Mating and selection schemes when rates of inbreeding are constrained

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Abstract

The effect of five mating schemes on genetic gain was compared for populations with discrete generations. Selection and mating were made in two steps. Parents were first selected with the Optimum Contribution selection method, where genetic gain is maximised while the average coancestry of selected animals is constrained. Thereafter, the mating algorithms were applied for the selected animals only. This two-step selection and mating strategy requires less computer time, compared to a one-step selection and mating scheme, where all selection candidates are also included in the mating step. Minimum coancestry (MC), Minimum coancestry with a maximum of one offspring per fullsib family (MC1) and Minimum variance of the relationships of offspring (MVRO) mating schemes resulted in a delay in inbreeding of about two generations compared to Random and Random factorial (R1) mating. In breeding schemes where selection is constraining rates of inbreeding ΔF, any improvement in family structure due to non-random mating increases genetic gain. For schemes with ΔF constrained to 1.0%, h^2=0.25 and 100 selection candidates (50 males and 50 females), genetic gain was 22% higher for the MC1 and MVRO schemes compared to Random mating schemes. For schemes with a less stringent constraint on ΔF (2.5%) or more selection candidates (200), the superiority of the MC1 and MVRO schemes was smaller (5-6%). In general, MC1 seemed the preferred mating method, since it almost always yielded the highest genetic gain.

1. Introduction

Mating and selection schemes attempt to reduce rates of inbreeding and/or increase genetic gain. Optimum Contribution selection methods are maximising genetic gain while constraining inbreeding by restricting coancestry among selected parents (Wray and Goddard, 1994; Brisbane and Gibson, 1995; Meuwissen, 1997; Meuwissen and Sonesson, 1998; Grundy *et al.*, 1998; Sonesson *et al.*, 1999; Grundy *et al.*, 1999). These authors assumed however random mating among selected parents, whereas non-random mating schemes may provide more opportunities for Optimum Contribution selection to select superior animals in the next generation. Caballero *et al.* (1996) concluded that minimum coancestry and compensatory mating strategies generally reduce rates of inbreeding and that they have a small effect on the genetic response to selection.

Caballero *et al.* (1996) used phenotypic and BLUP selection. With Optimum Contribution selection schemes, rates of inbreeding are however set to a desired value in the selection scheme and are not expected to change for different mating schemes. Hence, we expect that the Optimum Contribution selection will increase rates of genetic gain by using any by mating achieved improvement in structure of the relationships of the selection candidates.

The aim of this paper is to investigate rates of genetic gain and rates of inbreeding for five mating schemes that are combined with Optimum Contribution selection in a two step selection and mating optimisation procedure, i.e. only selected animals are included in the mating step. For all schemes, the number of offspring for each selected animal is given by the selection scheme. The five mating schemes are:

1. Random mating;
2. Random mating with only one offspring per full sib family (i.e. the factorial mating design of Woolliams (1989));
3. Minimum coancestry mating where the least related animals are mated;
4. Minimum coancestry mating with only one offspring per full sib family, and
5. A mating scheme that minimises variance of coancestry among the progeny.

The mating schemes mainly affect the family structure of the selection candidates, either by permitting only one offspring per full-sib family (schemes 2 and 4), by connecting certain families (schemes 3 and 4) or by reducing extreme relationships (scheme 5).

2. Material and Methods

2.1. Selection method

The method of Meuwissen (1997) was used to select animals. This method maximises the genetic level of next generation of animals, $G_{t+1} = c_t'EBV_t$, where c_t is a vector of genetic contributions of the selection candidates to generation t+1 and EBV_t is a vector of BLUP estimated breeding values of the candidates for selection in generation t. Rates of inbreeding are controlled by constraining the average coancestry to $\overline{C}_{t+1} = c_t'A_tc_t / 2$, where A_t is a (n x n) relationship matrix among the selection candidates, $\overline{C}_{t+1} = 1 - (1 - \Delta F_d)^t$, and ΔF_d is the desired rates of inbreeding (Grundy *et al*., 1998). Note that the level of the constraint $\overline{C}_{t+1}$, can be calculated for every generation, before the breeding scheme commences. For optimisation of c_t, it is also necessary to constrain the sum of the contributions of males (females) to ½, i.e. $Q'c_t = ½$ where Q is a (n x 2) incidence matrix of the sex of the selection candidates (the first column yields ones for males and zeros for females, and the second column yields ones for females and zeros for males) and ½ is a (2 x 1) vector of halves.

