Genet. Sel. Evol. 32 (2000) 231–248
© INRA, EDP Sciences

Original article

Mating schemes for optimum contribution selection with constrained rates of inbreeding

Anna K. SONESSON*, Theo H.E. MEUWISSEN

Institute for Animal Science and Health, Box 65, 8200 AB Lelystad,
The Netherlands

(Received 13 September 1999; accepted 21 January 2000)

Abstract – The effect of non-random mating on genetic response was compared for populations with discrete generations. Mating followed a selection step where the average coancestry of selected animals was constrained, while genetic response was maximised Minimum coancestry (MC), Minimum coancestry with a maximum of one offspring per mating pair (MC1) and Minimum variance of the relationships of offspring (MVRO) mating schemes resulted in a delay in inbreeding of about two generations compared with Random, Random factorial and Compensatory mating. In these breeding schemes where selection constrains the rate of inbreeding, ΔF, the improved family structure due to non-random mating increased genetic response. For schemes with ΔF constrained to 1.0% and 100 selection candidates, genetic response was 22% higher for the MC1 and MVRO schemes compared with Random mating schemes. For schemes with a less stringent constraint on ΔF or more selection candidates, the superiority of the MC1 and MVRO schemes was smaller (5–6%). In general, MC1 seemed to be the preferred mating method, since it almost always yielded the highest genetic response. MC1 mainly achieved these high genetic responses by avoiding extreme relationships among the offspring, *i.e.* fullsib offspring are avoided, and by making the contributions of ancestors to offspring more equal by mating least related animals.

breeding program / inbreeding / selection / mating / genetic response

Résumé – **Étude de schémas d'accouplement consécutifs à une sélection optimisée avec maintien d'un taux constant d'accroissement de consanguinité.** On a étudié dans des populations à générations séparées, l'effet de modes d'accouplement non aléatoires. Les accouplements étaient consécutifs à une phase de sélection où on maximisait la réponse attendue mais en contraignant la parenté moyenne des animaux sélectionnés à une valeur désirée. Les schémas d'accouplements « à parenté minimum entre conjoints » (MC), « à parenté minimum avec au plus un descendant par accouplement » (MC1), « à variance minimum des relations de parenté entre l'ensemble de toutes les descendances » (MVRO) ont eu pour effet de retarder la consanguinité de deux générations par rapport aux schémas « Aléatoire », « Aléatoire

---

* Correspondence and reprints
E-mail: a.k.sonesson@id.wag-ur nl

factoriel» et «Compensatoire». Dans ces schémas où la sélection est pratiquée tout en contraignant le taux d'accroissement de la consanguinité ΔF, l'amélioration de la structure familiale procurée par ces accouplements non aléatoires a augmenté la réponse génétique. Pour les schémas où ΔF était contraint à 1 % et où il y avait 100 candidats à la sélection, la réponse génétique a été supérieure de 22 % pour les schémas MC et MVRO par rapport au schéma «Aléatoire». Pour les schémas à contrainte moins forte sur ΔF ou avec davantage de candidats, la supériorité des schémas MC et MVRO a été plus faible (5–6 %). En général, MC1 semble devoir être la méthode préférée parce qu'elle a presque toujours procuré la réponse la plus élevée. MC1 a permis ces réponses élevées principalement en évitant les parentés extrêmes parmi la descendance, c'est-à-dire en évitant la production de plein-frères (sœurs) et en nivelant la contribution des différents ancêtres (par accouplement des animaux les moins parents entre eux).

schéma de sélection / consanguinité / sélection / accouplement / réponse à la sélection

1. INTRODUCTION

Selection and mating schemes attempt to reduce rates of inbreeding and/or increase genetic response. Optimum Contribution selection methods [1,6,7, 12,13,18,19,23] maximise genetic response while constraining inbreeding by restricting the coancestry among selected parents. These authors assumed however random mating among selected parents, whereas non-random mating may improve family structure of the next generation, and thus affect the results of subsequent selection. Caballero *et al.* [2] concluded that for phenotypic and BLUP selection, minimum coancestry and compensatory mating strategies generally have a small effect on genetic response to selection, but that they reduce rates of inbreeding. The effect of non-random mating on rates of inbreeding may, however, be reduced with Optimum Contribution selection schemes, because the increase of the average coancestry of the population is restricted. Because Optimum Contribution selection does not use an improvement of family structure due to non-random mating to achieve a lower coancestry of the selected parents (which is restricted), it may use the improvement of family structure to increase selection differential, *i.e.* to increase genetic response. Three different effects of non-random mating in combination with Optimum Contribution selection may therefore be envisaged: 1. genetic response may increase [2]; 2. level of inbreeding may decrease [2,3,21]; 3. rates of inbreeding may decrease [2].

One step mating and selection strategies have been proposed [20,21] that used the linear programming algorithm to optimise selection response, while restricting inbreeding coefficients of the offspring. Restricting inbreeding coefficients of offspring does not control long term inbreeding, because the increase of the average coancestry of the population, which equals the increase of the long-term inbreeding, may still increase too rapidly [1,6,12,19,21,23]. Furthermore, optimising mating schemes by linear programming is rather computationally intensive [3], which makes it unpractical for large populations. One way to reduce the needed computer time is to optimise selection and mating in two separate steps so that when optimising the mating step, only the selected animals have to be considered, although this method may not result in maximum genetic response because all possible matings of selection candidates are not considered.

