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Long-term effects of selection based on the animal model BLUP in a finite population

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Abstract. Monte Carlo simulation was used to assess the long-term effects of truncation selection within small populations using indices ($I = \omega f + m$) combining mid-parent [$f = (a_s + a_d)/2$] and Mendelian-sampling ($m = a - f$) evaluations provided by an animal model BLUP ($a = f + m$). Phenotypic values of panmictic populations were generated for 30 discrete generations. Assuming a purely additive polygenic model, heritability (h^2) values were 0.10, 0.25 or 0.50. Two population sizes were considered: five males and 25 females selected out of 50 candidates of each sex (small populations, S) and 50 males and 250 females selected out of 500 candidates in each sex (large populations, L). Selection was carried out on the index defined above with $\omega = 1$ (animal model BLUP), $\omega = 1/2$, or $\omega = 0$ (selection on within-family deviations). Mass selection was also considered. Selection based on the animal model BLUP ($\omega = 1$) maximized the cumulative genetic gain in L populations. In S populations, selection using $\omega = 1/2$ and mass selection were more efficient than selection under an animal model (+3 to +7% and +1 to +4% respectively, depending on h^2). Selection on within-family deviations always led to the lowest gains. In most cases, the variance of response to selection between replicates did not depend on the selection method. The within-replicate genetic variance and the average coefficient of inbreeding (F) were highly affected by selection with $\omega = 1$ or $1/2$, especially in populations of size S. As expected, selection based on within-family deviations was less detrimental in that respect. The number of copies of founder neutral genes at a separate locus, and the probability vector of origin of the genes in reference to the founder animals, were also observed in addition to F values. The conclusion was that selection procedures placing less emphasis on family information might be interesting alternatives to selection based on animal model BLUP, especially for small populations with long-term selection objectives.

Key words: Animal model BLUP – Genetic response – Genetic variability – Inbreeding

Introduction

Mid- and long-term responses to selection depend on changes in additive genetic variance. Under a purely additive polygenic model, and even for an infinite population, directional selection modifies the genetic variance by inducing linkage disequilibrium (Lush 1945; Bulmer 1971). If populations are of finite size, selection affects the family structure, increasing the loss of genetic variability by inbreeding (Lush 1946; Robertson 1961). In this case, the choice of a selection criterion should be made on the basis of the expected cumulative genetic gain in the long term rather than the response to one generation of selection. Some simulation results (Dempfle 1975; Toro and Perez-Enciso 1990) or deterministic prediction results (Verrier et al. 1989a) suggest that using the conventional weights (according to selection index theory) for individual and family information does not lead to maximum response in the long term. Furthermore, a too-high rate of inbreeding might have direct economic consequences as a result of inbreeding depression which mainly affects reproduction and viability traits.

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Mixed model methodology is currently used for predicting breeding values, and genetic evaluation procedures for livestock are now worldwide based on the animal model BLUP[1] (Van Raden 1990). It has been shown that the mixed model methodology and the animal model have optimal properties regarding the expected genetic gain after one generation of selection (See for example, Henderson 1975; Fernando and Gianola 1986; Kennedy and Sorensen 1988; Kennedy et al. 1988). However, since all genetic relationships are accounted for, more-related animals are likely to be selected, leading to higher inbreeding rate and loss of genetic variance, as verified by Belonsky and Kennedy (1988) and Quinton et al. (1992) from Monte Carlo simulation.

How to choose an optimal selection criterion for long-term purposes should be investigated via prediction algorithms taking into account the effects of both drift and selection on genetic variance (See Verrier et al. 1991, for a review). However, even in simple cases, these algorithms do not deal correctly with selection procedures based on estimated breeding values (EBV) computed by BLUP. Therefore, our investigation of the long-term effects of selection based on AM-BLUP evaluation was carried out via Monte Carlo simulation. Alternatives to EBVs derived from the conventional animal model were introduced by assigning different weight to the pedigree information.

Simulation processes

Panmictic populations of constant size (N) with separate generations (N_m sires and N_f dams per generation) were simulated. No fixed environmental effects were considered, as they are not relevant to the problem addressed here. The underlying genetic model was the additive polygenic model, i.e., one assuming a very large number of independent loci with additive effects, and with no mutation.

