Collaboration of breeding programs with genotype by environment interaction: possibilities and limitations.

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ABSTRACT: Dairy cattle breeding programs are often selecting sires and dams across environments. Genotype by environment interaction (G × E) might limit the possibilities for collaboration of breeding programs in different environments. This study investigated the possibilities for collaboration of breeding programs with G × E. A dairy cattle situation with two breeding programs and two environments was simulated using a deterministic pseudo-BLUP selection index model.

Long-term collaboration with G × E was beneficial for both breeding programs, when genetic gain in both breeding programs was equal for performance in one of the environments. A simple selection index model overestimated the possibilities of collaboration as a consequence of neglecting reduction of genetic variances and covariances due to selection. Collaboration of breeding programs was possible in the long-term, when the genetic correlation was higher than 0.80-0.90, resulting in up to 15% extra genetic gain. On the contrary, in the first generations breeding programs could mutually select each other sires and dams, when the genetic correlation was higher than 0.40-0.60. With more intense selection, breeding programs were less likely to benefit from collaboration. Small breeding programs had larger benefits from collaboration than large breeding programs and collaboration was possible with lower values of the genetic correlation.

INTRODUCTION

Dairy cattle breeding programs and dairy farmers are selecting sires from all over the world. To facilitate selection of sires from different countries, Interbull (Uppsala, Sweden) converts EBV from one country to another using multiple-trait across country evaluation (MACE) accounting for genotype by environment interaction (G × E) (Schaeffer, 1994). When G × E is not important between different countries, it is advantageous when breeding programs collaborate and select sires and dams worldwide. The same number of sires and dams can be selected from a larger population of selection candidates resulting in a higher selection intensity and genetic gain (Banos and Smith, 1991; Smith and Banos, 1991; Lohuis and Dekkers, 1998). Substantial G × E between environments can hamper long-term selection of sires and dams worldwide, because populations in different environments tend to diversify leading to separation of breeding programs in the long-term (Smith and Banos, 1991). Smith and Banos (1991) concluded that genetic correlations less than 0.8-0.9 would be large enough to remove benefits of worldwide selection.

Banos and Smith (1991) and Lohuis and Dekkers (1998) primarily focused on short-term benefits in genetic gain due to collaboration of dairy breeding programs, but did not investigate the effect of G × E on collaboration of breeding programs after a number of generations of selection. Smith and Banos (1991) focused more generally on benefits of collaboration of livestock breeding programs. They studied the effect of G × E as one of the constraints for collaboration, but did not study in detail the effects of other parameters (e.g. heritability, proportion of selected animals) at possibilities for collaboration of breeding programs in the presence of G × E. Furthermore, Smith and Banos (1991) simulated mass selection with only selection of sires across environments, whereas in dairy cattle breeding sires and dams might be selected across environments using BLUP-EBV.

The objective of this study was to compare simple selection index model and a pseudo-BLUP selection index model in prediction of possibilities for collaboration of dairy breeding programs in the presence of G × E, and to identify factors (e.g. heritability, proportion of selected animals) affecting collaboration of dairy cattle breeding programs in the short and long-term with BLUP-selection and to quantify the effect of collaboration on genetic gain.

MATERIAL AND METHODS

Breeding scheme

A classical dairy cattle breeding situation with four selection paths was considered: sires to breed sons (SS), sires to breed daughters (SD), dams to breed sons (DS) and dams to breed daughters (DD). Two breeding programs were operating in two environments in the presence of G × E interaction. The breeding goal of breeding program 1 was milk yield in environment 1; the breeding goal of breeding program 2 was milk yield in environment 2. Bulls in breeding program 1 were progeny tested in environment 1; bulls in breeding program 2 were progeny tested in environment 2. Performances in both environments were assumed to follow a multivariate normal distribution. Sires and dams were selected by truncation on animal model BLUP-EBV across environments. The EBV of sires were based on performance of progeny and pedigree information; EBV of dams were based on own performance in first lactation in one environment and pedigree information. Selection of SS, SD and DS was by truncation across environments, while DD were completely selected within their own environment. Generations were assumed to be discrete.

Table 1. Values of genetic correlation, heritability, phenotypic variance, number of bulls, number of progeny per bull, number of cows in each population and proportions of selected animals in each selection path for the basic situation and alternative situations.