The aim of this paper is to investigate the rates of genetic response and rates of inbreeding for eight mating schemes that are combined with Optimum Contribution selection in a two-step selection and mating optimisation procedure. For all schemes, the number of offspring for each selected animal was given by the Optimum Contribution selection algorithm. The mating schemes were: 1. Random mating; 2. Compensatory mating, where sires with the highest genetic contribution were mated to dams with the lowest genetic contribution, in sequence [17]; 3. Compensatory mating, where sires, which were most related to all the selection candidates were mated to dams that were least related to all the selection candidates, in sequence [17]. 4. Minimum coancestry mating, where least related animals were mated; 5. A mating scheme which minimises variance of coancestry among the progeny. For scheme 1, 3 and 4, a restriction of only having one offspring per mating pair was added (1b, 3b, 4b), *i.e.* paternal and maternal halfsib families were created instead of fullsib families, as in the factorial mating design of Woolliams [22]. The non-random mating mainly affects the family structure of the selection candidates, either by permitting only one offspring per mating pair (schemes 1b, 3b and 4b), by connecting certain families (schemes 2, 3, 3b, 4 and 4b) or by reducing extreme relationships (scheme 5).

2. MATERIALS AND METHODS

2.1. Selection method

The method of Meuwissen [12] was used to select animals. This method maximises the genetic level of the next generation of animals, $\mathbf{G_{t+1}} = \mathbf{c'_t EBV_t}$, where $\mathbf{c_t}$ is a vector of genetic contributions of the selection candidates to generation $t+1$ and $\mathbf{EBV_t}$ 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 $\overline{C}_{t+1} = \mathbf{c'_t A_t c_t}/2$, where $\mathbf{A_t}$ is a $(n \times n)$ relationship matrix among n selection candidates, $\overline{C}_{t+1} = 1-(1-\Delta \mathrm{F}_d)^t$, and $\Delta \mathrm{F}_d$ is the desired rate of inbreeding [6]. The constraint is based on the normal A matrix here instead of on the augmented A matrix, but both matrices yield very similar results [6,18]. 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 $\mathbf{c_t}$, it was also necessary to constrain the sum of the contributions of males (females) to 1/2, *i.e.* $\mathbf{Q'c_t} = (1/2)\mathbf{1_2}$, where $\mathbf{Q}$ is an $(n \times 2)$ 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 $\mathbf{1_2}$ is a (2×1) vector of ones.

In order to obtain the optimal $\mathbf{c_t}$ that maximises G_{t+1}, Lagrangian multipliers were used, which yield the following quadratic index, I_t [12]:

$$I_t = \mathbf{c'_t EBV_t} - \lambda_0(\mathbf{c'_t A_t c_t} - 2\overline{C}_{t+1}) - (\mathbf{c'_t Q} - (1/2)\mathbf{1'_2})\lambda, \qquad (1)$$

Table I. Summary of restrictions and objectives for the mating schemes. For all mating schemes, the restriction apply that the number of progeny per selected animal are as calculated by the Optimum Contribution selection method.

Name	Abbreviation	Restriction	Objective
Random	R	None	Randomise matings
Factorial	R1	Max one progeny per full-sib family	As objective of R
Compensatory	CREL	None	Mate sires with highest relationship to other selected animals to dams with lowest relationship to other selected animals
Compensatory	CREL1	Max one progeny per full-sib family	As objective of CREL
Compensatory	C	None	Mate sires with highest genetic contribution to dams with lowest genetic contribution
Minimum coancestry	MC	None	Mate animals that are least related
Minimum coancestry	MC1	Max one progeny per full-sib family	As objective of MC
Minimum variance of relationship of offspring	MVRO	None	Mate animals such that the variance of coancestry among progeny is minimised

where λ_0 and λ are Lagrangian multipliers (λ = (2×1) vector of Lagrangian multipliers). The objective function, $\mathbf{c'}_t\mathbf{EBV}_t$, is maximised for $\mathbf{c}_t$ 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 is explained in [12]. The output from the selection method is a vector with genetic contribution to next generation for each selection candidate, $\mathbf{c}_t$.

2.2. Random mating (R)

A summary of restrictions and objectives for the mating schemes is given in Table I. 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, $\mathbf{c}_t$.

2.3. Compensatory mating on genetic contributions (C)

In the compensatory mating scheme, as originally described by Santiago and Caballero [17], the selected offspring from families with largest contributions are mated to selected offspring from families with smallest contributions, in sequence. When Optimum Contribution selection is used, the contributions of selected animals differ, as indicated by their c_t value, and the compensatory mating scheme can be based on contributions of individuals instead of contributions of families. The number of progeny per sire (dam) is obtained from its optimum contribution, c_t, which is calculated by the selection algorithm by multiplying the contributions of the sire (dam) with the number of selection candidates and rounding to integers. Normally the truncation point for rounding up versus down is 0.5, but if the total number of progeny does not sum up to the intended number, the truncation point is adjusted such that the intended number of progeny results. Thereafter, sires and dams are ranked according to their number of offspring. Sires with the highest number of progeny are mated to dams with the lowest number, in sequence. For example, if the highest ranked sire obtains ten progeny and the two lowest ranked dams three and eight progeny, this sire obtained three progeny with the lowest ranked dam and seven with the second lowest ranked dam. The second highest ranked sire will be the sire of the eighth and last progeny of the second lowest ranked dam.