The base population was assumed to be in linkage equilibrium, with an initial genetic variance ($\sigma^2_{A_0}$) chosen as unity. Genetic values in the initial generation were, therefore, randomly chosen out of a $N(0, 1)$ distribution. Afterwards, the genetic value of an animal (a_i) was generated from the values of its sire (a_s) and dam (a_d) according to the usual formula:

$$a_i = \tfrac{1}{2}a_s + \tfrac{1}{2}a_d + \theta_i\sigma_w,$$

where θ_i is an independent random number taken from an $N(0, 1)$ distribution, and σ_w is the within full-sib family genetic standard deviation. σ^2_w was calculated, for any pair of parents, according to the usual formula (Foulley and Chevalet 1981):

$$\sigma^2_w = \tfrac{1}{2}\sigma^2_{A_0}\left(1 - \frac{F_s + F_d}{2}\right),$$

where F_s and F_d are the coefficients of inbreeding of the sire and the dam respectively. This formula was shown to be valid for the genetic model assumed here, even under selection (Verrier et al. 1989b; Langlois 1990). For any animal with a genetic value a_i, the corresponding phenotypic value (y_i) was:

$$y_i = a_i + \varepsilon_i\sigma_e,$$

where ε_i is a random number taken from an $N(0, 1)$ distribution, and σ_e is the environmental standard deviation, assumed to be constant over generations. Three values of the initial heritability of the selected trait (h^2) were chosen: 0.10, 0.25 and 0.50, corresponding to $\sigma_e = 3$, $\sqrt{3}$ and 1 respectively.

An independent neutral locus was simulated: each of the $2N$ variants present in the N base animals was labelled from 1 to $2N$. Transmission to offspring was simulated as a random sampling, with replacement, from labelled genes of the sire and dam.

In each generation, N_m males and N_f females were selected out of T candidates of each sex ($T = N/2$). Matings were hierarchical and at random: a given dam was mated to only one male, which was chosen with replacement in the list of N_m possible sires. The number of offspring per dam was constant and equal to two males and two females. Two population sizes were considered:

populations of size S: $N_m = 5$, $N_f = 25$, $T = 50$;
populations of size L: $N_m = 50$, $N_f = 250$, $T = 500$.

Populations of size L are similar to pooling ten populations of size S, with the same familial structure and the same selection pressure, i.e., 1/10 for males and 1/2 for females. For simplicity, the simulated populations were named S10, S25 and S50 for populations of size S (with $h^2 = 0.10$, 0.25 and 0.50 respectively) and, correspondingly, L10, L25 and L50 for populations of size L.

Mass selection was used as a reference selection method, keeping in mind that data were free from systematic environmental effects.

For other selection procedures, the animals were evaluated according to the following animal model:

$$\mathbf{y} = \mu + \mathbf{Z}\mathbf{a} + \mathbf{e},$$

where $\mathbf{y}$ is the vector of observations, μ the overall mean, $\mathbf{a}$ the vector of individual genetic values, $\mathbf{Z}$ the incidence matrix and $\mathbf{e}$ the vector of errors. Henderson's (1976) rules were used for computing the inverse of the relationship matrix ($\mathbf{A}^{-1}$), accounting for the individual inbreeding coefficients. Since generations did not overlap, the inverse of the relationship matrix was block-tridiagonal, and a block Gauss-Seidel procedure was used to solve the mixed model equations. Then, a selection index (I_i) was computed by combining the estimates of the mid-parent genetic value (f_i) and of the Mendelian sampling genetic value (m_i):

$$I_i = \omega\hat{f}_i + \hat{m}_i,$$

with

$$\hat{f}_i = \tfrac{1}{2}(\hat{a}_s + \hat{a}_d) \text{ and } \hat{m}_i = \hat{a}_i - \hat{f}_i,$$

where $\hat{a}_i$, $\hat{a}_s$, $\hat{a}_d$ are the predictors of the candidate ($\hat{a}_i$), its sire ($\hat{a}_s$), and its dam ($\hat{a}_d$) respectively, from applying a conventional animal model. Three values were given to the weight ω:

$\omega = 1$, i.e., a conventional animal model;
$\omega = 0$, i.e., selection on within-family deviations (Hill 1985), also called "unrestricted within-family selection" by Dempfle (1990);
$\omega = 1/2$, i.e., a modified animal model with less emphasis on family information.

Emphasis on within-family deviation (m_i) is a simple way to achieve the real objective of choosing parents with less relationship.

At each generation, and for each replicate, the genetic mean and the genetic variance of the selected trait and the average

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[1] From now on referred to as AM-BLUP

coefficient of inbreeding were computed from the individual values. Furthermore, the proportion of inbred animals at the independent neutral locus was calculated by comparing paternal- and maternal-labelled genes. The males and females chosen at generation zero were considered to be founders of the population. At a given generation, the proportion of original genes at the independent locus still existing with at least one copy in the population was computed by comparing existing labelled genes with the 2 $(N_m + N_f)$ genes in the founders. For populations of size S only, at each generation, the probability matrix of gene origin [N offspring $\times (N_m + N_f)$ founders] was computed. At generations 5, 10, ..., 30, the probability vector of gene origin (of size $N_m + N_f$) was recorded, through ranking the founders by their decreasing contribution to the gene pool.

