Genetic gain of pure line selection and combined crossbred purebred selection with constrained inbreeding

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Abstract

Using deterministic methods, rates of genetic gain (ΔG) and inbreeding (ΔF) were compared between pure line selection (PLS) and combined crossbred purebred selection (CCPS), for the sire line of a three-way crossbreeding scheme. Purebred performance and crossbred performance were treated as genetically correlated traits assuming the infinitesimal model. Breeding schemes were compared at a fixed total number of purebred selection candidates, i.e. including crossbred information did not affect the size of the purebred nucleus. Selection was by truncation on estimated breeding values for crossbred performance. Rates of genetic gain were predicted using a pseudo-BLUP selection index. Rates of inbreeding were predicted using recently developed methods based on long-term genetic contributions. Results showed that changing from PLS to CCPS may increase ΔF by a factor of 2·14. In particular with high heritabilities and low purebred-crossbred genetic correlations, CCPS requires a larger number of parents than PLS, to avoid excessive ΔF. The superiority of CCPS over PLS was judged by comparing ΔG from both selection strategies at the same ΔF. At the same ΔF, CCPS was superior to PLS and the superiority of CCPS was only moderately reduced compared with the situation without a restriction on ΔF. This paper shows that the long-term genetic contribution theory can be used to balance ΔF and ΔG in animal breeding schemes within very limited computing time.

Keywords: *crossbreeding, effective population size, genetic gain, inbreeding, selection.*

Introduction

In crossbreeding programmes, the primary aim is to increase the performance of the crossbred animals. For this reason, the breeding goal should be defined on the crossbred level, though some weight may be given to purebred performance in particular cases (Jiang and Groen, 1999). Several studies have shown that selection response in crossbred performance can be increased by including both purebred and crossbred information in the selection criterion (Wei and van der Werf, 1994; Baumung *et al.*, 1997; Bijma and van Arendonk, 1998; Uimari and Gibson, 1998). Purebred performance and crossbred performance can be treated as genetically different traits, and selection may be based on an estimated breeding value for crossbred performance (EBV), which uses both purebred and crossbred information (Wei and van der Werf, 1994; Bijma and van Arendonk, 1998). Such a selection strategy is referred to as combined crossbred purebred selection (CCPS), whereas

selection based solely on information from the pure line is referred to as pure line selection (PLS). None of the studies mentioned above, however, has considered the effect of CCPS on the rate of inbreeding. As will be argued next, the use of CCPS may substantially increase the rate of inbreeding compared with PLS.

In a CCPS programme, an important information source is the phenotypic information on crossbred half sibs of the selection candidate (Wei and van der Werf, 1994). For example, in a three-way crossbreeding system, sires from the sire line may simultaneously be mated to dams of the sire line and to F1 dams from the multiplier level of the dam line. In that case, sires from the sire line produce two types of offspring; purebred offspring within the sire line, which are the selection candidates for the next generation, and commercial crossbred offspring which provide information on crossbred performance. When estimating breeding values for

the purebred selection candidates, the information on their crossbred half-sibs can be included in the EBV, which results in a higher accuracy of selection. Wei and van der Werf (1993) and Spilke *et al.* (1998) show how mixed model equations can be set up to estimate genetic parameters and breeding values with CCPS.

When the breeding goal is crossbred performance and the genetic correlation between purebred and crossbred performance (r_{pc}) is low, the information coming from crossbred half sibs will dominate the EBVs of selection candidates. As a consequence, there will be a high intraclass correlation between EBVs of full- and half-sibs present among the purebred selection candidates. Depending on the value of r_{pc}, therefore, selection in a CCPS programme may tend to between family selection, resulting in increased rates of inbreeding. To maintain genetic variation and to limit inbreeding depression in the pure line, rates of inbreeding have to be restricted in animal breeding programmes. The relevant question, therefore, is whether the superiority of CCPS schemes over PLS schemes can be sustained when rates of inbreeding are restricted. This question has not been addressed so far.

The aim of this paper is to compare CCPS schemes to PLS schemes while restricting the rate of inbreeding. First, we will compare the intraclass correlation between EBVs of sibs for PLS and CCPS schemes. Subsequently, rates of genetic gain and rates of inbreeding will be compared between CCPS and PLS schemes which have the same size of pure line. Finally, we will maximize genetic gain from PLS and CCPS schemes by optimizing the number of selected parents while restricting the rate of inbreeding. The superiority of CCPS schemes over PLS schemes will be judged by comparing rates of gain from both selection strategies at the same rate of inbreeding.