2.4. Compensatory mating on relationships (CREL and CREL1)

For CREL, the original method [17] was modified as described in [2]. Firstly the average relationship of each selected animal to all other selected animals was calculated. Thereafter, sires and dams were ranked on this relationship and sires with the highest rank were mated to dams with the lowest rank, in sequence. Each candidate was given as many progeny as was optimised by the selection process. However, many fullsib relationships in a scheme result in either less genetic response or more inbreeding compared with the situation where the fullsib relationships are replaced by paternal and maternal halfsib relationships [22]. A higher inbreeding in generation t can lead to problems for the selection algorithm to constrain the inbreeding in generation $t + 1$. Hence, for CREL1, an additional constraint was imposed, namely that each mating pair should obtain only one offspring. However, this cannot 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.

2.5. 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 $\mathbf{F}$ of size $(N_s \times N_d)$ is set up, where N_s (N_d) is the number of selected sires (dams) and element $\mathbf{F}_{ij}$ is the coefficient of coancestry of the selected individuals i and j, which is also the inbreeding coefficient of their progeny. MC schemes can result in many fullsib offspring, because a sire has only minimum coancestry with one dam. For MC1, an additional restriction was included, restricting the number of offspring per mating pair to a maximum of one.

Minimum coancestry matings were obtained by applying the simulated annealing algorithm [14]. The implementation of the annealing algorithm is described in the appendix. The alternative solutions that were tried by the annealing algorithm differed from the current optimal solution by replacing mating pairs according to the scheme in Figure 2. These conditions reduce the number of alternative solutions substantially, and thus reduce the parameter space for the annealing algorithm, which saves computer time.

2.6. Mating which achieves minimum variance of relationship of offspring (MVRO)

The MVRO mating method minimises 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 fullsibs are made because of their strong relationship. Note that the Optimum Contribution selection algorithm calculates the average relationship of the offspring, which cannot be changed by the mating algorithm. For MVRO schemes, a symmetric matrix **V** is set up that yields the term that a pair of possible future offspring would contribute to the variance of the relationship of offspring, *i.e.*

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

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 $(N_s * N_d \times N_s * N_d)$ and $\overline{a}$ is the average relationship of selected animals. Note that $a_{ij} = 1/4\left[a_{s_i s_j} + a_{s_i d_j} + a_{d_i s_j} + a_{d_j s_j}\right]$, where s_i and d_i (s_j and d_j) denote the sire and dam of $i(j)$. Let the vector **m** contain the number of offspring from mating pair ij. Now, the variance of the relationships of the offspring is proportional to $\mathbf{m}'\mathbf{V}\mathbf{m}$. The minimisation of $\mathbf{m}'\mathbf{V}\mathbf{m}$ is again done by the annealing algorithm (see appendix). The alternative solutions that were evaluated by annealing were the same as for MC mating.

2.7. Factorial mating (R1)

For the factorial mating scheme [22], the simulated annealing algorithm is used as explained in the minimum coancestry mating section, but without an objective function, *i.e.* all suggested changes of matings (1 000) are accepted, in order to randomise the initial solution. This randomisation by the annealing algorithm is preferred over simply sampling at random a sire and dam for each offspring according to the contributions of the sires and dams as in R, with the additional restriction that a sire and dam pair can only be sampled once. The latter often results in a not feasible solution, *i.e.* fullsibs cannot be avoided anymore because of unfortunate sampling of earlier matings. Furthermore, it results (more often than by chance) in the mating of sires and dams with low contributions, since after some sampling of matings according to the contribution of the sires and dams, only sires and dams with low contribution matings are still available.

Table II. Parameters of the closed nucleus scheme.

Size of selection scheme	
Number of selection candidates	100 or 200
Number of generations over which the breeding scheme was run	20
Number of replicated simulations	100
Parameters of trait	
Phenotypic variation, σ_p^2	1.00
Heritability, h^2	0.10, 0.25 or 0.50
Recording of trait	on both sexes, before selection
Inbreeding constraint	1.0 or 2.5% per generation

2.8. The simulated breeding schemes

The simulated breeding schemes are described in Table II. The general structure is that of a closed nucleus scheme with discrete generation structure. The number of selection candidates per generation is 100 or 200. Genotypes, g_i, of the base animals were sampled from the distribution $N(0,\sigma_a^2)$, where σ_a^2 is base generation genetic variance of 0.10, 0.25 or 0.50. Later generations are obtained by simulating offspring genotypes from $g_i = 1/2g_s + 1/2g_d + m_i$, where s denotes the sire and d the dam of offspring i, and m_i is the Mendelian sampling component, which is sampled from $N\big(0,1/2(1-\overline{F})\sigma_a^2\big)$, where $\overline{F}$ is the average inbreeding coefficient of parents s and d. Phenotypes are simulated by adding an error term to the genotypes, which is sampled from $N(0,\sigma_e^2)$. The base generation phenotypic variance $\sigma_p^2 = \sigma_a^2 + \sigma_e^2$ is always equal to 1. Estimates of breeding values (EBVs) are obtained using the BLUP-breeding value estimation procedure [9].

