Omega = \exp(-\Delta/T)$ where Δ is the difference between values of the alternative and actual solutions and T is a 'cooling' factor or temperature. (iii) This step is repeated several times; then the value of T is reduced by a factor and the process continues. At the beginning many alternatives are accepted but as T decreases it becomes more difficult to accept an alternative that is worse than the actual solution.

The nature of the simulated annealing algorithm makes it able to avoid local minima in the first steps and therefore is superior to other algorithms based on following the direction with the highest slope.

A combined objective function was used to make an easy simultaneous control of response and inbreeding possible. The routine started with a value of $T = 1$ and it was reduced by a factor of 0.9 each step (as in PRESS et al. 1989). Up to one hundred of such steps were allowed with 10 000 alternative solutions generated in each of them. The optimal solution was supposed to be found when the solution was not changed during the 10 000 suggested modifications of one step. If the solution does not change further, the current solution is very unlikely to be improved upon, and the temperature has reached a sufficiently low value.

The alternative solutions were obtained by choosing at random one individual. If its contribution was not zero it was decreased in one unit; then choosing at random another

individual of the same sex and increasing its contribution in one unit. Control can be established so no male generates more than $(ss + sd)$ offspring and no female more than $(ds + dd)$ offspring; in this way the structure is comparable with other selection schemes.

Linear and quadratic programming was computed using the routines package OSL from IBM (highly recommendable for its power and flexibility). The simulated annealing and Hungarian algorithms were computed with routines created by the authors.

Example breeding population

All of these designs were implemented in a small example. The population of evaluated individuals at generation t consisted of 16 males and 16 females structured into eight full-sib female families and four male families. The number of selected sires s (when limited) was four and the selected dams d equal to eight. The maximum number of male offspring per sire, female offspring per sire, male offspring per dam and female offspring per dam were, respectively, $ss = 4$, $sd = 4$, $ds = 2$ and $dd = 2$.

The co-ancestry coefficients among all the individuals were arbitrarily chosen. The trait under selection was assumed to have a heritability of 0.2 and a unit of genetic variance. The EBVs of all individuals were generated according to the additive relationship matrix (A) and the genetic parameters following this procedure: the vector of phenotypic values was the sum of a vector of random numbers from a normal distribution with zero mean and standard deviation equal to two (the environmental deviation) and a vector of genetic values. The latter was the result of multiplying Cholesky's decomposition of A by a vector of normally distributed random numbers with zero mean and standard deviation equal to one (the genetic deviation). The vector of EBVs was calculated as

$$EBV = (A\sigma_u^2) \cdot (A\sigma_u^2 + I\sigma_e^2)^{-1} \cdot y \quad (16)$$

where y is the vector of phenotypic values and I an identity matrix. EBVs for all individuals are given in Table 1 together with the family structure.

Results

As previously explained, the selection strategies implemented were: truncation selection (TS), modified within-family selection (MWFS), restricted co-ancestry selection (RCS), weighted selection (WS), restricted co-ancestry weighted selection (RCWS) and pair weighted selection (PWS).

Results arising from truncation selection in the example considered are summarized as follows. The expected accumulated response (the expected offspring mean EBV) was $R_e = 0.6405$, the effective population size in the transition between selected individuals in generation $t-1$ and selected individuals in generation t (calculated using eqn (7)) was $N_e = 8.5333$. The average co-ancestry coefficient between all selected individuals of generation t (including self co-ancestries and reciprocals) was $\bar{f} = 0.1238$. The mean inbreeding coefficient in generation $t+1$ when random matings were performed (equivalent to the mean co-ancestry between selected individuals of different sex) was $F_r = 0.0896$, and the value when matings were planned to give the minimum global co-ancestry between couples was $F_{mc} = 0.0137$. The response reached with truncation selection was the highest possible for any design because in all of them a selected sire could contribute a maximum of four males and females to the evaluated individuals of generation $t+1$ and two of each sex if it was a selected dam.