In order to obtain the optimal c_t that maximises G_{t+1}, LaGrangian multipliers are used, which yields the following quadratic index, I_t (Meuwissen, 1997):

$$I_t = c_t'EBV_t - \lambda_0(c_t'A_tc_t - 2\overline{C}_{t+1}) - (c_t'Q - 1/2')\lambda \quad (1)$$

where λ_0 and λ are LaGrangian multipliers (λ = (2 x 1) vector of LaGrangian multipliers). The objective function, $c_t'EBV_t$, is maximised for c_t under two restrictions; the first one is on the average relationship of the selection candidates and the second one is on the contribution per sex. The optimisation procedure was explained in Meuwissen (1997). The number of selection candidates per generation, T, is 100 or 200 in all breeding schemes. The output from the selection method is a vector with genetic contribution for each selection candidate, c_t.

2.2. Random mating (R)

For the R scheme, a sire and a dam are allocated at random for each new born progeny with a probability that is proportional to the genetic contribution that they received from the selection algorithm, c_t. This scheme is not a strictly hierarchical scheme, since dams can be mated to multiple sires. This scheme is therefore expected to have lower inbreeding and/or higher genetic gain than the commonly studied hierarchical breeding schemes.

2.3. Minimum coancestry mating (MC and MC1)

With minimum coancestry mating, MC, the average relationship of sires and

dams and therefore also the inbreeding of their progeny is minimised. A matrix **F** of size (N_s x N_d) is set up, where N_s (N_d) is the number of selected sires (dams) and element **F_{ij}** is the coefficient of kinship of selection candidates which is also the inbreeding coefficient of their progeny. MC schemes can result in many full sib offspring, because a sire has only minimum coancestry with one dam. However, many full sib relationships in a scheme result in either less genetic gain or more inbreeding compared to the situation where the full sib relationships are replaced by paternal and maternal half sib relationships (Woolliams, 1989). A higher inbreeding in generation t can lead to problems for the selection algorithm to constrain the inbreeding in generation t+1. Hence, for MC1 an additional constraint is imposed, namely that each mating pair should obtain only one offspring. However, this can not always be achieved, e.g. when a sire should obtain more offspring than the number of dams that are selected, i.e. one offspring per dam does not suffice. In the latter case, the sire will obtain more than one offspring per dam.

Minimum coancestry matings were obtained by applying the simulated annealing algorithm (Press *et al.*, 1989). The implementation of the annealing algorithm is described in the **Appendix**. The alternative solutions that are tried by the annealing algorithm differ from the current optimal solution by replacing mating pairs according to the scheme in Figure A1. These conditions reduce the number of alternative solutions substantially, and thus reduce the parameter space for the annealing algorithm, which saves computer time.

2.4. Factorial mating (R1)

For the factorial mating scheme (Woolliams, 1989), a sire and a dam are allocated for each progeny in the same way as for random mating, but with the restriction that only one full sib per family

is made. The simulated annealing algorithm was here used to sample mating pairs as shown in Figure A1 of the **Appendix**, but changes were made at random and an optimal solution was not searched for as for the MC and MVRO schemes.

2.5. Minimum variance of relationship of offspring mating (MVRO)

This mating method reduces the variance of relationships of progeny of selected sires and dams, which reduces the number of extremely high relationships among the progeny. The latter also reduces the probability that two full sibs are made because of their strong relationship. Note that the average relationship of the offspring is calculated by the Optimum Contribution selection algorithm and it can not be changed by the mating algorithm. For MVRO schemes, a symmetric matrix **V** is set up that yields the term that a pair of offspring contributes to the variance of the relationship of offspring, i.e.

$$V_{ij} = (a_{ij} - \bar{a})^2 \text{, for } i \neq j \text{ and } V_{ij}=0 \text{ for } i=j,$$

where a_{ij} is the relationship of offspring i and j, and i(j) denotes every possible offspring from all N_s*N_d mating combinations, i.e. **V** is of size (N_s*N_d x N_s*N_d) and $\bar{a}$ is the average relationship of selected animals. The minimisation of terms that are selected from the **V** matrix, i.e. selecting from the matings that are performed, is again done by the annealing algorithm (see **Appendix**). The alternative solutions that are tried by the annealing are the same as for MC mating.