3. RESULTS

3.1. Inbreeding trend

For MC, MC1 and MVRO, there was a delay in inbreeding of about two generations compared with R, R1, C, CREL and CREL1 schemes (Fig. 1). For the MC scheme there was a somewhat lower F than for the MC1 scheme. The latter was probably due to the extra restriction of having only one offspring per mating pair in MC1, which reduced the opportunities for MC1 of mating animals that were least related, *i.e.* its opportunity to generate offspring with lowest inbreeding. In Figure 1, ΔF was constrained to 1.0%, the number of selection candidates was 100 and the trait had a heritability of 0.25, but similar results were obtained for all other schemes (results not shown).

For all schemes, the realised rates of inbreeding were close to the desired rates of inbreeding (Tabs. III and IV), which justifies the comparison of genetic response between the different schemes.

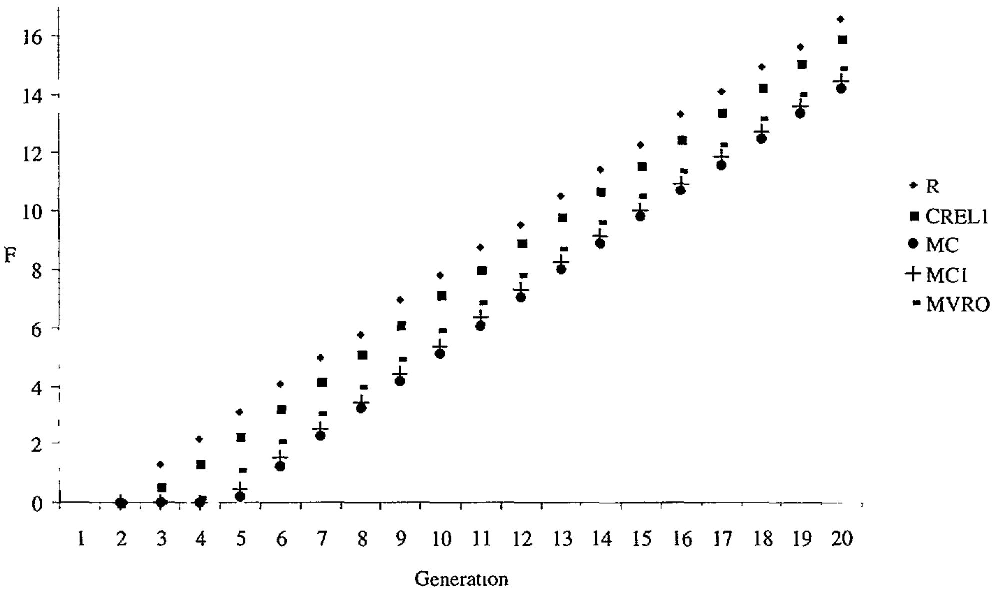

Figure 1. Coefficient of inbreeding (F) for schemes where ΔF was constrained to 1.0% per generation, the number of selection candidates was 100 and the heritability was 0.25. The F of the R1, C and CREL was always between F of the R (◆) and CREL1 (■) schemes and has been omitted to increase readability of the graph. R: Random, CREL1: Compensatory, MC and MC1: Minimum coancestry, MVRO: Minimum variance of relationship of offspring.

3.2. Genetic response in small schemes with low inbreeding

The genetic level at year 20, G_{20}, was significantly higher for the non-random mating schemes than for the random mating scheme when ΔF was constrained to 1.0% and the number of selection candidates was 100 (Tab. III). For $h^2 = 0.25$, G_{20} was the highest for the MC1 ($4.01\sigma_p$ units) and MVRO ($4.02\sigma_p$ units) schemes, which corresponds to 22.3 and 22.6% higher G_{20} than with the R scheme ($3.28\sigma_p$ units), respectively. The G_{20} was somewhat lower for the R1, CREL1 and MC schemes than for the MC1 and MVRO schemes, although this difference was not significant. The G_{20} for the C and CREL schemes was significantly lower than for the other non-random mating schemes. In general, for the other levels of heritability, the same pattern between the schemes was seen, although the superiority of the non-random mating schemes over the R schemes was slightly higher for $h^2 = 0.10$ and lower for $h^2 = 0.50$. The G_{20} for the CREL1 scheme was as high as for the MC1 and MVRO schemes for the lowest h^2 of 0.10, but for the higher heritabilities of 0.25 and 0.50, G_{20} was lower than for the MC1 and MVRO schemes, although this difference was not significant.

For all breeding schemes, there was a linear increase of genetic response over generations (results are not shown).

Table III. Average rate of inbreeding (ΔF), genetic level at generation 20 (G_{20}), number of selected sires and dams and variance of relationship of offspring at generation 20 (V_{rel}) for schemes with ΔF constrained to 1% per generation and 100 selection candidates[1].