In all schemes several points were obtained by changing the restriction about inbreeding or selection responses to study the trade-offs between average co-ancestry and response. In Figure 1, with selected individual mean coancestry (f) in y-axis, the curves for minimization of co-ancestry, maximization of response and parametrical (combining selection response

Table 1. Estimated breeding values of individuals in generation 0 classified by sex and family. Also selected individuals [for modified within-family selection (MWFS) and restricted co-ancestry selection (RCS)] or individual's contributions [for weighted selection (WS), restricted co-ancestry weighted selection (RCWS) and restricted co-ancestry weighted selection without limits in the number of offspring (RCWS*)] to reach 95% of the response obtained with truncation selection

Sex	Male family	Female family	No.	EBV	MWFS	RCS	WS	RCWS	RCWS*
Sires	1	1	1	0.0233	0	0	0	0	1
			2	-1.3626	0	0	0	0	0
			3	-0.4330	0	0	0	0	0
			4	-0.4154	0	0	0	0	0
	2	3	5	0.4351	0	0	3	3	3
			6	0.3506	0	0	2	0	1
			7	0.5726	1	1	5	4	1
			8	1.3617	1	1	8	8	11
	3	5	9	0.7587	1	1	8	8	5
			10	0.5503	1	1	4	4	2
			11	-0.3105	0	0	0	0	0
			12	0.2220	0	0	0	0	0
	4	7	13	0.2740	0	0	1	3	4
			14	-0.3135	0	0	0	0	0
			15	0.1238	0	0	0	0	1
			16	0.2341	0	0	1	2	3
Dams	1	1	1	0.0969	1	1	2	3	4
			2	-1.6444	0	0	0	0	0
			3	-0.9203	0	0	0	0	0
			4	0.2905	1	1	4	4	6
	2	3	5	0.4351	1	1	4	4	3
			6	0.0051	0	0	0	0	0
			7	0.4814	1	0	4	4	1
			8	0.1513	0	0	2	0	0
	3	5	9	-0.0796	0	0	0	0	0
			10	0.5245	0	1	4	4	3
			11	1.0000	1	1	4	4	6
			12	0.7169	1	1	4	4	3
	4	7	13	-0.1664	0	0	0	0	0
			14	0.1623	1	1	2	4	4
			15	0.0647	1	1	2	1	2
			16	-0.0542	0	0	0	0	0

and inbreeding in the objective function) approaches in the MWFS method are compared. Lines are almost identical and the only differences are due to points corresponding to a particular level of response calculated in some of the schemes but not in the others. This means the same results are obtained using either the minimization of co-ancestry, maximization of response or parametric form of the problem. So any of the approaches will be used when comparing selection schemes in the present work.

In Figure 2 results from MWFS (solid lines) and RCS (dashed lines) methods are compared. The figure shows the behaviour of mean co-ancestry between selected individuals of generation t as expected response changes. Vertical lines mark (from right to left) 95, 90 and 75% of the highest possible response. Comparable results are given by the two strategies along the whole range of variation of the expected response (no differences greater than 10^{-3} are found in mean co-ancestry for the same level of response). However, although RCS gave a constant decrease in co-ancestry as response decreased, intervals can be found

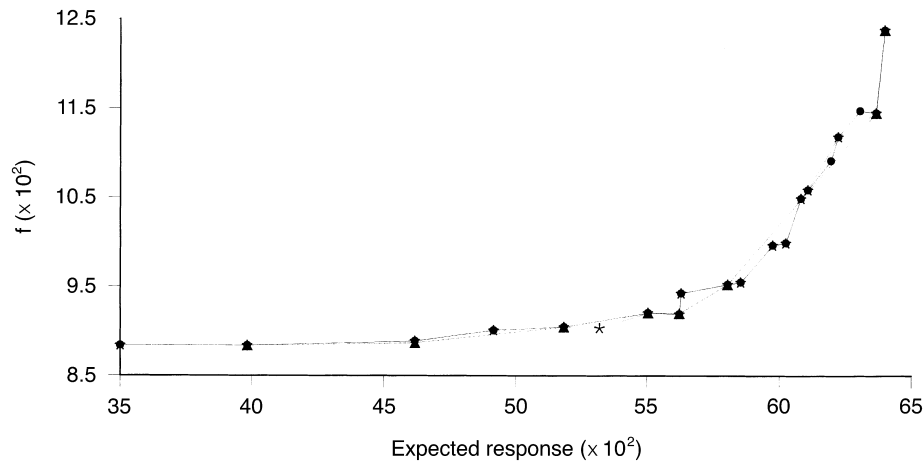


Fig. 1. Trade-offs between mean co-ancestry of selected individuals and expected response for minimization of co-ancestry (—), maximization of response (---) and parametrical (-·-·-) approach in the MWFS scheme