2.6. The simulated breeding schemes

The general structure of the breeding schemes was that of a closed nucleus

scheme with 100 or 200 selection candidates. Genotypes, g_i, of the base animals are sampled from the distribution $N(0, \sigma^2_a)$, where σ^2_a is base generation genetic variance (0.25). Later generations are obtained by simulating offspring genotypes from $g_i = \frac{1}{2}g_s + \frac{1}{2}g_d + m_i$, where s denotes the sire and d the dam of the offspring i, and m_i is the Mendelian sampling component, which is sampled from $N(0, \frac{1}{2}(1-\bar{F})\sigma^2_a)$, where $\bar{F}$ is the average inbreeding coefficient of parents s and d. Phenotypes are simulated by adding an error term to the genotypes, which was sampled from $N(0, \sigma^2_e)$. The base generation phenotypic variance $\sigma^2_p = \sigma^2_a + \sigma^2_e$ is equal to 1. Estimates of breeding values (EBVs) are obtained using the BLUP- breeding value estimation procedure (Henderson, 1984). The simulated trait was recorded on both sexes, before selection. One hundred replicates of the scheme were run for 20 years with an inbreeding constraint of 1 or 2.5%.

3. Results

3.1. Inbreeding trend

For MC1, MC and MVRO, there was a delay in inbreeding of about two generations compared to for the R and R1 schemes. For MC there was somewhat lower F than for MC1. The latter is probably due to the extra restriction of having only one offspring per mating in MC1, which reduces the opportunities for MC1 of mating animals that are least related, i.e. its opportunity to generate offspring with lowest inbreeding. For all schemes, the realised rates of inbreeding were close to the constraint on the rates of inbreeding (Table 1), so a comparison of genetic gain between the different schemes is justified.

3.2. Genetic gain in small schemes with low inbreeding

For schemes where ΔF was constrained to 1.0% and the number of selection candidates was 100, the highest genetic level at year 20, G_{20}, was achieved for the MC1 and MVRO schemes and the lowest for the R schemes (Table 1). G_{20} was 22.3% higher for the MC1 (4.01 σ^2_p units) and 22.6% higher for the MVRO schemes (4.02 σ^2_p units) than for the R scheme (3.28 σ^2_p units). For the R1 and MC schemes, genetic gain was somewhat lower than for the MC1 and MVRO schemes, i.e. G_{20} was 21.1% higher for the R1 and MC schemes (3.98 σ^2_p units) than for the R scheme.

For all breeding schemes, genetic gain showed a linear increase over the years (results are not shown).

3.3. Genetic gain in small schemes with high inbreeding

As expected, a less stringent constraint on ΔF of 2.5% resulted in higher G_{20} (Table 1). With this less stringent constraint on ΔF, the superiority of the non-random mating schemes was much lower. The highest G_{20} was achieved by the MC1 and MVRO schemes (6.9% higher than R) followed by the R1 (4.9% higher than R) and MC schemes (4.3% higher than R).

3.4. Genetic gain in a large scheme with low inbreeding

For the larger schemes where ΔF was constrained to 1% per generation and the number of selection candidates was 200, the same pattern of G_{20} over the heritabilities was seen as for schemes where ΔF was constrained to 2.5% per generation and the number of selection candidates was 100. As expected, G_{20} was in general higher than for the smaller schemes. The highest G_{20} was achieved for the MC1 (on average 6.7% higher than R over the three heritabilities) and MVRO

schemes (6.6% higher than R), followed by the MC schemes (5.8% higher than R) and R1 scheme (5.4% higher.

Table 1. **Average rate of inbreeding (ΔF), genetic level at generation 20 (G_{20}), number of selected sires and dams (h^2=0.25)**

	ΔF/gen[i] (%)	G_{20} (σ_p-units (s.e.))	Sel. sires/ dams[i] (no)
ΔF=1.0%, 100 selected candidates			
R	1.00	3.28 (.0296)	32.2/32.1
R1	1.01	3.98 (.0249)	26.2/26.0
MC	1.00	3.98 (.0263)	26.0/25.9
MC1	1.00	4.01 (.0266)	26.5/26.6
MVRO	1.00	4.02 (.0291)	26.2/26.4
ΔF=2.5%, 100 selected candidates			
R	2.50	4.94 (.0396)	14.7/14.8
R1	2.48	5.18 (.0346)	13.3/13.4
MC	2.49	5.15 (.0391)	13.5/13.6
MC1	2.49	5.28 (.0394)	13.9/13.6
MVRO	2.48	5.28 (.0355)	13.3/13.4
ΔF=1.0%, 200 selected candidates			
R	1.00	5.07 (.0279)	36.5/36.1
R1	0.99	5.34 (.0229)	31.8/32.1
MC	1.00	5.33 (.0327)	31.3/31.6
MC1	1.00	5.42 (.0266)	32.5/32.6
MVRO	1.00	5.43 (.0265)	32.8/33.1