	ΔF/gen[2] (%)	G_{20} (σ_p-units (s.e.))	Number of selected sires/dams[2]	V_{rel}
		$h^2 = 0.10$		
R	1.00	1.42 (0.0177)	34.2/34.0	0.00687
R1	1.00	1.72 (0.0157)	27.1/27.4	0.00447
C	0.97	1.70 (0.0168)	30.3/30.2	0.00620
CREL	1.01	1.69 (0.0160)	31.7/31.6	0.00571
CREL1	1.00	1.74 (0.0168)	30.8/30.6	0.00411
MC	0.99	1.69 (0.0187)	27.5/27.4	0.00542
MC1	1.00	1.74 (0.0176)	27.9/27.7	0.00331
MVRO	0.99	1.74 (0.0166)	27.8/27.8	0.00332
		$h^2 = 0.25$		
R	1.00	3.28 (0.0296)	32.2/32.1	0.00701
R1	1.01	3.98 (0.0249)	26.2/26.0	0.00465
C	1.00	3.92 (0.0249)	28.4/28.2	0.00672
CREL	1.00	3.86 (0.0264)	29.6/29.8	0.00615
CREL1	1.01	3.96 (0.0290)	29.1/28.7	0.00441
MC	1.00	3.98 (0.0263)	26.0/25.9	0.00570
MC1	1.00	4.01 (0.0266)	26.5/26 6	0.00348
MVRO	1.00	4.02 (0.0291)	26.2/26.4	0.00351
		$h^2 = 0.50$		
R	0.96	6.31 (0.0376)	30.5/30.5	0.00716
R1	1.00	7 53 (0.0345)	24.5/24.7	0.00500
C	0.96	7.50 (0.0362)	26.1/26.1	0.00728
CREL	1.01	7.28 (0.0353)	27.9/28.1	0.00650
CREL1	1.02	7.52 (0.0398)	26.9/27.0	0.00483
MC	1.00	7.53 (0.0409)	24.4/24.4	0.00607
MC1	1.00	7.61 (0.0345)	25.0/25.2	0.00372
MVRO	1.00	7.60 (0.0332)	25.1/25.3	0.00373

[1] See Table I for abbreviations of the mating schemes.

[2] Average of generation 16–20.

3.3. Genetic response in small schemes with high inbreeding

A less stringent constraint on ΔF, 2.5 compared with 1.0% for the more stringent schemes, resulted in higher G_{20} (Tab. IV). The superiority of the non-random mating schemes was, however, much lower than for the more stringent schemes, although G_{20} was still significantly higher for the R1, CREL1, MC,

Table IV. Average rate of inbreeding (ΔF), genetic level at generation 20 (G_{20}), number of selected sires and dams and variance of relationship of offspring at generation 20 (V_{rel}) for schemes with ΔF constrained to 2.5% per generation and 100 selection candidates or ΔF constrained to 1 0% and 200 selection candidates[1].

	ΔF/gen[2] (%)	G_{20} (σ_p-units (s.e.))	Number of selected sires/dams[2]	V_{rel}
	ΔF constrained to 2.5% and 100 selection candidates			
R	2.50	4.94 (0.0396)	14.7/14.8	0.00777
R1	2.48	5.18 (0.0346)	13.3/13.4	0.00637
C	2.48	4.92 (0.0366)	13.7/13.8	0.00937
CREL	2.49	4.94 (0.0370)	15.7/15.6	0.00711
CREL1	2.50	5.11 (0.0412)	14.0/14.1	0.00608
MC	2.49	5.15 (0 0391)	13.5/13.6	0.00608
MC1	2.49	5.28 (0.0394)	13.9/13.6	0.00440
MVRO	2.48	5.28 (0.0355)	13.3/13.4	0.00482
	ΔF constrained to 1.0% and 200 selection candidates			
R	1.00	5.07 (0.0279)	36.5/36.1	0.00595
R1	0.99	5.34 (0.0229)	31.8/32.1	0.00463
C	1.00	5.33 (0.0277)	33.7/34.1	0.00678
CREL	1.00	5.18 (0.0269)	37.2/37.1	0.00591
CREL1	0.99	5.37 (0.0264)	34.9/34.7	0.00435
MC	1.00	5.33 (0.0307)	31.3/31.6	0.00580
MC1	1.00	5.42 (0.0266)	32.5/32.6	0.00346
MVRO	1.00	5.43 (0.0265)	32.8/33.1	0.00353

[1] See Table I for abbreviations of the mating schemes.

[2] Average of generation 16–20.

MC1 and MVRO schemes compared with the R scheme. 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), MC schemes (4.3% higher than R) and CREL1 scheme (3.4% higher than R). The G_{20} was similar for the C, CREL and R schemes.

3.4. Genetic response in large schemes with low inbreeding

The G_{20} was in general higher for larger schemes (Tab. IV), when the number of selection candidates was 200, compared with 100 for the smaller schemes, and ΔF was constrained to 1.0%. The superiority of the non-random schemes was about the same as for the schemes with a less stringent constraint on ΔF (2.5%) and 100 selection candidates. The G_{20} was significantly higher for the non-random mating schemes than for the R scheme; the G_{20} was the highest for the MVRO and MC1 schemes (7.1 and 6.9% higher than R, respectively), although differences between the non-random mating schemes were mostly not significant.

3.5. Number of selected animals

The highest number of animals was selected for the R scheme and the lowest number for the MC scheme when ΔF was constrained to 1% and the number of selection candidates was 100 (Tab. III). This suggests that the increase of genetic response due to non-random mating resulted (partly) from the selection of fewer animals, *i.e.* increased selection differential. There was a small trend of selecting more animals with decreasing heritability. This was probably because the lower heritability resulted in a higher correlation between EBV of relatives. Hence, the selected animals would be more related, which was compensated here by selecting more animals. The number of animals selected was about half when ΔF was constrained to 2.5% per generation, compared with when ΔF was constrained to 1.0% per generation (Tab. IV), 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 with the smaller schemes (Tab. IV), which indicates that the intensity of selection has increased for the larger schemes. Meuwissen and Sonesson [13] found a similar result for Optimum Contribution selection schemes with overlapping generations.