Methods

Traits
Purebred and crossbred performance will be treated as two different traits having a genetic correlation of r_{pc}. It is assumed that both traits are determined by the infinitesimal model, that phenotypic variance equals one for both traits and that heritability is equal for both traits.

Population structure
The population structure was the same as the structure considered by Bijma and van Arendonk (1998), and will be described briefly here. The sire line of a three-way crossbreeding system in pigs was modelled. Mating structure was hierarchical and generations were discrete. Sires from the sire line

were mated to n_{pd} purebred dams from the sire line to produce n_{po} purebred offspring per dam ($\frac{1}{2}n_{po}$ of each sex). At the same time, the same sires were also mated to F1-dams from the multiplier level of the dam line, to produce n_{cb} crossbred fattening pigs per sire. Each purebred selection candidate, therefore, had n_{cb} crossbred half sibs providing crossbred information. Purebred performance was measured on animals within the sire line, and crossbred performance was measured on fattening pigs. Information on purebred and crossbred individuals was assumed to be available at the same time. The traits were measured on both sexes and each sire had the same number of offspring tested. Each generation, n_s males and $n_s n_{pd}$ females were selected out of the $\frac{1}{2}N = \frac{1}{2}n_s n_{pd} n_{po}$ purebred selection candidates of each sex, to become parents of the next generation. Selection was by truncation on EBV for crossbred performance, without a restriction on the number of parents contributed by a single family.

Rates of gain
Throughout this paper, rate of genetic gain in crossbred performance with PLS is denoted as ΔG_{pls} and rate of genetic gain in crossbred performance with CCPS is denoted as ΔG_{ccps}. Rates of genetic gain in crossbred performance were predicted using the pseudo-BLUP selection index of Bijma and van Arendonk (1998). This index is an extension of the single trait pseudo-BLUP index of Wray and Hill (1989) to CCPS, and combines phenotypic information of the selection candidate and its full- and half-sibs together with EBVs of parents into a pseudo-BLUP EBV for crossbred performance of the selection candidate. The pseudo-BLUP index predicts response in crossbred performance for a situation with multi-trait animal model BLUP evaluation, including all purebred, crossbred and pedigree information, and where selection is by truncation on the EBV for crossbred performance. Detailed equations of the index are described by Bijma and van Arendonk (1998).

A minor modification was made to the index of Bijma and van Arendonk (1998). Bijma and van Arendonk (1998) explicitly modelled the F1-dams, but here we will assume that EBVs of F1-dams are not available, which is likely to be the situation in practice. Consequently, the F1-dams were omitted from the index, and the total number of information sources equalled 9, whereas the index of Bijma and van Arendonk (1998) contained 10 information sources.

Selection intensities accounted for finite population size and intraclass correlations between EBVs of relatives, and were calculated using the method of

Meuwissen (1991). Selection and mating were iterated until Bulmer's (1971) equilibrium parameters were reached, using the equations described by Bijma and van Arendonk (1998). Rates of genetic gain were predicted for the equilibrium situation.

Rates of inbreeding

Rates of inbreeding (ΔF) were predicted deterministically using the long-term genetic contribution theory (Woolliams *et al.*, 1999; Woolliams and Bijma, 2000). The application of this theory to CCPS is a direct analogy of the method to predict ΔF for single trait BLUP selection as described by Bijma and Woolliams (2000). Here we will only outline the main steps involved in predicting ΔF, detailed equations can be found in Bijma and Woolliams (2000).

The procedure for predicting ΔF consisted of the following steps. First, Bulmer's (1971) equilibrium genetic parameters were obtained by iterating on the pseudo-BLUP index of Bijma and van Arendonk (1998). Subsequently, the intraclass correlation between EBVs of full- and half-sibs were calculated from the selection index equations, following the approach described in appendix A of Bijma and Woolliams (2000). Finally, rates of inbreeding were predicted using equations 1 through 13 and appendix B of Bijma and Woolliams (2000). In equations 2 and 3 of Bijma and Woolliams (2000), the single trait breeding value was replaced by the breeding value for crossbred performance. For single trait BLUP selection, an example of computation is given in appendix B of Bijma and Woolliams (2000). In the present paper, the accuracy of the predicted rate of inbreeding will be evaluated by means of stochastic simulation for a number of CCPS schemes.