Each situation was run with 200 replicates for the very small populations and with 100 replicates for the larger populations. The reason for this difference lies in the observed standard deviation between replicates which was lower for populations of size L than for populations of size S. For a given parameter, these numbers of replicates allowed the detection of significant differences of the means of about the same magnitude in populations of both sizes. For each generation, homogeneity among selection procedures for the variance between replicates was examined using Bartlett's test, assuming a normal distribution of the simulated results.

Results

After 30 generations, mass selection provided the following cumulative genetic gains: 7.3, 11.1 and 15.2 units of initial genetic standard deviation in populations S10, S25 and S50 respectively; 10.8, 16.1 and 21.3 units of initial genetic standard deviation in L10, L25 and L50 respectively. Increasing initial heritability or population size enhanced these gains, as expected. Figure 1 shows the relative cumulative gains obtained by using different selection methods, compared with mass selection as a reference. As expected, animal model evaluations ($\omega = 1$) always led to maximum genetic gains during the first generations. In larger size populations (L), the AM-BLUP gave the highest cumulative response. This result was not true for very small populations (S), because selection with $\omega = 1/2$ led to higher cumulative genetic gains: this phenomenon occurred from generations 8, 8 and 16 onwards in S10, S25 and S50 respectively. At the end of the process, the relative superiority of this procedure compared to a conventional animal model was $+7.4\%$ $+7.0\%$ and $+3.5\%$ in S10, S25 and S50 respectively; these differences were highly significant ($P < 0.001$). In populations of both sizes, unrestricted within-family selection ($\omega = 0$) always led to the lowest genetic gains ($P < 0.001$). In populations of size S, the effect of mass selection was found to be intermediate between those of $\omega = 1$ and $\omega = 1/2$: after 30 generations, mass selection was better than selection on an animal model by $+4.2\%$ and $+2.4\%$ in S25 and S50 respectively ($P < 0.001$ in each case), but the difference in final genetic mean was not significant in S10. In populations of size L, mass selection was less efficient than selection on an animal model ($P < 0.001$).

Figure 2 shows the plot of the standard deviation among replicates of the genetic mean against the generation number. As expected, the higher the population size, the smaller the variance between replicates of the genetic mean ($P < 0.001$). At a given generation, the variance between replicates was not found to depend on selection method, except for population L10: from the third generation onwards, selection with $\omega = 1$ or

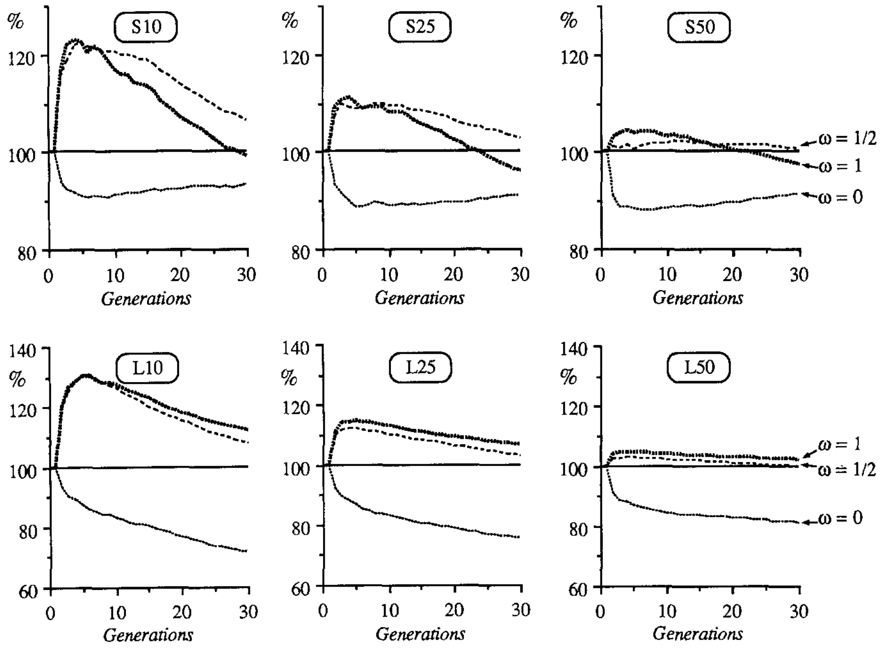

Fig. 1. Change in the genetic mean in simulated populations with different values of ω (see text). The observed values are expressed as percentages of means obtained under mass selection. Mean of 200 and 100 replicates in populations of size S and L respectively. Note that the scale is not the same for populations of size S and L