3.6. Variance of relationship of the selection candidates

Optimum Contribution selection accounts for relationships among the animals while selecting for high EBV. If there are no extreme relationships in the population, *i.e.* the variance of the relationships, V_{rel}, is low, selection is expected to put more emphasis on the differences in EBVs and yield higher selection differentials. There was a general tendency for schemes with low V_{rel} to obtain high G_{20} (Tabs. III and IV), which confirmed that a lower V_{rel} is an indication of a better family structure. More specifically, V_{rel} was the lowest for the MC1 and MVRO schemes and generally the highest for the R scheme, but V_{rel} was also high for the C schemes.

4. DISCUSSION

4.1. Inbreeding

Although non-random mating can reduce rates of inbreeding in phenotypic or BLUP selection schemes [2], it did not reduce the rate of inbreeding in combination with Optimum Contribution selection (Fig. 1). This was probably because the Optimum Contribution selection method enforces a constant rate of increase of coancestry in the population and mating schemes can only reduce coancestry of mated animals by a fixed amount compared with the average of the selected animals (about 2% points in Fig. 1). Hence, the rate of inbreeding has to follow the rate of increase of coancestry, although possibly with some delay. Although Optimum Contribution selection makes sure that the increase of the coancestry is as predefined, it does take advantage of any improvement in family structure, due to the mating schemes. It takes this advantage by selecting fewer animals (Tabs. III and IV), and thus increasing selection differentials, which is suggested by the increased genetic response.

4.2. Genetic response

Non-random mating schemes yielded an increase in genetic response of up to 22% compared with random mating schemes (Tab. III). This increase in genetic response was probably due to three effects, which were to some degree achieved by all the non-random mating schemes:

1. Connecting contributions of unrelated families (especially for minimum coancestry mating). If a sire and dam are unrelated, ancestors that contributed to the sire are different than those that contributed to the dam, and *vice versa*, but the offspring of this sire and dam will have contributions from both groups of ancestors, which will make contributions in the progeny generation more equal. The latter reduces the effect of selection of certain offspring on the contributions of the ancestors to the next generation. Hence, selection of offspring becomes more independent from that of earlier generations, giving the Optimum Contribution algorithm more opportunity to increase genetic response, without affecting optimum contributions of previous generations.
2. Avoiding extreme relationships of offspring (especially for mating which achieves minimum variance of relationship of offspring and for schemes with one offspring per mating pair) makes the offspring more independent, giving the Optimum Contribution algorithm more opportunity to increase genetic response within a generation. In a sense, it increases the effective number of offspring. The restriction of having only one offspring per mating pair, *i.e.* factorial mating, also avoids extreme relationships, since there are no fullsib offspring.
3. Reduced inbreeding levels of the offspring and thus of the parents of the next generation (especially for minimum coancestry mating). Reduced inbreeding levels will achieve larger Mendelian sampling variances, *i.e.* the term $1/2(1 - \overline{F})\sigma_a^2$ is larger, resulting in more genetic variance, and thus also in more genetic response. 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 response. Because of these two opposite impacts on genetic response and because schemes do not differ much in levels of inbreeding, this third effect of non-random mating is probably the 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.* compensatory mating will also lead to mating of less related animals. The above effects of non-random mating can be quantified as follows. MC1 mating combines the first and second effect, since it avoids fullsib relationships of the offspring. Hence, the ratio $[G_{20}(\mathrm{MC}) - G_{20}(\mathrm{R})]/[G_{20}(\mathrm{MC1}) - G_{20}(\mathrm{R})]$, which ranges from 0.62 to 1.00 depicts the proportion of the effect of MC1 that is achieved by minimum coancestry mating. Similarly, the ratio $[G_{20}(\mathrm{R1}) - G_{20}(\mathrm{R})]/[G_{20}(\mathrm{MC1}) - G_{20}(\mathrm{R})]$, which ranges from 0.71 to 0.96 depicts the proportion of the effect of MC1 that is due to the avoidance of fullsib relationships. Since these two fractions do not add to one, the effects of minimum coancestry mating and avoidance of fullsib relationships are not additive. If minimum coancestry mating is introduced in addition to the restriction of one offspring per mating pair, it yields less extra genetic response compared with when it replaces an R scheme. Similarly, the restriction of one offspring per mating pair yields less extra genetic response when introduced in an MC scheme compared with when it is introduced in an R scheme.

Because MVRO schemes result in as much as or less response than MC1 schemes, it seems that avoidance of fullsib mating is a sufficient measure to avoid extreme relationships. The fact that MVRO also attempts to avoid other high relationships than fullsibs does not seem to yield extra genetic response. There are three categories of relationships in a population, namely fullsibs, halfsibs and other less related animals. Fullsib relationships may be avoided at the expense of more halfsib relationships, but halfsib relationships cannot be avoided when animals have more than one offspring. The avoidance of strong relationships within the category of other relationships does probably not improve family structure much, such that avoidance of fullsib matings results in about all response that can be achieved by avoiding extreme relationships.