Parameter	Basic	Alternative range
Genetic correlation (r_g)	0 – 1	
Heritability (h^2)	0.3	0.1, 0.3 and 0.5
Phenotypic variance (σ_p^2)	1.0	
Number of test-bulls per breeding program	200	100-300 (sum always 400)
Number of progeny per bull	100	10-100
Population size cows per environment	1.000.000	
Proportion selected sires to breed sons (p_{SS})	0.05	0.01, 0.05, 0.10, 0.20
Proportion selected sires to breed daughters (p_{SD})	0.10	0.01, 0.05, 0.10, 0.20
Proportion selected dams to breed sons (p_{DS})	0.005	0.01, 0.05, 0.10, 0.20
Proportion selected dams to breed daughters (p_{DD})	0.80	

Values of parameters in the basic situation are summarized in Table 1. In the basic situation breeding program 1 tested 200 bulls annually with 100 daughters per bull in environment 1. Analogously, breeding program 2 tested 200 bulls annually with 100 daughters per bull in environment 2. The proportions of selected animals were chosen to represent practical dairy cattle breeding programs and were similar to Dekkers (1992), Lohuis and Dekkers (1998) and Vargas and Van Arendonk (2004). In each breeding program, the best 20 SS were selected each year out of 400 bulls in total ($p_{SS} = 0.05$), while the best 40

SD were selected out of 400 bulls in total ($p_{SD} = 0.10$). To produce 400 test-bulls, 1000 DS were selected each year out of 200.000 cows in both environments together ($p_{DS} = 0.005$). Each dam population consisted of a million cows, from which 10% was considered as potential DS. Other dams were excluded for various reasons not directly related to the breeding goal. The 80% best cows were selected as DD each year within their own environment to produce female replacements using artificial insemination ($p_{DD} = 0.80$). The heritability (h^2) of milk yield was 0.3 in both environments and the genetic correlation (r_g) was varied between 0 and 1. For simplicity, the phenotypic variance was set to 1.0 in both environments. Alternative situations were created by changing one parameter at a time while keeping other parameters constant.

Prediction of genetic gain

Genetic gain in both environments was predicted deterministically approximating BLUP-selection under an animal model using a pseudo-BLUP selection index model (Wray and Hill, 1989; Villanueva et al., 1993). The model accounted for changes in genetic variances and covariances due to linkage disequilibrium caused by selection (Bulmer, 1971), but also due to selection of SS, SD and DS across environments with different genetic means (Mueller and James, 1983).

Selection across environments was simulated by finding a common truncation point using Ridders' Method (Press et al., 1992). The common truncation point was translated into proportions of selected animals using Brascamp (1978). Subsequently, selection intensities (i) were calculated, which were corrected for finite population size using the method of Burrows (1972) and for correlated EBV among relatives using the method of Meuwissen (1991).

Genetic means of selected animals (μ_x*) in one environment for performance in environment x were calculated as $\mu_x + R_x$, where μ_x was the genetic mean before selection and R_x was the selection differential, which was $R_x = \frac{i \times \mathbf{b}'\mathbf{G}_x}{\sigma_I}$, where $\mathbf{b}$ is a vector with selection index weights, $\mathbf{G}_x$ is a column of the $\mathbf{G}$-matrix with the covariances between the information sources and the true breeding value of environment x and σ_I^2 is the variance of the selection index. The genetic mean of all selected animals for one of the breeding programs was a weighted average of genetic means of selected animals within environment 1 and 2 weighted by the fraction of selected animals of each environment. The genetic mean of newborn animals was calculated as the average genetic mean of both parents. Genetic gain was calculated as the difference in genetic mean in generation t and generation $t-1$. The equilibrium was reached when genetic gain in both breeding programs in subsequent generations did change less than 1.0 * 10^{-10}. Results were based on equilibrium values, unless mentioned differently.

Collaboration of breeding programs and split-point genetic correlation

Collaboration of both breeding programs was defined as selection of sires and dams across environments resulting in a higher genetic gain for both breeding programs in comparison to selection of sires and dams only within environments. In the presence of G × E, populations can diverge in terms of genetic means leading to separated breeding programs in the equilibrium. The highest value of the genetic correlation, where breeding programs were separated in the equilibrium, was in this study called the split-point genetic correlation.