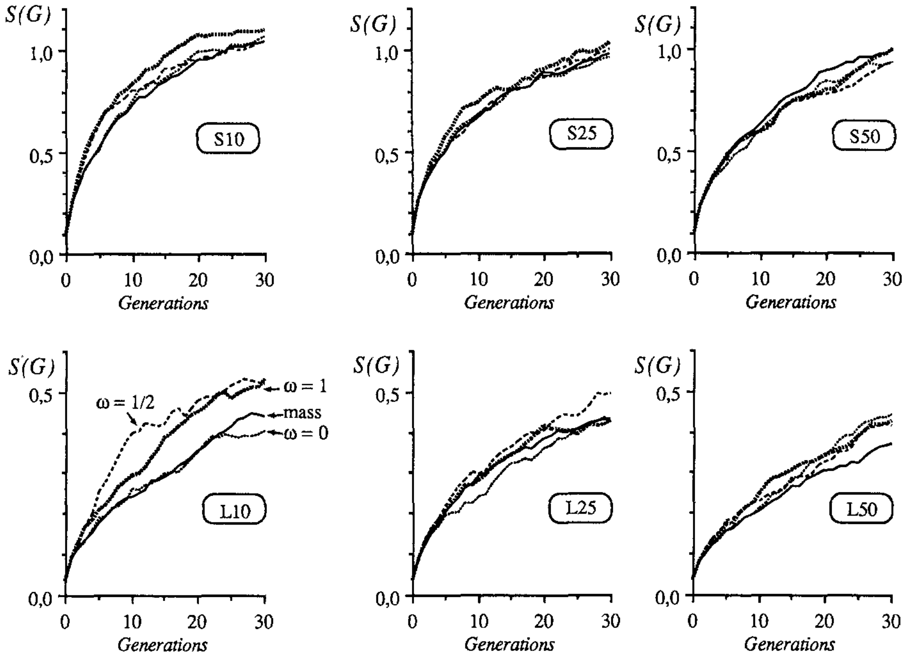

Fig. 2. Change in the standard deviation among replicates of the genetic mean [$S(G)$] for simulated populations. Note that the scale is not the same for popualtions of size S and L

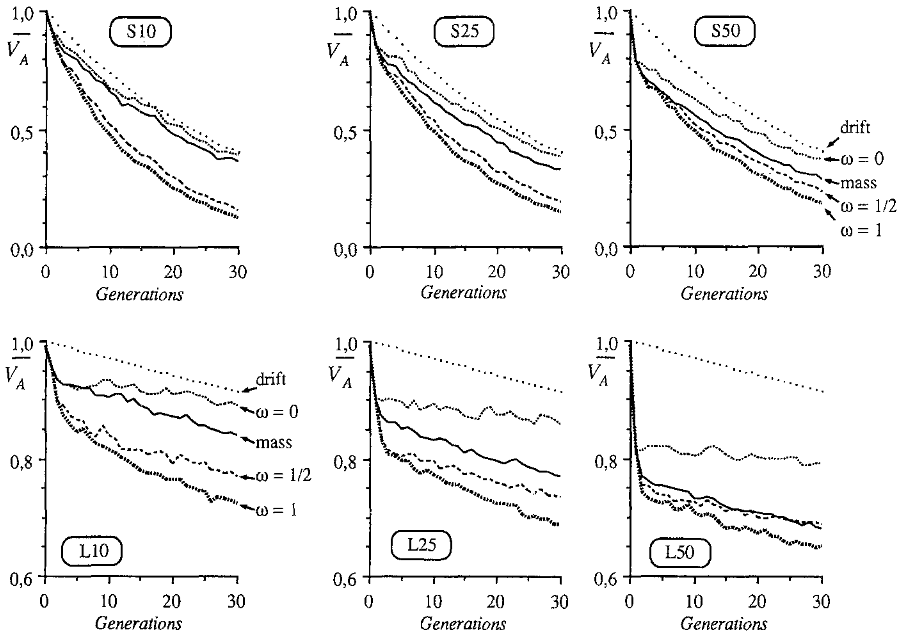

Fig. 3. Change in the genetic variance ($\overline{V_A}$) in simulated populations. Mean of 200 and 100 replicates in populations of size S and L respectively. Note that the scale is not the same for populations of size S and L

$\omega = 1/2$ led to more-variable response in population L10 ($P < 0.05$ or $P < 0.001$, depending on the generation number).