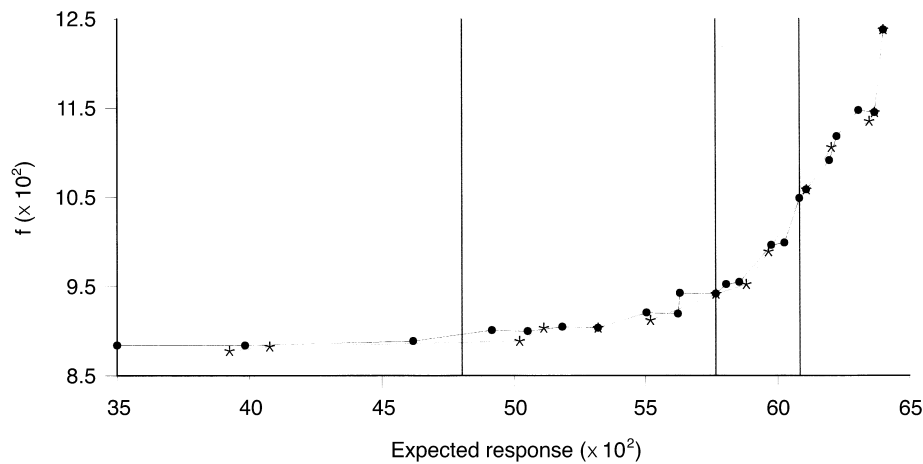


Fig. 2. Comparison between MWFS (●) and RCS (*). Trade-offs between mean co-ancestry and expected response. Vertical lines mark 95, 90 and 75% of the highest possible response

in the curve for MWFS where a decrease in expected response implies a local increase in the average co-ancestry of selected individuals of generation t . The same pattern is observed for the mean inbreeding coefficient of evaluated individuals of generation $t + 1$ either with random mating or with minimum co-ancestry mating (data not shown). Obviously, lower levels of inbreeding are reached if couples with minimum global co-ancestry are mated (this is true for all designs).

In Figure 3 performances of WS (solid lines) and RCWS (dashed lines) are shown. Trade-offs between mean co-ancestry of selected individuals and expected response show that better solutions (lower co-ancestry for the same level of response) are to be found using the RCWS method than using WS for the whole range of responses considered. In this graphic

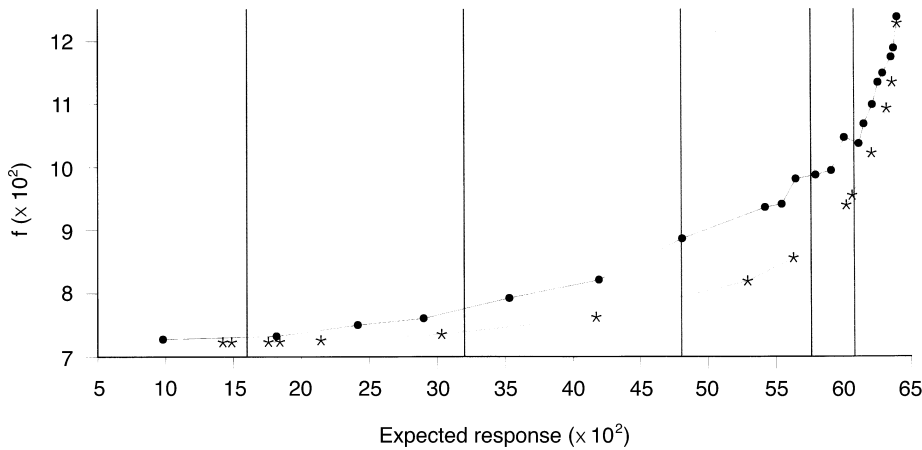


Fig. 3. Comparison between WS (●) and RWCS (*). Trade-offs between mean co-ancestry and expected response. Vertical lines mark 95, 90, 75, 50 and 25% of the highest possible response