R = random mating, R1 = random mating with maximum one full-sib per couple, MC = Minimum coancestry mating, MC1 = minimum coancestry mating with maximum one full-sib per couple, MVRO = minimum variance of relationship of offspring
[i] average of generation 16-20

3.5. Number of selected animals

For schemes where ΔF was constrained to 1% and the number of selection candidates was 100, the highest number of animals was selected for the R scheme and the lowest number for the MC scheme. The number of animals that were selected for the MVRO and MC1 schemes was somewhat higher than the number of animals that were selected for the MC scheme. The number of animals selected was about halved when ΔF was constrained to 2.5% per generation,

compared to when ΔF was constrained to 1.0% per generation, although the number of selection candidates was 100 in all schemes. There were about the same number of animals selected for the larger schemes with 200 selection candidates compared to for the smaller schemes, which indicates that the intensity of selection has increased for the larger schemes. Meuwissen and Sonesson (1998) found a similar result for Optimum Contribution selection schemes with overlapping generations.

4. Discussion

4.1. Genetic gain

Non-random mating schemes yielded an increase in genetic gain of up to 22% compared to random mating schemes (Table 1). This increase in genetic gain is probably due to three effects of non-random mating:

1. MC mating connects contributions of unrelated families. Offspring resulting from these matings will have more equal contributions from their ancestors. The latter facilitates their selection, because then selection affects contributions of ancestors less than with random mating. Hence, selection of offspring becomes more independent from that of earlier generations, giving the Optimum Contribution algorithm more opportunity to increase genetic gain without affecting optimum contributions of previous generations.

2. MVRO mating avoids extreme relationships of offspring, which makes the offspring more independent, giving the Optimum Contribution algorithm more opportunity to increase genetic gain within a generation. In a sense it increases the effective number of offspring. The restriction of having only one offspring per full-sib family (factorial mating) also avoids extreme

relationships obtained by mating full sibs.

3. Especially MC mating minimises inbreeding levels of the offspring and thus of the parents of next generation. This mating scheme will therefore achieve larger Mendelian sampling variances, i.e. the term $\frac{1}{2}(1-\bar{F})\sigma^2_a$ is larger, resulting in more genetic variance, and thus also in more genetic gain. Since larger Mendelian sampling variances lead to more within family drift, the Optimum Contribution algorithm needs however to restrict the between family drift more in order to achieve the constraint on inbreeding. The latter will decrease genetic gain. Because of these two opposite impacts on genetic gain and because schemes do not differ much in levels of inbreeding, this third effect of non-random mating is probably least important of the three effects.

Although some of the non-random mating schemes are especially designed to achieve one (or two) of the above effects, all non-random mating schemes will achieve all three effects to some extent, because the effects are highly related, e.g. MVRO will also lead to the mating of less related animals. The above effects of non-random mating schemes can be quantified. MC1 mating combines the first and second effect, since it avoids full-sib relationships of the offspring. Hence, the ratio $[G_{20}(MC)-G_{20}(R)]/[G_{20}(MC1)-G_{20}(R)]$ ranges from 0.62 to 1.00 and depicts the proportion of the effect of MC1 that is achieved by minimum coancestry mating. Similarly, the ratio $[G_{20}(R1)-G_{20}(R)]/[G_{20}(MC1)-G_{20}(R)]$ ranges from 0.50 to 0.96 and depicts the proportion of the effect of MC1 that is due to the avoidance of full-sib relationships. Since these two fractions do not add to one, the effects of minimum coancestry mating and avoidance of full-sib relationships are not additive. If minimum coancestry mating is introduced in