Figure 3 shows the change over time in the genetic variance (denoted $\overline{V_A}$ and computed as the mean over replicates of the within-replicate variance) in the simulated populations. The predicted values of $\overline{V_A}$ under pure drift (Wright 1931) are also reported in this figure. Due to the effect of selection, the observed (simulated) values of $\overline{V_A}$ under selection were always lower than those predicted under drift. This observation holds even for $\omega = 0$, because the first generation of selection corresponds to a mass selection in any case (the parents of the animals of the base population are unknown). Due to a larger number of parents, $\overline{V_A}$ decreased less in populations of size L than in populations of size S. Selection procedures based on $\omega = 1$ and $\omega = 1/2$ resulted in the largest decrease in genetic variance over time while, on the contrary, unrestricted within-family selection ($\omega = 0$) resulted in the smallest decrease in genetic variance, as expected. The smaller the initial heritability and the population size, the bigger the differences in $\overline{V_A}$ among selection methods. Expressed as a percentage of the value obtained under mass selection, the difference in values of $\overline{V_A}$ at generation 30 between animal model and mass selection were −66%, −55% and −37% in S10, S25 and S50 respectively, and −13%, −10% and −5% in L10, L25 and L50 respectively.

As pointed out by Hill (1977), it is not only the average within-line genetic variance that contributes to the variability of response between lines, but also the variance between lines of the within-line variance [Var (V_A)]. Both of these parameters depend largely on linkage disequilibrium induced by both selection and random sampling (Bulmer 1976; Avery and Hill 1977). For populations without selection, Avery and Hill (1977) derived a formula for Var (V_A):

$$\text{Var}(V_{A_t}) = 2\overline{r_t^2}[E(V_{A_t})]^2,$$

where t refers to the generation number and $(\overline{r_t^2})$ is the average squared correlation among all loci affecting the trait, depending on linkage disequilibrium. Because Var (V_A) is proportional to $(\overline{V_A})^2$, an attempt to investigate the change in the variance in genetic variance independently from the average value was made by observing the change in the coefficient of variation [CV (V_A)] over time (Fig. 4). In fact, it seems that the observed change in $CV(V_A)$ was not related to the significant decrease in $(\overline{V_A})$ which occurred in all populations. As expected, the higher the population size, the smaller the $CV(V_A)$. This coefficient increased from generation zero to generation 1; the observed values at this generation were within the range of the numerical values predicted by Hill (1977). Next, the change in $CV(V_A)$ was erratic, especially in populations of size L. In the late generations in populations of size S, higher values of $CV(V_A)$ were obtained when selecting with $\omega = 1$ or $\omega = 1/2$, whereas in L populations the situation was much more complex.

Figure 5 shows the change in the average coefficient of inbreeding (F). As expected, the smaller the number of parents, the higher the rate of inbreeding. An important increase in F occurred over time under selection based on $\omega = 1$ or $\omega = 1/2$. On the other hand, selecting on within-family deviations ($\omega = 0$) generated the lowest values of F throughout the selection process. Actually, the values obtained with $\omega = 0$ were very similar to those expected under pure genetic drift (the observed values were higher than the expected ones only by 0.5% to 3% in S populations and 0.5% to 4% in L populations) so that the choice of families under that selection procedure does not appear to differ from a random process. The absolute differences between selection methods were all the more important as the initial heritability and the population size were small (as for the genetic variance). Expressed as a percentage of the value obtained under mass selection, the difference in the final average coefficient of inbreeding between the animal model and mass selection was +40%, +31% and +20% in S10, S25 and S50 respectively, and +124%, +82% and +36.1% in L10, L25 and L50 respectively. From the second generation, and