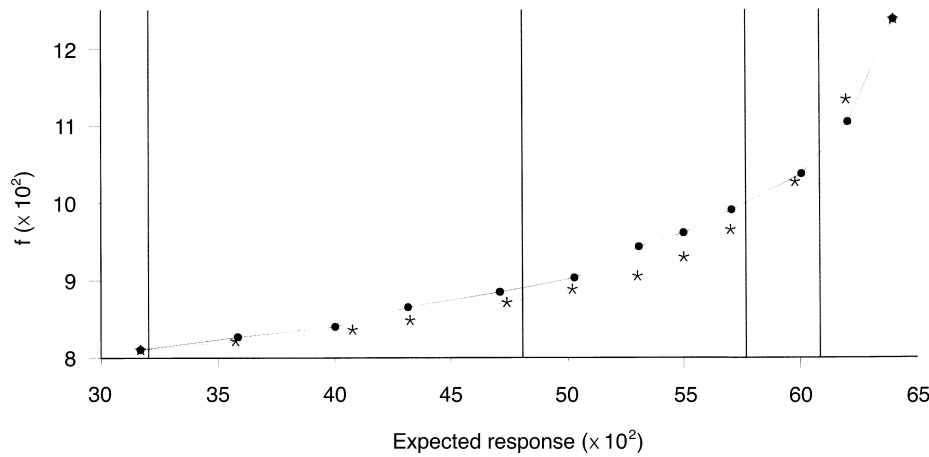


Fig. 4. Comparisons between PWS with minimum co-ancestry mating (●—) and PWS with random mating (*). Trade-offs between mean co-ancestry and expected response. Vertical lines mark 95, 90, 75 and 50% of the highest possible response

the vertical lines mark (from right to left) 95, 90, 75, 50 and 25% of the highest possible response. Levels of inbreeding in generation $t + 1$, either with random mating or with minimum co-ancestry mating, also confirm the superiority of the RCWS method (data not shown).

Results for PWS for couples with the minimum global co-ancestry (solid line) and one example of random-mated couples (dashed line) are shown in Figure 4. Percentages of the highest possible response are marked with vertical lines as in previous figures. Trade-offs indicate that evolution of mean co-ancestry for different expected responses is quite similar, independently of the mating criteria used with the selected individuals. However, minimum

co-ancestry mating yields lower levels of inbreeding in generation $t + 1$ than random mating does (data not shown).

Discussion

Increased rates of inbreeding in selection programmes may have an important effect on medium- and long-term response to selection and on reproductive performance through a reduction in genetic variability and an increased inbreeding depression. Therefore the importance of the joint control of response and inbreeding has been emphasized repeatedly in recent years.

This work has shown how some of the proposed strategies can be implemented through mathematical programming. All of them have proved to be effective at balancing the expected response and the inbreeding of the population. Furthermore, Figures 2, 3 and 4 present a common feature: a high slope in the right side of trade-offs for all strategies. This means that a substantial reduction in co-ancestry can be attained with a small loss in response. Further relaxation in the expected level of response gives little advantage in the observed decrease of co-ancestry. Data on the mean inbreeding coefficient of the next generation also show, although less clearly, that almost all reduction in the level of inbreeding is reached with little reduction of the expected response (data not shown). Table 2 shows, for different schemes, the percentage reduction in the co-ancestry of selected individuals when limits of the 95, 90 or 50% with respect to the highest possible response are imposed.

For all strategies, the three suggested approaches (minimization of co-ancestry, maximization of response and a combined objective) provide the same solutions, as could be seen in Figure 1. So the choice between strategies will depend on response or inbreeding being the real limitation. In most breeding programmes efforts must be focused on maximizing selection response while restricting inbreeding (TORO and PÉREZ-ENCISO 1990; TORO and SILIÓ 1992), but sometimes breeders might be interested in minimizing inbreeding but maintaining acceptable levels of expression of the traits (KLIEVE et al. 1994) as in some conservation programmes. Using the parametric approach has the additional difficulty of finding the appropriate value of factor λ as no clear relation has been discovered in this work. As an example, values of λ from zero to 550 were used to obtain trade-offs in the design controlling the family size (MWFS) and from zero to 10 in the RCWS scheme. Preliminary simulations must be carried out to determine the correct value to use depending on the breeding program aim.