Optimization of breeding schemes

Breeding schemes were optimized by maximizing genetic gain while restricting the rate of inbreeding. Optimization was performed at different fixed values of the mating ratio (n_{pd}) and of the total number of selection candidates (N). The optimization variable was the number of sires, i.e. the number of sires was increased until the inbreeding constraint was achieved. The number of dams and the number of offspring per dam was a result of the number of sires and the mating ratio, i.e. the number of dams was $n_s n_{pd}$ and the number of offspring per dam was $n_{po} = N/(n_s n_{pd})$. The number of offspring per dam was allowed to be a non-integer value, because the primary purpose of this paper is to examine trends, and not to present values for specific actual breeding schemes.
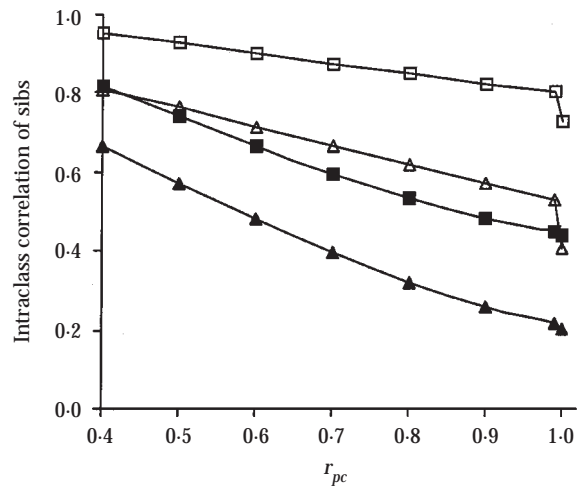

Figure 1 Intraclass correlations between EBVs of full- and half-sibs with CCPS, as a function of r_{pc}, for $n_s = 20$, $n_{pd} = 3$, $n_{po} = 4$ and $n_{tb} = 60$. —□— full-sibs, $h^2 = 0.15$; —△— half-sibs, $h^2 = 0.15$; —■— full-sibs, $h^2 = 0.6$; —▲— half-sibs, $h^2 = 0.6$; The symbols at $r_{pc} = 1$ represent intraclass correlations for PLS.

The optimization is in one dimension, i.e. the only variable is the number of sires, and from $n_s \geq 12$ and higher, ΔF and ΔG are continuously decreasing functions of n_s, which makes it easy to identify the optimum scheme. With increasing n_s, the optimum scheme, i.e. the optimum n_s, is the first scheme where ΔF is smaller than or equal to the constraint, and the maximum possible ΔG given the constraint on ΔF is the rate of gain from this scheme. The optimality of CCPS *v.* PLS was judged by comparing ΔG_{pls} and ΔG_{ccps} for the optimum schemes of both selection strategies, at the same rate of inbreeding and for the same total number of selection candidates.

Results

Intraclass correlation between EBVs of sibs

Figure 1 shows the intraclass correlation between EBVs of full- and half-sibs with CCPS, as a function of the purebred-crossbred genetic correlation (r_{pc}) and for two different heritabilities, $h^2 = 0.15$ or $h^2 = 0.6$. (Note that purebred and crossbred performance were assumed to have the same heritability.) With $r_{pc} = 1$, purebred and crossbred performance are the same trait, so for this situation, CCPS corresponds to single trait selection. With $h^2 = 0.15$ and $r_{pc} = 1$, intraclass correlations are high, which shows that with low heritability single trait BLUP selection puts substantial emphasis on family information. With $h^2 = 0.6$ and $r_{pc} = 1$, intraclass correlations are substantially lower, because

BLUP-EBV are largely determined by individual performance when heritability is high. With decreasing r_{pc}, the intraclass correlation increases rapidly for $h^2 = 0.6$, because emphasis shifts from the purebred individual performance to family information for crossbred performance. For $h^2 = 0.15$, the increase is smaller because family information already receives substantial emphasis for $r_{pc} = 1$. With PLS the intraclass correlation is slightly smaller than with CCPS and $r_{pc} = 1$, because with CCPS there are an additional 60 half-sibs included in the EBV. In conclusion, intraclass correlations increase with decreasing r_{pc} and the increase is largest for high heritabilities.