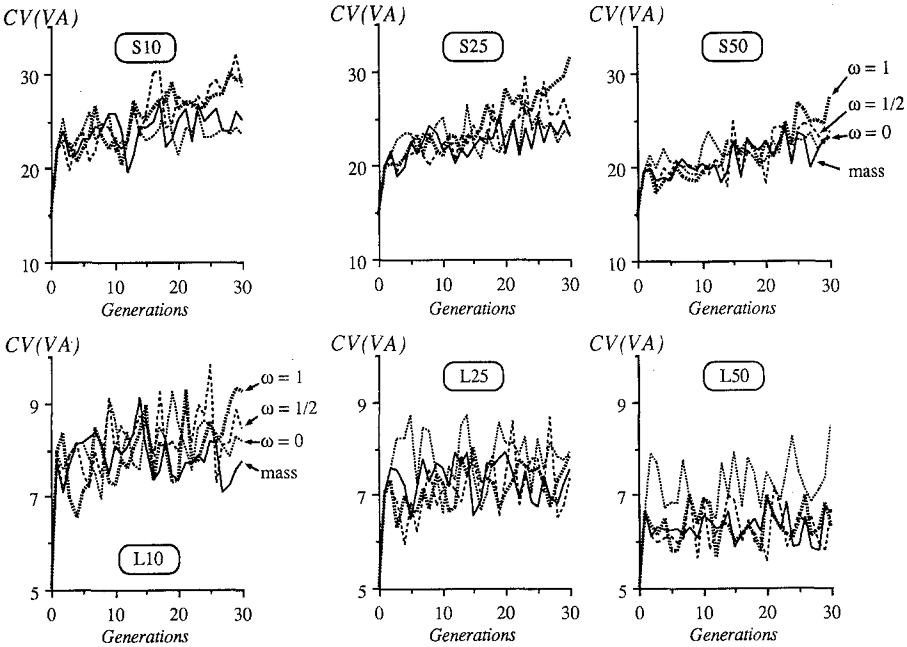

Fig. 4. Change in simulated populations in the coefficient of variation between replicates [$CV(VA)$] of the within-replicate genetic variance. $CV(VA)$ is expressed as a percentage of the average value over replicates. Note that the scale is not the same for populations of size S and L

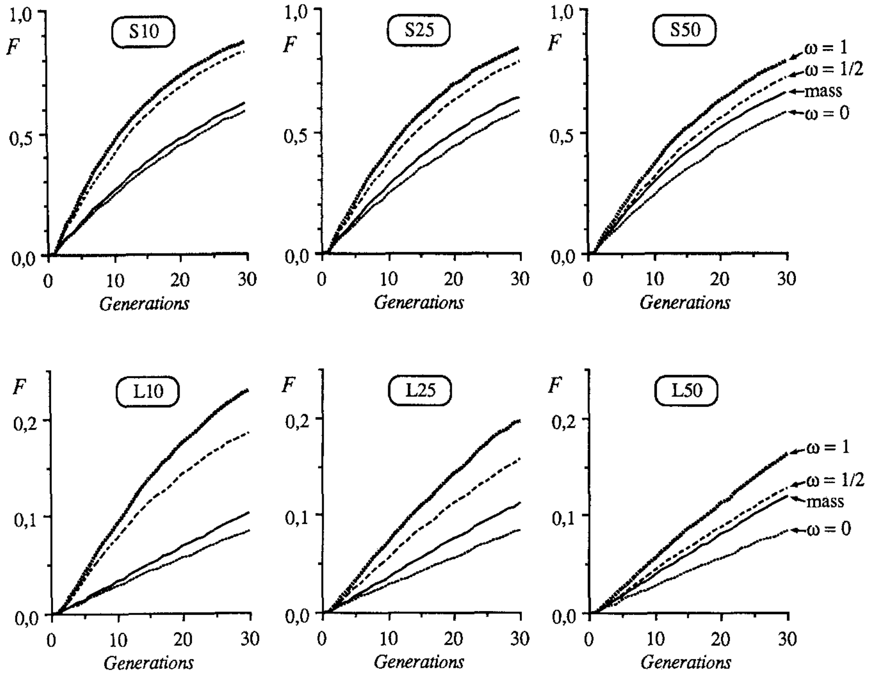

Fig. 5. Change in the average coefficient of inbreeding (F) in simulated populations. Mean of 200 and 100 replicates in populations of size S and L respectively. Note that the scale is not the same for populations of size S and L

Table 1. Proportion of founder genes (%) with at least one copy after 10 and after 30 generations of selection in simulated populations (200 and 100 replicates in populations of size S and L respectively)

Generation	Population	Mass selection	Selection on BLUPs Weight (ω) given to the mid-parent value $\omega = 1$	 $\omega = 1/2$	 $\omega = 0$
10	S10	11.3	6.6	7.5	12.0
	S25	10.6	7.3	8.4	11.8
	S50	10.5	8.4	9.8	11.8
	L10	10.2	4.9	5.9	11.1
	L25	9.7	5.8	7.1	11.3
	L50	9.2	7.0	8.4	11.4
30	S10	4.0	2.4	2.6	4.3
	S25	3.7	2.6	2.9	4.4
	S50	3.8	2.8	3.4	4.6
	L10	3.2	1.5	1.9	3.8
	L25	3.0	1.7	2.2	3.7
	L50	2.8	2.1	2.6	3.8

for all populations, the selection method was found to have a significant effect ($P < 0.001$) on the variance of F between replicates: the animal model ($\omega = 1$) always led to the highest variance among replicates whereas unrestricted within-family selection ($\omega = 0$) always led to the smallest variance among replicates.