Table 2. Percentage of decrease in mean co-ancestry between selected individuals for 95, 90 and 50% of maximum expected response achieved for different designs

	95%	90%	50%
MWFS	84.8	75.9	71.9
RCS	84.8	75.9	71.9
WS	84.0	80.0	63.0
RCWS	77.5	71.1	60.6
PWS	87.6	80.2	66.2

MWFS, modified within-family selection; RCS, restricted co-ancestry selection; WS, weighted selection; RCWS, restricted co-ancestry weighted selection; PWS, pair weighted selection

Equal contributions

Theoretically, when no relation exists between families and the only considered co-ancestry is between full-sibs and half-sibs then RCS is identical to MWFS. Results indicate that, in the example examined, both methods are also similar either for mean co-ancestry of selected individuals in generation t or for mean inbreeding in the evaluated individuals of generation $t + 1$. Some small discrepancies were found for MWFS with local increases in the mean co-ancestry when reducing the expected response. The similarity of both methods can be confirmed in Table 1 where solutions for 95% of truncation selection only differ in one of the selected dams.

In computational terms implementing MWFS through linear programming implies the use of $[s \cdot (ss + 1) \cdot (sd + 1)] + [d \cdot (ds + 1) \cdot (dd + 1)]$ variables being s and d , the number of male and female families and ss , sd , ds , dd the maximum number of males and females that can be selected from each kind of family. However, RCS requires a number of variables equal to $(N^2 + 4N)/2$ where N is the total number of evaluated individuals. As population size increases the number of variables in the latter case becomes huge and almost impossible to deal with; in the MWFS design the number of variables does not increase as quickly as in RCS. Therefore, as the handling of the population and the results are similar, MWFS would be more practical in most situations.

Differential contributions

Although, in parallel with the previous section, the two methods (WS and RCWS) compared here should yield similar results, better responses were obtained with the RCWS than with the WS strategy, as can be seen in Figure 3. The superiority of RCWS is due to the fact that it takes account of the co-ancestries among different individuals of the population. In Table 1, with WS method, contributions per individual are proportional to their EBV while with RCWS, although better individuals tend to contribute more, the relation is not straight and contributions are conditioned by co-ancestries among an individual and the rest. RCWS can be implemented through integer quadratic programming and the appropriate software for it exists (OSL by IBM). Therefore RCWS would be the method of choice.

To transform the integer quadratic program into a linear integer one is not feasible because of the magnitude of the problem even in a population as small as the one considered. Some authors have tried to solve the problem by using iterative methods dealing with quadratic expressions and approximate noninteger solutions (WRAY and GODDARD 1994; BRISBANE and GIBSON 1995a,b; MEUWISSEN 1997) or by making noninteger quadratic programming and then arranging contributions to the nearest integer; this last possibility as well as MEUWISSEN's strategy were also tested by the authors giving quite good solutions (data not shown). Finally the simulated annealing algorithm has provided the same solutions as integer quadratic programming without spending much computing time. So this kind of approach could be an appropriate way of dealing with RCWS.

Some comments must be made about differences between schemes with equal and differential contributions. Allowing differential contributions obviously gives more flexibility and higher restrictions on inbreeding can be imposed for the same level of response; this can be clearly seen by comparing results from implementing the RCS and RCWS method, but it implies keeping a greater and variable number of individuals as parents with an increase in the cost of the breeding program.

Furthermore, the use of unequal contributions could lead to factorial matings where every evaluated individual would contribute offspring by mating with different individuals. Nowadays, this is not feasible in most situations although the development of AI and MOET techniques can help in the introduction of factorial designs (WOOLLIAMS 1989; TORO et al. 1991). To arrange the mating scheme in the present work the following procedure was used. Once the contributions per individual to the next generation were