Robertson [16] showed that with phenotypic selection, the genetic superiority of some families increases their contributions for many generations, at the expense of less successful families. Compensatory mating is designed to reduce this cumulative effect of phenotypic selection on genetic contributions (Robertson's [16] Q^2 term) by linking contributions from unsuccessful families to those of successful. Optimum Contribution selection controls the contributions of ancestors and thus also the cumulative effect of selection. Therefore, compensatory mating schemes without the restriction of only one offspring per mating pair (C and CREL schemes) that reduce the cumulative effect of selection with BLUP or phenotypic selection, are partly redundant when applied with Optimum Contribution selection. On the other hand, compensatory mating will also often result in mating of rather unrelated animals and its effect are therefore to some extent similar to that of minimum coancestry mating. This difference in mechanisms between selection methods may explain why compensatory mating schemes often ranked lowest of the non-random mating schemes (Tabs. III and IV), although these differences were mostly not significant.

4.3. Effects of breeding scheme

There was a large difference in how much genetic response increased between schemes, mainly depending on the size of schemes and on the constraint on ΔF. Benefits of non-random mating strategy were smallest for large schemes and for schemes with high rates of inbreeding, (Tabs. III and IV). This was probably because there is 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, which may be denoted by lower variance of the relationships of the offspring, V_{rel}, has large effect on genetic response in schemes with low ΔF and/or small numbers of selection candidates (see Results section).

For larger schemes with 200 selection candidates, the larger families (twice as many animals per generation, but about the same number of selected animals) in combination with the same number of families results in more within family selection, even if selection is for BLUP-EBV. Hence, the weight of family relationships in the quadratic index (1) is smaller and the structure of selection candidates is less important. Therefore, the effect of non-random mating was also reduced to about the same level as for schemes with 100 selection candidates and less constrained ΔF (2.5%).

4.4. Variance of the relationships of the offspring

In general, there was a tendency for mating schemes with low variance of relationship of offspring, V_{rel}, to have high G_{20} (Tabs. III and IV). The MVRO scheme was developed to minimise V_{rel}, but V_{rel} tended to be lower for the MC1 schemes than for the MVRO schemes. To test the efficiency of the MVRO algorithm of achieving lowest V_{rel}, V_{rel} was calculated separately for a particular set of candidates by the MC1 and MVRO algorithms. Here, V_{rel} was lowest for MVRO in the next generation, but in later generations V_{rel} was somewhat lower for MC1. This might be because the number of animals being selected was somewhat smaller for MVRO (Tabs. III and IV), which reduces its opportunities for achieving a low V_{rel}.

4.5. Simultaneous optimisation of selection and mating

The Optimum Contribution selection program gives the number of offspring per selected animal. This is computationally an advantage for the mating algorithms presented here as compared to those that optimise selection and mating simultaneously [3,10,21]. Current algorithms do not have to optimise over all selection candidates, but only over selected animals. This and the use of the simulated annealing algorithm probably make the current mating algorithm computationally faster than for example the linear programming algorithm of Toro and Pérez-Enciso [21] and Fernández and Toro [3], which have to include all selection candidates. Kinghorn [10] facilitated the computation by first making a selection out of clusters of animals, grouped on for example age, breed, herd and EBV, and thereafter selecting and mating animals out of these preselected animals. Fernández and Toro [3] found that simultaneous selection and mating give similar results to first selection and then mating as was applied here. There are however also differences in computer time between the mating algorithms presented here. R1 was fast, because the annealing algorithm did not have to lead to an optimal solution, but it only had to randomise mating pairs. The C, CREL and CREL1 algorithms were fast, because selected animals just had to be ranked and mated according to their compensatory mating criterion. The MC, MC1 and MVRO algorithms were much slower than the other algorithms, and the MVRO algorithm needed the most computer time. This difference in computer time can be explained by that MC and MC1 only have to consider a matrix of relationships of size $(N_s \times N_d)$, whereas MVRO optimises over a matrix of size $(N_s * N_d \times N_s * N_d)$.

4.6. Practical breeding schemes

In most practical 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 [11] may yield both the required number of offspring per dam and the control over parentage of every offspring. Similarly, for pig schemes, embryo transfer [8] may result in an increased control of numbers of offspring and their parentage.

Assortative and disassortative matings based on EBV or phenotype have also been suggested as alternative mating methods, see [4,15,24] and others. These methods do not, however, directly affect and/or improve family structure, which renders them outside the scope of this paper, where improvements of family structure are expected to improve selection response when rates of inbreeding are restricted.

Of the schemes considered here, MC1 and MVRO consistently yielded the highest genetic response, although the differences with the other schemes were not always statistically significant. The MC1 scheme may be preferred over the MVRO scheme, because of its lower computational costs.

ACKNOWLEDGEMENTS

We would like to thank Pim Brascamp, Ab Groen, Kor Oldenbroek and Piter Bijma for their useful comments on the manuscript.

REFERENCES

[1] Brisbane J.R., Gibson J.P., Balancing selection response and rate of inbreeding by including genetic relationships in selection decisions, Theor. Appl. Genet. 91 (1995) 421–431.

[2] Caballero A., Santiago E., Toro M.A., Systems of mating to reduce inbreeding in selected populations, Anim. Sci. 62 (1996) 431–442.

[3] Fernândez J., Toro M.A., The use of mathematical programming to control inbreeding in selection schemes, J. Anim. Breed. Genet. 116 (1999) 447–466.

[4] Fisher R.A., The correlation between relatives on the supposition of Mendelian inheritance, Trans. R. Soc. Edinb. 52 (1918) 399–433.

[5] Grundy B., Villanueva B., Woolliams J.A., Maximising response with a predefined rate of inbreeding for overlapping generation structure, in: Proc. British Society of Animal Science, Scarborough, 1997, p. 27.