Table 1 shows the proportion of founder genes with at least one copy at generations 10 and 30. Founder genes were lost dramatically in the first generations (about 90%). Additionally, from generation 10 to generation 30, approximately one-half to two-third of the remaining founder genes were lost (Table 1). In constrast with F, there was not a large effect of population size or of initial heritability of the selected trait on the loss of genes: for all populations, the proportion of genes still present was very low. In generation 30, the maximum proportion observed was only 4.6%. The number of genes still present in generation 30 was very low for populations of size S: from 1.4 to 2.8, which is near fixation. Different selection criteria led to different values, with a maximum loss of genes provided by selection based on BLUP evaluation with $\omega = 1$ or $\omega = 1/2$.

Table 2. Proportion of founder animals (%) with a non-null contribution to the vector of probabilities of origin of the genes in the 30th generation (populations of size S, mean of 200 replicates)

Population	Mass selection	Selection on BLUPs Weight (ω) given to the mid-parent value $\omega = 1$	 $\omega = 1/2$	 $\omega = 0$
S10	64.9	34.4	41.0	67.5
S25	61.2	38.5	45.8	68.6
S50	57.9	45.4	54.3	71.1

In populations of size S, where it was recorded, the average probability vector of gene origin (with reference to the founder animals) became unbalanced from the first generations. The vector remained unchanged from the 15th generation onwards. As shown in Table 2, the probability vector of gene origin was the most unbalanced with $\omega = 1$ (AM-BLUP), especially when initial heritability of the selected trait was low.

Discussion

Expected cumulative response to selection

The results presented in this paper illustrate the conflict between short- and long-term goals. The AM-BLUP provides EBVs which used as a selection criterion will maximize the expected genetic value of a given number of candidates (Goffinet and Elsen 1984; Fernando and Gianola 1986). This is typically a short-term property which is valid only for one cycle of selection and may not apply to long-term cumulative response after many cycles of selection.

Using AM-BLUP evaluations leads to an important change in the family structure of the population, and consequently to higher inbreeding coefficients. The lower the heritability of the selected trait, the larger this change, due to increased emphasis on family information that results in larger correlations between EBVs of candidates from the same family. In this respect, our results are in agreement with the simulation data of Belonsky and Kennedy (1988) and Quinton et al. (1992) who compared the consequences of mass selection and selection based on AM-BLUP, but for a smaller number of generations. The increase in selection accuracy also magnified the loss of genetic variance through linkage disequilibrium induced by selection (Bulmer 1971). The combined effect of selection on inbreeding and linkage disequilibrium leads to a decrease in genetic variance, which is particularly large when using AM-BLUP. Genetic gains depend on genetic standard deviation adjusted for selection and inbreeding: higher gains obtained at the beginning of the selection with the animal model are, therefore, balanced with the reduced gains obtained later. In populations of size S, the effect of drift is large and genetic variance decreases quickly, with considerable differences among selection methods. In such populations, using AM-BLUP has a large impact on long-term gains, whereas selection methods that preserve genetic variance provide higher final cumulative gains. In contrast, in populations of size L, the effect of drift is not large and genetic variance remains substantial, with small differences among selection methods. Therefore, in populations of size L, even after 30 generations, selection criteria not based on the AM-BLUP cannot compensate for lower gains in the first generations with a greater maintenance of genetic variability. Other alternatives, such as selecting with $\omega = 1/2$, lead to similar cumulative gains with lower inbreeding coefficients, which may also be a parameter to consider in the choice of selection criteria.

Some technical factors not considered in this study, e.g., selection intensity, male/female ratio, and the prolificacy of females, could modify the conclusions for the long term. In particular, for a given number of selected parents, a higher selection intensity (i.e., from increasing the number of candidates) is expected to increase the probability that two selected parents come from the same family and, therefore, to lead to higher inbreeding coefficients. This conjecture is supported both by theoretical (Robertson 1961; Burrows 1984; Verrier et al. 1990; Wray and Thompson 1990) and by simulation (Quinton et al. 1992) results. In such a situation, one would be inclined to pay more attention to the ability of selection methods to maintain genetic diversity in the long term.

The conclusion about cumulative gain may also be modified for different assumptions. For example, including mutations should modify the expected evolution of genetic variance by providing a small additional amount of variation at each generation. Likewise, including dominance effects in the model could result in less decrease of the genetic variance under selection. However, it should be kept in mind that the hypotheses used in this study are the same as those underlying linear mixed model and BLUP theory. In particular, the property of BLUP, via the genetic relationship matrix among individuals, to adjust automatically for drift and selection effects back to the base population relies on the assumption of the infinitesimal model with purely additive gene effects (for a discussion, see Kennedy and Sorensen 1988; Verrier et al. 1989b). Therefore, it seems natural at first to use these genetic assumptions to question the AM-BLUP in the long run.