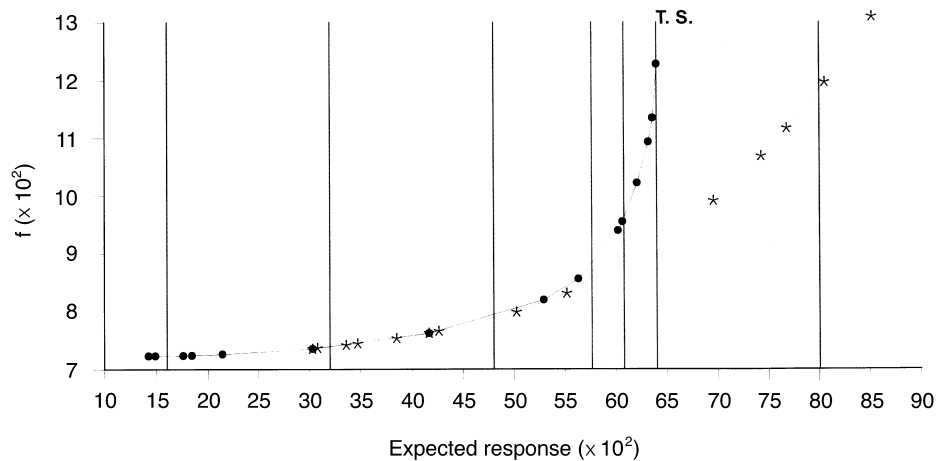


Fig. 5. Comparison between RCWS (●) and RCWS* (*). Trade-offs between mean co-ancestry and expected response. Vertical line labelled T. S. marks the highest response with truncation selection. Line to the right marks 125% of that response and to the left 95, 90, 75, 50 and 25%

decided, two vectors were constructed (one for sires and one for dams) where every individual appears as many times as the number of sons and daughters was to leave. Then the positions of both vectors were matched at random (if performing random mating) or in order to minimize the global parents co-ancestry (using the *Hungarian algorithm*).

If parents can leave as many sons and daughters as desired, the RCWS method can be implemented without limitations about the maximum number of offspring every sire or dam can contribute (it will be denoted as RCWS* method hereafter). Trade-offs between selected individuals mean co-ancestry and expected response obtained when using RCWS (solid line) or RCWS* (dashed line) are drawn in Figure 5. Lower co-ancestry levels were expected for the same response in the RCWS* scheme. Unlimited strategy allows reaching higher responses than truncation selection (up to twice as much). Thus, solutions with an expected response that is 30% higher than with truncation selection can be obtained ensuring the same level of co-ancestry. The solution for RCWS* in Table 1 shows that an unlimited strategy allows 'elite' individuals to contribute much more than the rest. The behaviour observed for the next generation mean inbreeding was similar, either with random mating or with minimum co-ancestry mating (data not shown): again less inbreeding was found with an unlimited design.

Additional restrictions on the number of mates per dam can be imposed. This can be done by performing mate selection (deciding in just one step the selected individuals and their contributions together with the mating scheme). To implement this design the authors developed a quadratic program, but the number of variables needed was too large to make it practical [$(ds + dd + 1) \cdot N^2/4 + N/2$ if a dam can mate to just one sire]. Therefore, simulated annealing was used to choose the optimal contributions and the mating scheme for different levels of response. Results for average co-ancestry were almost equal with those of the RCWS method in the population considered in this work (data not shown).

The problem of reproductive limitations could also be simplified using the PWS strategy. All strategies studied previously assume first optimizing contributions (per family or per individual) and then arranging matings. PWS implies deciding on the mating criteria prior to looking for optimum contributions. As matings are planned in a first step, a female can only mate to one male and reproductive limitations are avoided. The results indicate co-ancestry trade-offs are similar for random mating and minimum co-ancestry mating. This

could be due to the fact that the selected individuals in both schemes are the same (the eight best males and all the females) so similar contributions are expected to fulfil the restrictions and therefore similar levels of global co-ancestry. However, lower inbreeding is to be found in next generation with minimum co-ancestry mating as it occurs in all designs.

When comparisons are made between mean inbreeding in generation $t + 1$ using designs with predetermined mating scheme (PWS) and schemes which imply deciding couples to mate after selection of the parents and their contribution, it can be clearly seen that greater inbreeding levels are to be found in the first case than in the rest of schemes (either for random mating or for minimum co-ancestry mating).