[6] Grundy B., Villanueva B., Woolliams J.A., Dynamic selection procedures for constrained inbreeding and their consequences for pedigree development, Genet. Res. 72 (1998) 159–168.

[7] Grundy B., Villanueva B., Woolliams J.A., Dynamic selection for maximizing response with constrained inbreeding in schemes with overlapping generations, Anim. Sci. (in press).

[8] Hazeleger W., Kemp B., State of the art in pig embryo transfer, Theriogenology 51 (1999) 81–90.

[9] Henderson C.R., Applications of Linear Models in Animal Breeding, University of Guelph Press, Guelph, 1984.

[10] Kinghorn B.P., Mate selection by groups, J. Dairy. Sci. 81 (1998) 55–63.

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

[12] Meuwissen T.H.E., Maximizing the response of selection with a predefined rate of inbreeding, J. Anim. Sci. 75 (1997) 934–940.

[13] Meuwissen T H E., Sonesson A.K., Maximizing the response of selection with a predefined rate of inbreeding: overlapping generations, J. Anim. Sci. 76 (1998) 2575–2583

[14] Press W.H , Flannery B.P., Teukolsky S.A., Vetterling W.T., Minimization or maximization of functions, in: Numerical recipes- the art of scientific computing. University of Cambridge Press, 1989, pp. 274–334.

[15] Reeve E.C.R., Studies in quantitative inheritance. III. Heritability and genetic correlation in progeny tests using different mating systems, J. Genet. 51 (1953) 520–542.

[16] Robertson A., Inbreeding in artificial selection programmes, Genet. Res. 2 (1961) 189–194.

[17] Santiago E., Caballero A., Effective size of populations under selection, Genetics 139 (1995) 1013–1030.

[18] Sonesson A.K., Grundy B., Woolliams J.A., Meuwissen T.H.E., Selection with control of inbreeding in populations with overlapping generations: a comparison of methods, Anim. Sci. 70 (2000) 1–8.

[19] Toro M.A., Nieto B., A simple method for increasing the response to artificial selection, Genet. Res. 44 (1984) 347–349.

[20] Toro M.A., Nieto B , Salgado C., A note on minimisation of inbreeding in small-scale selection programmes, Livest. Prod. Sci. 20 (1988) 317–323

[21] Toro M., Pérez-Enciso M., Optimisation of selection response under restricted inbreeding, Genet. Sel. Evol. 22 (1990) 93–107.

[22] Woolliams J.A., Modifications to MOET nucleus breeding schemes to improve rates of genetic progress and decrease rates of inbreeding in dairy cattle, Anim. Prod. 49 (1989) 1–14.

[23] Wray N.R., Goddard M.E., Increasing long-term response to selection, Genet Sel. Evol. 26 (1994) 431–451.

[24] Wright S., Systems of mating. I. The biometric relations between parent and offspring, Genetics 6 (1921) 111–123.

APPENDIX

Implementation of the simulated annealing algorithm

Minimum coancestry matings were obtained by applying the simulated annealing algorithm [14]. In a feasible starting solution, each sire and dam obtained the number of offspring that was assigned by the Optimum Contribution selection method (and only one offspring per mating pair 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, in sequence. This was similar to C schemes, but with the difference that for

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

Figure 2. Suggested modifications of the current solution for the annealing algorithm. All indicated changes have to be made simultaneously to maintain the total number of offspring selected for each sire and dam. 1 → 0 indicates that the mating conducted in the present solution is not conducted in the alternative solution, and 0 → 1 indicates the opposite.

MC1 schemes, more than one offspring per mating pair was not allowed when it could be avoided, whereas it was allowed for the MC and C schemes.

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 one alternative set of matings at a time, where the changes of matings are sampled randomly, although the number of progeny per each specific sire and dam must remain constant. This is achieved by the modifications in Figure 2, which shows that an alternative set of matings contains four changes compared with the original set. Sires 1 and 2 and dam 1 and 2 were randomly chosen, with the restriction that their matings in the current solution were as indicated in Figure 2. 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.* $\delta = a_{s_1d_2} + a_{s_2d_1} - a_{s_1d_1} - a_{s_2d_2}$, where $a_{s_id_j}$ is the coancestry coefficient of sire i and dam j. When δ is smaller than zero, replace 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 is large or Temp is small.
3. When the current set of matings was replaced $10 * n_{\max}$ times by an alternative set of matings or when $100 * n_{\max}$ alternative set of matings have been evaluated, the "temperature", Temp, is decreased by 10%, $n_{\max}$ is the maximum of the number of sires and 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 solution and Temp is too low to accept a reduction of V_0. Otherwise go to step 2.

To achieve a solution for MC1, the annealing algorithm will not accept an alternative solution, which contains more than one offspring per mating pair.

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 $V_0 = \mathbf{m}'\mathbf{V}\mathbf{m}$ over sets of matings, where $\mathbf{m}$ contains the number of offspring of the mating pair ij, and the $\mathbf{V}$ matrix yields the term that a pair of possible future offspring would contribute to the variance of the relationship of offspring, as defined in Section 2.6. 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

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

where $\sum_{\substack{i\in\text{mating}\\ j\neq i_1 i_4}}$ denotes summation over all progeny that are produced by the current set of matings, except for mating pairs i_1 and i_4. The mating pair 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 (Fig. 2). 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 [14].