Rates of inbreeding and gain
Figure 2 shows the rate of inbreeding with CCPS as a function of r_{pc}, for different heritabilities and for two different selection intensities, $n_{po} = 4$ or 8. To evaluate the accuracy of the deterministic predictions (lines in Figure 2), Figure 2 also shows ΔF estimated from stochastic simulation (symbols in Figure 2), which reveals that predictions and simulations are in close agreement. A discussion on the origin of prediction errors is in Bijma and Woolliams (2000).

Figure 2 shows that ΔF increases with decreasing r_{pc} and that the relative increase is largest with high

heritabilities and high selection intensities. For example, with $n_{po} = 8$ and $h^2 = 0.6$, the rate of inbreeding increased by a factor of 2·14 when r_{pc} decreased from 1 to 0·4; whereas with $h^2 = 0.15$, the rate of inbreeding increased only by a factor of 1·42. The large increase of ΔF for high heritabilities agrees with the trend in the intraclass correlations observed in Figure 1.

Figure 2 also shows a rapid increase of ΔF when selection intensity increases. For example, with $h^2 = 0.15$ and $r_{pc} = 1$, ΔF increased by a factor of 1·81 when the number of purebred offspring per dam was doubled from 4 to 8; and for $r_{pc} = 0.4$, ΔF increased by an even greater factor 2·06. This shows that, with BLUP selection, doubling the number of selection candidates while keeping the number of parents constant may double the rate of inbreeding. Obviously, the rate of inbreeding with PLS (results not shown) is independent of r_{pc} and was slightly lower than ΔF for CCPS with $r_{pc} = 1$. In conclusion, Figure 2 shows that, when keeping the number of parents constant, changing from PLS to CCPS may substantially increase ΔF, in particular for small r_{pc}, high h^2 and high selection intensity.

Figure 3 shows ΔG_{pls} and ΔG_{ccps} as a function of r_{pc} and for different heritabilities. With PLS, genetic gain
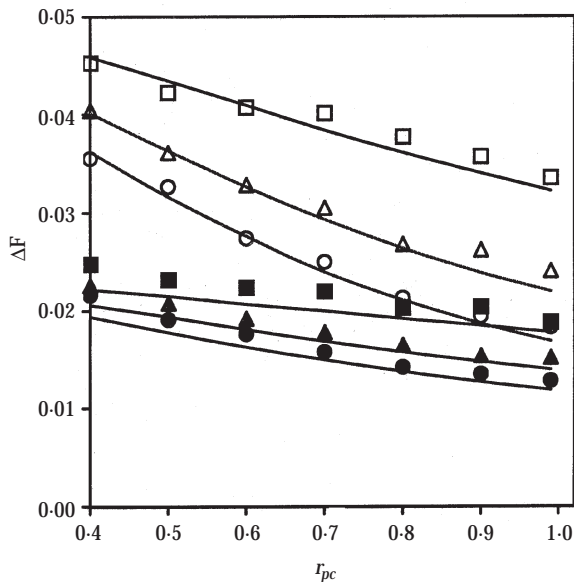

Figure 2 Rates of inbreeding (ΔF) with CCPS as a function of r_{pc}, for $n_s = 20$, $n_{pd} = 3$ and $n_{cb} = 60$. ——□—— $n_{po} = 8$, $h^2 = 0.15$; ——△—— $n_{po} = 8$, $h^2 = 0.4$; ——○—— $n_{po} = 8$, $h^2 = 0.6$; ——■—— $n_{po} = 4$, $h^2 = 0.15$; ——▲—— $n_{po} = 4$, $h^2 = 0.4$; ——●—— $n_{po} = 4$, $h^2 = 0.6$. Lines represent predictions, symbols represent results from simulation.
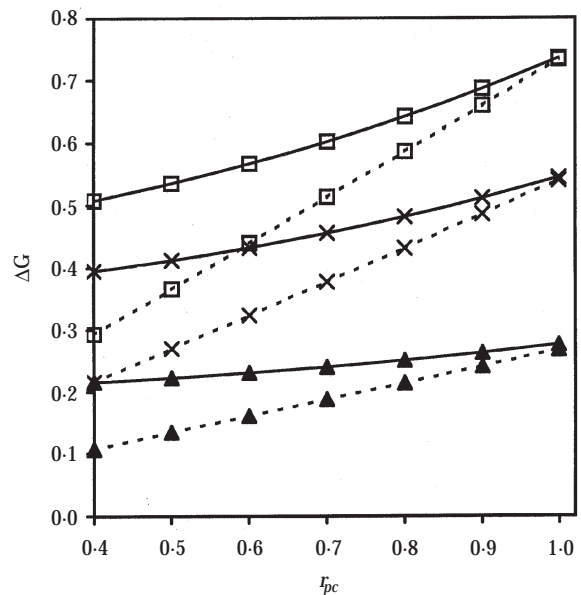