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Summary

In recent years, different strategies have been proposed to reduce the rates of inbreeding in genetic improvement although keeping genetic gains at a substantial level. The strategies considered here were MWFS (modified within-family selection), RCS (restricted co-ancestry selection), WS (weighted selection), RCWS (restricted co-ancestry weighted selection) and PWS (pair weighted selection) and it has been shown how all of them can be implemented through integer mathematical programming (either linear or quadratic). An example involving a small selection scheme was given as an illustration. For larger designs approximated algorithms, such as simulated annealing, could yield good solutions without great computational or memory cost. Important reductions of inbreeding with no substantial losses in response were reached with all strategies. If there are no reproductive or economic limitations (all individuals can be engaged in factorial matings and high numbers of sons and daughters can be obtained from them) the best strategy resulted in optimizing contributions from all evaluated individuals in generation t to evaluated individual in $t + 1$. A simplified strategy with matings planned first and then optimizing each couples' contribution does not seem to be a good alternative. A mate selection strategy, solved by simulated annealing, with additional restrictions on the number of sires that can be mated to a dam would probably be the best feasible solution.

Resumen

En los últimos años se han propuesto diferentes estrategias para reducir el incremento de la consanguinidad en programas de mejora manteniendo las ganancias genéticas a un nivel substancial. En este artículo se consideran las estrategias MWFS (selección intrafamiliar modificada), RCS (selección con parentesco restringido), WS (selección ponderada), PWS (selección ponderada de parejas) y RCWS (selección ponderada con parentesco restringido) y se expone como dichos esquemas se pueden implementar a través de programación matemática entera (ya sea lineal o cuadrática). Se presenta un ejemplo en el que las diferentes estrategias se aplicaron sobre un pequeño esquema de selección. Para diseños mayores, algoritmos aproximados, como el del temple simulado (*simulated annealing*), pueden proporcionar buenas soluciones sin grandes requerimientos computacionales. Con todas las estrategias se pueden alcanzar importantes reducciones en consanguinidad sin pérdidas substanciales en respuesta. Si no hay limitaciones reproductivas ni económicas (todos los individuos pueden aparearse según diseños factoriales y se puede obtener un gran número de hijos e hijas de cualquiera de ellos) la mejor estrategia consiste en optimizar las contribuciones de todos los individuos evaluados en la generación t a los individuos evaluados en $t + 1$. Una estrategia simplificada en la que primero se deciden los apareamientos y después se optimiza la contribución de cada pareja no parece ser una buena solución. Probablemente la solución factible óptima sea una estrategia basada en selección de apareamientos (*mate selection*), resuelta con *simulated annealing*, con restricciones adicionales acerca del número de machos con los que puede aparearse una hembra.

Zusammenfassung

In letzter Zeit sind verschiedene Vorgangsweisen zur Reduktion des Inzuchtzuwachses bei substantiellen genetischen Fortschritt vorgeschlagen worden. Hier werden MWFS (modifizierte innerhalb Familien Selektion), RCS (restringierte Verwandtschaftsselektion), WS (gewichtete Selektion), RCWS (restringierte gewichtete Verwandtschaftsselektion) und PWS (Parungspaar gewichtete Selektion) betrachtet. Die Anwendung der Systeme durch Integer mathematische Programmierung (linear oder quadratisch) wird gezeigt. Ein kleines Selektionsschema wird zur Illustration verwendet. Bei umfan-

greicheren Plänen bieten approximative Algorithmen gute Lösungen ohne große Rechenoder Speicherkosten. Erhebliche Inzuchtinderung ohne erhebliche Verluste an Fortschritt wurden mit allen Vorgangsweisen erreicht. Ohne reproduktive oder ökonomische Begrenzungen (alle Tiere können faktoriell verpaart werden und zahlreiche männliche und weibliche Nachkommen sind möglich) ist die beste Vorgangsweise die Optimierung der Beiträge aller bewerteten Individuen in Generation t zu jenen in Generation $t+1$. Der einfachere Ansatz vorweg geplanter Paarung mit folgender Optimierung des Beitrages eines jeden Eltenpaares scheint keine gute Alternative zu sein. Partner Selektion über simulierte Paarung mit zusätzlicher Restriktion der Zahl von Vatertieren je Muttertier ist wahrscheinlich die günstigste Lösung.

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