Variability of response to selection

The variability of response to selection could be a parameter of interest when choosing an optimal selection criterion, e.g., by assessing the probability to realize cumulative genetic gain above a target threshold (Nicholas 1980) or by penalizing variability for a given expected gain (Meuwissen 1991). The most striking result of the present study is that the selection method had no effect on the variability of response between lines in five out of the six simulated populations. In particular, selection on EBVs from the AM-BLUP does not contribute to a higher variability of selection response, a result that was not at all obvious when beginning this study.

In order to explain this result, an investigation of the effect of selection on the variance between replicates of the within-replicate variance was made. As shown by Hill (1977), selection as compared to drift is expected to have two opposite effects on the variance between lines of the within-line genetic mean: (1) a decrease in variance due to a reduction in differences among selected animals and (2) an increase in variance due to variation in within-line genetic variance. The more accurate the selection method, the more alike will be the selected parents and the larger the first effect of selection. Results observed in populations of size S tend to support the second effect since a higher selection accuracy seems to correspond to a larger variation coefficient between lines for V_A. This second effect might originate from increased variation in linkage disequilibrium (Hill 1977). The reason why this effect does not appear in populations of size L is unclear.

From a practical point of view, it would be interesting to compare observed values of the variance between lines of the genetic mean [$\mathrm{Var}(\overline{A_t})$] with the values predicted by the well known formula given by Wright (1931) for an ideal population of finite size and for a neutral trait determined by a purely additive model:

$$\mathrm{Var}(\overline{A_t}) = 2\overline{F_t}\sigma^2_{A_0},$$

where $\overline{F_t}$ is the average coefficient of inbreeding over lines and $\sigma^2_{A_0}$ is the genetic variance in the base population. On one hand, using for $\overline{F_t}$ the values predicted under pure drift (Crow and Kimura 1970, Eq. 7.1.4, with $N_e = 50/3$ and $500/3$ for populations of size S and L respectively) gives predicted values of the variance between replicates that are generally not in agreement with the observed values: in populations S10, L10 and L25, the variance was generally underestimated (by 10% to 50%), especially when selecting with $\omega = 1$; in populations S25, S50 and L50, the variance was generally overestimated (by 5% to 45%), especially when selecting on within-family deviations ($\omega = 0$). On the other hand, the variance between replicates was generally overestimated by the above equation when substituting for $\overline{F_t}$ the values of the average coefficient of inbreeding over replicates observed in the simulated populations; especially, when the selection is based on AM-BLUP evaluations ($\omega = 1$), the variance between replicates was overestimated by 25% to 100% in populations of size S and by around 100% in populations of size L.

Genetic variability for independent neutral loci

When choosing a selection method, one may also be concerned with the genetic diversity of the whole genome, and in particular with that of independent neutral loci. For a trait independent from the selected trait, the change in the average coefficient of inbreeding represents a good measure of the change in its genetic variability, though additive genetic variance is not exactly proportional to $1 - F$ in dioecious populations. However, consideration of alternative criteria to F may be worthwhile because, as pointed out by Chevalet and Rochambeau (1985), the same value of F can result from different genetic structures vis-à-vis the origin of genes.

The results observed for the probabilities of gene origin and the number of copies of original genes are worrying, especially the loss of founder genes after 30 and even 10 generations. More acute problems occur with selection based on the AM-BLUP. Actually, both parameters gave the same ranking as F for the selection methods in terms of their effect on the genetic variability. However, the parameters differed greatly in rate of change over time, with most changes occurring within the first generations for the additional parameters considered. This result suggests that if maintenance of genetic diversity has mainly long-term effects, its consequences may also occur in the short term.

Conclusion

Simulation results presented indicate that, for an additive polygenic model, selection based on the full AM-BLUP is able to maximize response, but procedures placing less emphasis on family information might be interesting alternatives to consider, especially for optimal management of small populations (e.g., closed selection nuclei) for long-term objectives. The selection rules proposed here involve truncation selection on EBVs calculated from the components of the AM-BLUP but with a lower weight on pedigree index. Other procedures have been suggested, such as direct use of pedigrees and search of mating designs minimizing the average coefficient of inbreeding in the next generation of selection (Toro and Perez-Enciso 1990). However, such procedures could be difficult to implement.

The relevance of a systematic use of AM-BLUP should be analyzed for other genetic models (e.g., major genes, non-additivity), by investigating both direct effects on the expected response to selection, and its variability, and indirect effects on unselected traits of possible interest for the future. In this respect, the results obtained here suggest that preserving genetic variation should deserve much more emphasis in the future.

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