Figure 3 Rates of genetic gain in crossbred performance (ΔG) as a function of r_{pc}, for $n_s = 20$, $n_{pd} = 3$, $n_{po} = 8$ and $n_{cb} = 60$. For CCPS: ——□—— $h^2 = 0.6$; ——✕—— $h^2 = 0.4$; ——▲—— $h^2 = 0.15$. For PLS: - -□- - $h^2 = 0.6$; - -✕- - $h^2 = 0.4$; - -▲- - $h^2 = 0.15$.

in crossbred performance is equal to the product of $\Delta G_{purebred}$ and r_{pc}, and, therefore, ΔG_{pls} increases linearly with r_{pc}. As expected from previous studies (e.g. Wei and van der Werf, 1994), CCPS gives more genetic gain than PLS and the superiority of CCPS over PLS increases with decreasing r_{pc}. The relative superiority of CCPS over PLS is largest for low heritabilities. For example, with $r_{pc} = 0.4$ and $h^2 = 0.15$, using CCPS instead of PLS increased genetic gain by a factor 2·02, whereas for $h^2 = 0.6$, genetic gain increased only by a factor of 1·73.

Combining Figures 2 and 3 shows, that for high heritabilities together with high selection intensities, ΔF increases more rapidly than ΔG when changing from PLS to CCPS. For example, for $h^2 = 0.6$, $r_{pc} = 0.4$ and $n_{po} = 8$, changing from PLS to CCPS increased ΔG by a factor of 1·73 and ΔF by a factor of 2·14.

PLS v. CCPS with constrained inbreeding
To make inferences on the superiority of CCPS over PLS when the rate of inbreeding is restricted, the ratio $\Delta G_{ccps}/\Delta G_{pls}$ was calculated for schemes where genetic gain was maximized while restricting ΔF. Figure 4 shows $\Delta G_{ccps}/\Delta G_{pls}$ for optimum schemes with a fixed total number of 768 pure line selection candiates, where ΔF was restricted to be smaller than 1%. To validate the deterministic optimization, a limited number of schemes was optimized using stochastic simulation (results not shown), which
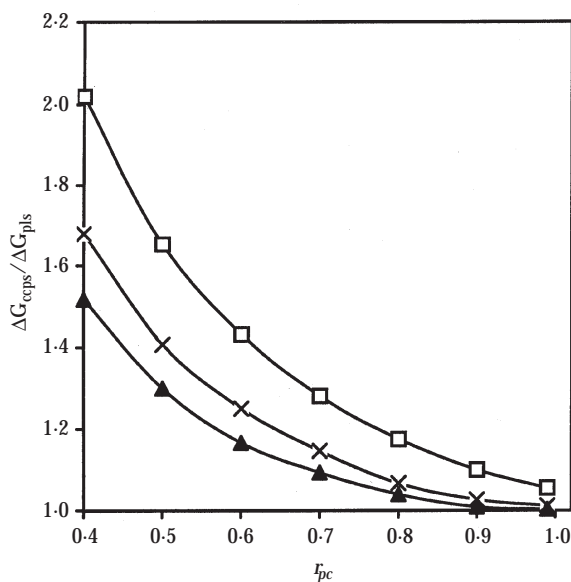

Figure 5 Ratio of genetic gain with CCPS over genetic gain with PLS ($\Delta G_{ccps}/\Delta G_{pls}$) as a function of r_{pc}, without a restriction on ΔF, for $n_s = 30$, $n_{pd} = 5$, $n_{po} = 6$, and $n_{cb} = 60$. —□— $h^2 = 0.15$; —✕— $h^2 = 0.4$; —▲— $h^2 = 0.6$.

revealed close agreement between predictions and simulations. Results in Figure 4 show that, with a restriction on the rate of inbreeding, CCPS remains superior over PLS, i.e. the ratio $\Delta G_{ccps}/\Delta G_{pls}$ exceeds one. The superiority of CCPS over PLS increases with decreasing r_{pc} and with decreasing h^2. The ratio $\Delta G_{ccps}/\Delta G_{pls}$ was also evaluated for other values of N and d, but the relation was almost identical, which indicates that with constrained inbreeding, the superiority of CCPS over PLS is determined almost entirely by r_{pc} and h^2. Results for other values of N and d, therefore, are not shown.