addition to schemes with the restriction of one offspring per full-sib family, it yields less extra genetic gain compared to when it replaced an R scheme. Similarly, the restriction of one offspring per full-sib family yields less extra genetic gain when introduced in an MC scheme compared to when it is introduced in an R scheme. Because MVRO achieves as much as or less response than MC1, it seems that avoidance of full-sib mating is a sufficient measure to avoid extreme relationships. The fact that MVRO also attempts to avoid other high relationships than full-sibs does not seem to yield extra genetic gain. There are three categories of relationships in a population, namely full-sibs, half-sibs and other less related animals. Full-sib relationships may be avoided at the expense of more half-sib relationships, but half-sib relationships can not be avoided when animals have more than one offspring. The avoidance of strong relationships within the category of other relationships does probably not improve the family structure much, such that avoidance of full-sib matings achieves about all response that is achievable by the second effect of the previous paragraph.

4.2. Effects of the breeding scheme

There was a large difference in how much genetic gain increased between the schemes, mainly depending on the size of the schemes and on the constraint on ΔF. Benefits of mating strategy were smallest for large schemes and for schemes with high rates of inbreeding. This is probably because there is a relatively higher weight on relationships in the quadratic index (1) when ΔF is low and/or the number of candidates is small. This means that an improved family structure has a large effect on genetic gain in schemes with low ΔF and/or small numbers of selection candidates.

For larger schemes with 200 selection candidates, the larger families (twice as many animals per generation, but about

the same number of selected animals) resulted in more within family selection, even if selection is for BLUP-EBV. Hence, the weight of the family relationships in the quadratic index (1) is smaller and the structure of selection candidates was less important. Therefore, the effect of mating was also reduced to about the same level as for the schemes with 100 selection candidates and less constrained ΔF (2.5%).

4.3. Practical breeding schemes

In most breeding schemes, the control over matings is not as high as we have assumed in the general schemes simulated here. However, in dairy nucleus schemes, ova pick up and in vitro maturation and fertilisation (Kruip *et al.*, 1994) may yield both the required number of offspring per dam and the control over parentage of every offspring.

4.4. Conclusions

For MC, MC1 and MVRO schemes, there was a delay in inbreeding of about two generations compared to the R and R1 schemes, but rates of inbreeding were about the same for all schemes. In breeding schemes where there is selection with a constraint on rates of inbreeding, any improvement in family structure due to non-random mating increases genetic gain. For schemes with ΔF constrained to 1.0% and 100 selection candidates, genetic gain was up to 22% higher for the MC1 and MVRO schemes compared to the R scheme. For schemes with a less stringent constraint on ΔF or more selection candidates, the superiority of the non-random mating schemes compared to the random schemes was smaller (5-6%). In general, MC1 seemed to be the preferred mating method, since it almost always yielded the highest genetic gain and is simpler and computationally faster than MVRO. R1 and MC increased genetic

gains that ranged from 0.50 to 0.96 respectively 0.62 to 1.00 of that of MC1.

References

Brisbane, J.R. and Gibson, J.P., 1995. Balancing selection response and rate of inbreeding by including genetic relationships in selection decisions. Theor. Appl. Genet. 91: 421-431

Caballero, A., Santiago, E. and Toro, M.A., 1996. Systems of mating to reduce inbreeding in selected populations. Anim. Sci. 62: 431-442

Grundy, B., Villanueva, B. and Woolliams, J.A., 1998. Dynamic selection procedures for constrained inbreeding and their consequences for pedigree development. Genet. Res. (Camb) 72: 159-168

Grundy, B., Villanueva, B. and Woolliams, J.A., 1999. Dynamic selection for maximizing response with constrained inbreeding in schemes with overlapping generations. Submitted.

Henderson, C.R., 1984. *Applications of Linear Models in Animal Breeding*. University of Guelph Press, Guelph, Canada

Kruip, T.A.M., Boni, R., Wurth, Y.A., Roelofsen, M.W.M. and Pieterse M.C., 1994. Potential use of Ovum Pick-Up for embryo production and breeding in cattle. Theriogenology 42: 675-684

Meuwissen T.H.E., 1997. Maximizing the response of selection with a predefined rate of inbreeding. J. Anim. Sci. 75: 934-940

Meuwissen, T.H.E. and Sonesson, A.K., 1998. Maximizing the response of selection with a predefined rate of inbreeding: overlapping generations. J. Anim. Sci. 76: 2575-2583

Press, W.H., Flannery, B.P., Teukolsky, S.A. and Vetterling, W.T., 1989. Minimization or maximization of functions. In *Numerical recipes- the art of scientific computing*. University of Cambridge Press, 274- 334

Sonesson, A.K., Grundy, B., Woolliams, J.A. and Meuwissen, T.H.E., 1999. Selection with control of inbreeding in populations with overlapping generations: a comparison of methods. In press.