Figure 5 shows the superiority of CCPS over PLS without a restriction on the rate of inbreeding, for a scheme with $n_s = 30$, $n_{pd} = 5$ and $n_{po} = 6$. For $h^2 = 0.15$, the ratio $\Delta G_{ccps}/\Delta G_{pls}$ is very similar to the situation where ΔF is restricted, e.g. with $r_{pc} = 0.4$ and no restriction on ΔF the ratio was 2·06 (Figure 5), whereas with $\Delta F < 1\%$ the ratio was 2·02. For low heritabilities, therefore, restricting ΔF hardly affects the superiority of CCPS over PLS. For higher heritabilities the superiority of CCPS over PLS decreased when ΔF was restricted, e.g. with $h^2 = 0.6$, $r_{pc} = 0.4$ and no restriction on ΔF the ratio was 1·74 (Figure 5), whereas with $\Delta F < 1\%$ the ratio decreased to 1·51. Compared with the large increase of ΔF when changing from CCPS to PLS (Figure 2), the reduction of $\Delta G_{ccps}/\Delta G_{pls}$ when ΔF is restricted is strikingly small.

Figure 4 Ratio of genetic gain with CCPS over genetic gain with PLS ($\Delta G_{ccps}/\Delta G_{pls}$) as a function of r_{pc}, for optimum schemes with $\Delta F < 1\%$ and with $N = 768$, $n_{pd} = 5$ and $n_{cb} = 60$. —□— $h^2 = 0.15$; —✕— $h^2 = 0.4$; —▲— $h^2 = 0.6$.
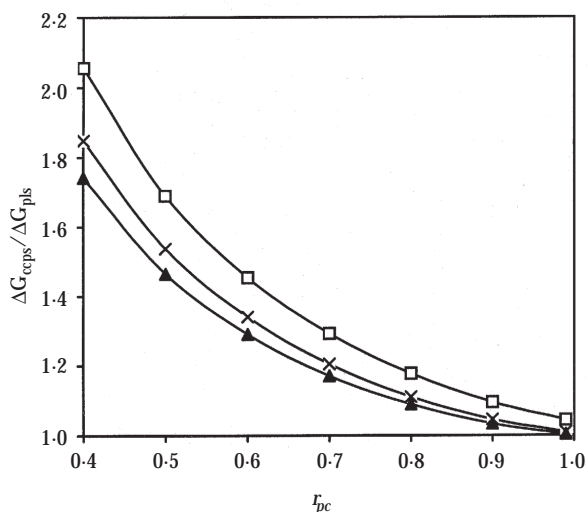
Table 1 shows the design of optimum breeding schemes, i.e. the optimum number of selected sires, for different constraints on the rate of inbreeding. With PLS, the optimum number of sires is always lower than with CCPS and decreases when h^2 increases. With CCPS the optimum number of sires decreases with increasing h^2 and r_{pc}. With decreasing r_{pc}, the required number of sires increased rapidly for $h^2 = 0.6$, whereas for $h^2 = 0.15$ there is only a small increase. This result agrees with the observation that the increase of intraclass correlations is largest for high heritabilities (Figure 1). Results in Table 1 indicate that, with a constraint on ΔF, the difference between the optimum number of sires with PLS and CCPS increases with heritability. For low heritabilities, this difference is relatively small because single trait BLUP selection already puts substantial emphasis on family information.

The comparison of CCPS v. PLS at fixed rates of inbreeding involves a trade off between accuracy and intensity of selection. Table 1 shows that with CCPS the constraint on ΔF is achieved by selecting more parents, which is at the expense of selection intensity. On the other hand, CCPS benefits from a higher accuracy of selection due to the use of crossbred
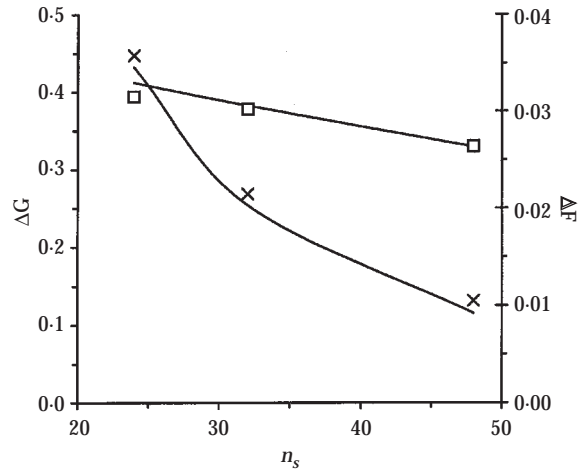

Figure 6 Relation of ΔF and ΔG with the number of selected sires n_s for a fixed test capacity of $N = 768$, with $n_{pd} = 4$, $h^2 = 0.4$, $r_{pc} = 0.4$ and $n_{cb} = 60$; ——□—— ΔG; ——✕—— ΔF. Lines represent predictions, symbols represent results from simulation.

Table 1 *Optimum number of selected sires for CCPS and PLS schemes with constrained inbreeding (ΔF)†*

h^2	r_{pc}	$\Delta F < 2\%$	$\Delta F < 1\%$	$\Delta F < 0.5\%$
0.15	0.4	32	44	61
	0.5	31	44	60
	0.6	30	43	59
	0.7	29	42	58
	0.8	28	41	57
	0.9	27	40	56
	0.99	26	39	55
	PLS‡	26	38	53
0.4	0.4	30	42	59
	0.5	28	41	58
	0.6	27	39	56
	0.7	25	37	54
	0.8	24	36	53
	0.9	22	34	51
	0.99	21	32	49
	PLS‡	21	32	49
0.6	0.4	28	41	58
	0.5	27	39	56
	0.6	24	37	54
	0.7	22	34	51
	0.8	20	32	49
	0.9	19	30	46
	0.99	17	28	44
	PLS‡	17	28	44

† For $N = 768$, $n_{pd} = 5$ and $n_{cb} = 60$, h^2 = heritability, r_{pc} = purebred-crossbred genetic correlation.
‡ With PLS the optimum design is independent of r_{pc}.

information. The superiority of CCPS vs. PLS at fixed rates of inbreeding (Figure 4) indicates that the increase of gain due to increased accuracy exceeds the decrease of gain due to decreased selection intensity.

Given the large differences in ΔF between CCPS and PLS (Figure 2), the difference between the optimum number of sires for both selection strategies (Table 1) is surprisingly small. This indicates that a small increase in the number of sires is sufficient to substantially reduce ΔF. Figure 6 shows the relation of ΔF and ΔG with the number of selected sires, for $h^2 = 0.4$, $r_{pc} = 0.4$ and $N = 768$, which shows that ΔF drops substantially when the number of sires increases, whereas ΔG decreases only moderately. There are two distinct mechanisms causing the sharp decrease of ΔF. First, in the absence of selection, ΔF approximately halves when the number of parents is doubled (Wright, 1969). Second, with fixed N, selection intensity decreases when the number of parents increases, which further reduces ΔF (see appendix B of Bijma and Woolliams (2000)). For the scheme in Figure 6, both mechanisms contribute approximately equally to the reduction of ΔF. The different relation of ΔF and ΔG with the number of sires also explains why the superiority of CCPS over PLS, i.e $\Delta G_{ccps}/\Delta G_{pls}$, reduces only moderately when ΔF is restricted (Figure 4 v. Figure 5).

Discussion

In this paper, we have compared CCPS to PLS with particular emphasis on the rate of inbreeding. When keeping the number of parents constant, changing from PLS to CCPS may substantially increase ΔF. In particular with high h^2 and low r_{pc}, CCPS requires a larger number of parents than PLS, to avoid excessive rates of inbreeding. When compared at the same rate of inbreeding, CCPS was superior to PLS and the superiority of CCPS was only moderately reduced compared with a situation without a restriction on ΔF.