Woolliams, J.A., 1989. Modifications to MOET nucleus breeding schemes to improve rates of genetic progress and

decrease rates of inbreeding in dairy cattle. Anim. Prod. 49: 1-14

Wray, N.R. and Goddard, M.E., 1994. Increasing long-term response to selection. Genet. Sel. Evol. 26: 431-451

Appendix

Implementation of the simulated annealing algorithm

Minimum coancestry matings are obtained by applying the simulated annealing algorithm, (Press et al., 1989). In a feasible starting solution, each sire and dam obtains the number offspring that was assigned by the Optimum Contribution selection method (and only one offspring per sire-dam couple for MC1). In order to achieve this, sires and dams were ranked according to their number of offspring and then sires with high rank were mated to dams with low rank.

Given this feasible starting solution, the simulated annealing algorithm optimises the mating scheme as follows:

1. Calculate the sum of coancestry of the mating pairs of start solution and set it to V_0. The initial 'temperature' is set to Temp=1.0.

2. Consider an alternative set of matings, where the changes of matings are sampled randomly, although the number of progeny per sire and dam must remain constant. Sires 1 and 2 and dam 1 and 2 are randomly chosen, with the restriction that their matings in the current solution are as indicated in Figure A1. Evaluate the alternative value, $V_a = V_0 + \delta$, where δ is the change of the coancestry if the alternative matings are accepted, i.e.

$\delta = a_{s_1 d_2} + a_{s_2 d_1} - a_{s_1 d_1} - a_{s_2 d_2}$, where $a_{s_1 s_2} =$ the coancestry coefficient of sire 1 and dam 2. When δ is smaller than zero, replace the current set of matings with the alternative set of matings and set V_0 equal to V_a. When δ is larger than zero, replace the current set of matings and V_0 with a probability equal to $\exp(-\delta/\text{Temp})$, which decreases when δ and/or Temp is small.

3. When the current set of matings was replaced $10*\max(N_s, N_d)$ times by an alternative set of matings or when $100*\max(N_s, N_d)$ alternative set of matings have been evaluated, the 'temperature', Temp, was decreased by 10%, where $N_s(N_d)=$ total number of sires(dams). When there was no accepted alternative set of matings since the last reduction of Temp: finish, because the algorithm did not find an improved distribution and Temp is too low to accept a reduction of V_0. Otherwise go to step 2.

For the MVRO schemes, simulated annealing algorithm is used to minimise the variance of relationship of the offspring that are produced by the matings, i.e.

minimise $V_0 = \sum\limits_{i \in \text{mating}} \sum\limits_{j \in \text{mating}} V_{ij}$ over sets of

matings, where $\sum\limits_{i \in \text{mating}}$ denotes summation

over all progeny that are produced by the current set of matings and the V_{ij} elements are as defined in the main text. The same changes of matings as for MC are evaluated by the simulated annealing algorithm. The alternative values are $V_a = V_0 + \delta$, with

$$\delta = 2 \left[\sum\limits_{\substack{j \in \text{mating} \\ j \neq i_1 i_4}} \left(-V_{i_1 j} - V_{i_4 j} + V_{i_2 j} + V_{i_3 j} \right) + V_{i_2 i_3} - V_{i_1 i_4} \right]$$

, where i_1 is defined as the progeny that is going to be cancelled with sire s_1, and dam d_1, i_2 is a new progeny by s_1 and dam d_2, i_3 is a new progeny of dam d_1 and sire s_2, and i_4 is the old progeny of s_2 and d_2, which is cancelled. Except for the above calculation of the δ values, the simulated annealing algorithm equals that of the MC mating.

For more details on the mechanisms of the annealing algorithm, see Press *et al.* (1989).

	Dam 1	*Dam 2*
Sire 1	1 → 0	0 → 1
Sire 2	0 → 1	1 → 0

Figure A1. **Suggested modifications of the current solution for the annealing algorithm. 1 → 0 indicates that the mating conducted in the present solution is not conducted in the alternative solution and 0 → 1 indicates the opposite. All indicated changes have to be made simultaneously to maintain the total number of offspring selected for each sire and dam.**