Until recently, balancing rates of gain and inbreeding in animal breeding programmes required computationally demanding stochastic simulation, which seriously restricted the number of alternative schemes involved in the optimization. This paper shows that the use of the long-term genetic contribution theory for predicting ΔF (Woolliams *et al.*, 1999; Bijma and Woolliams, 2000; Woolliams and Bijma, 2000) enables the optimization of rates of gain and inbreeding of breeding schemes, within very limited computing time with no restriction on the number of alternative schemes involved. For example, the results in Figure 4, which involved the evaluation of approx. 750 alternative breeding schemes, were generated within nine wall clock seconds.

Following the approach of Wei and van der Werf (1994), we have treated purebred performance and crossbred performance as correlated traits, assuming the additive infinitesimal model. Other studies have used finite locus models with several degrees of dominance, and generally with equal effects for all loci (Baumung *et al.*, 1997; Uimari and Gibson, 1998). Neither of these models is fully realistic, i.e. the true number of genes must be finite, but on the other hand we have little knowledge of the number of genes, their effects and the interactions between genes.

Prediction of short-term selection response by means of selection index theory does not require the infinitesimal assumptions, providing gene effects are not very large and gene frequency of favourable alleles is near 0·5 (Hill, 1998). When phenotypes and breeding values follow a multivariate normal distribution, the regression of breeding values on phenotypes, i.e. the selection index, is unbiased. With multivariate normality, therefore, selection index theory exactly predicts response to a single cycle of selection. Although selection may induce deviations from normality, Turelli and Barton (1994) show that the prediction of genetic gain by regression on phenotypes is robust against deviations from

normality, even with strong truncation selection. Therefore, prediction of response by means of selection index theory is expected to be adequate in the short term.

In the long-term, selection response depends on the nature of the genetic variation, i.e. the number of genes, their effects etc. However, we have little knowledge of those parameters, and it will be difficult to convince practitioners to sacrifice short-term response (i.e. by not using CCPS) when it remains doubtful whether doing so will indeed yield more long-term response. The most practical approach, therefore, seems to be the use of CCPS while restricting the rate of inbreeding, so as to maximize short-term response and simultaneously avoid rapid erosion of the genetic variation. To account for changing genetic parameters due to changing gene frequency, genetic parameters should frequently be re-estimated so that optimality of the CCPS EBV is guaranteed.

In this study, breeding schemes were optimized given a fixed total number of purebred selection candidates, whereas the number of recorded crossbred individuals varied between schemes. In other studies, crossbred individuals were tested at the expense of purebred individuals, thus reducing the number of selection candidates (Wei and van der Werf, 1994). Whether testing crossbred individuals is at the expense of purebred individuals depends on whether testing of crossbred individuals is part of the nucleus-breeding programme, or, alternatively, information from the commercial population is collected, e.g. at the slaughterhouses. Collecting information at the slaughterhouse has the advantage that one can directly measure the traits that determine the carcass price, e.g. carcass grade and lean%, instead of an ultrasonic measurement of backfat, which may increase accuracy of selection. Additionally, measuring crossbred performance on individuals of the commercial population has the advantage that G × E interaction is accounted for. When crossbred information is collected outside the nucleus, PLS and CCPS are not compared at the same total amount of resources, so the relevant question is whether the additional gain arising from using CCPS instead of PLS makes up for the cost of measuring crossbred individuals.

CCPS and PLS can be compared at the same level of resources by specifying the ratio of the costs of testing a purebred *v.* a crossbred individual and, subsequently, evaluating breeding schemes at the same total costs. In that case, testing crossbred individuals will reduce the number of purebred selection candidates, which reduces selection

intensity and has a decreasing effect on ΔF (Figure 2). When compared at the same level of resources, therefore, changing from PLS to CCPS will give smaller increases of ΔF than the values presented in Figure 2. Methods used in this study can as well be used to balance rates of inbreeding and gain for crossbreeding schemes with a fixed total level of resources.

In this study, constraints on ΔF were achieved by increasing the number of parents. Alternatively, one can use dynamic selection algorithms that directly constrain ΔF (Meuwissen, 1997; Grundy *et al.*, 1998). Though dynamic selection algorithms are expected to give higher ΔG at the same ΔF, optimization of breeding schemes using those algorithms can only be implemented by means of computationally demanding stochastic simulation, which limits the number of alternative schemes considered in the optimization. Our methods provide good insight into the impact of different parameters and as such provide a good starting point for the optimization of breeding schemes.

Acknowledgements

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