RESULTS

General

Figure 1 shows genetic gain in environment 1 for breeding program 1 and 2 as a function of the genetic correlation between environment 1 and 2. The Figure could be split up into two parts: genetic gain of two completely separated breeding programs when the genetic correlation was 0.90 (= split-point genetic correlation) or lower, and genetic gain of two collaborating breeding programs when the genetic correlation was higher than 0.90. When the genetic correlation was 0.90 or lower, genetic gain in environment 1 of breeding program 2 was a correlated response indicated by the linear decrease in genetic gain with decreasing genetic correlation. Genetic gain in environment 1 of breeding program 1 was constant, when the genetic correlation was 0.90 or lower. When the genetic correlation was higher than 0.90, genetic gains of both breeding programs were equal and increased curvilinear with the genetic correlation. Genetic gain increased up to 15%, because both breeding programs were collaborating, resulting in higher selection intensity.

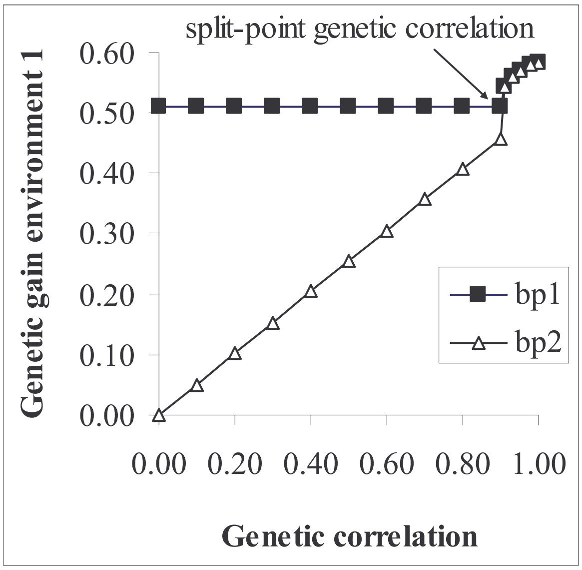

Figure 1. Genetic gain in environment 1 for breeding program 1 and 2 (bp1, bp2) as a function of the genetic correlation (heritability = 0.3; phenotypic variance = 1.0; number of test-bulls per breeding program = 200 (total = 400); number of progeny per bull = 100; population size cows each environment = 1.0 million; proportion of selected SS = 0.05; proportion of selected SD = 0.10; proportion of selected DS = 0.005; proportion of selected DD = 0.80).

Simple selection index versus pseudo-BLUP selection index

To illustrate the aspects of collaboration, separation and the split-point genetic correlation, a pseudo-BLUP selection index model was used in Figure 1. The question is whether it would be necessary to use such a complicated model or that a simple selection index would be sufficient. Therefore, different models were used varying from a simple selection index model to a pseudo-BLUP selection index model.

Figure 2 shows the split-point genetic correlation as a function of the proportion of selected sires and dams in SS, SD, and DS (all equal) for different models accounting for either Bulmer effect, pedigree information, correction of selection intensity for finite population size and correlated index values or accounting for all effects together (= pseudo-BLUP selection index). When the proportion selected increased, the split-point genetic correlation decreased for all models. Differences between curves were largest at a proportion selected of 0.2. The decrease in split-point genetic correlation was largest for the simple selection index model (‘simple’) and smallest for the pseudo-BLUP selection index model (‘full model’). When the selection index model accounted for decrease in genetic variance due to selection (‘bulmer’), the decrease in split-point genetic correlation was smaller than the decrease with the selection index, but was similar to the decrease with the pseudo-BLUP selection index. When the selection index model included pedigree information ('pedigree') or accounted for reduced selection intensity due to finite population size and correlated index values of relatives ('correction') the decrease in split-point genetic correlation was very similar to a simple selection index.

Overall, accounting for decrease in genetic variance due to selection increased mainly the split-point genetic correlation, comparing the pseudo-BLUP selection index model with the simple selection index model. The model used to predict genetic gain when breeding programs are collaborating or separating in the presence of G × E, therefore, should account for decrease in genetic variance due to selection. Selection does not only decrease genetic variances due to linkage disequilibrium, but also decrease the genetic correlation between both environments (Villanueva and Kennedy, 1990), resulting in less opportunity for breeding programs to collaborate with breeding programs in other environments. Using a simple selection index would predict a lower split-point genetic correlation and would therefore over predict genetic gain, when the genetic correlation is in the range between the split-point genetic correlation of the simple selection index model and the split-point genetic correlation of a pseudo-BLUP selection index model.

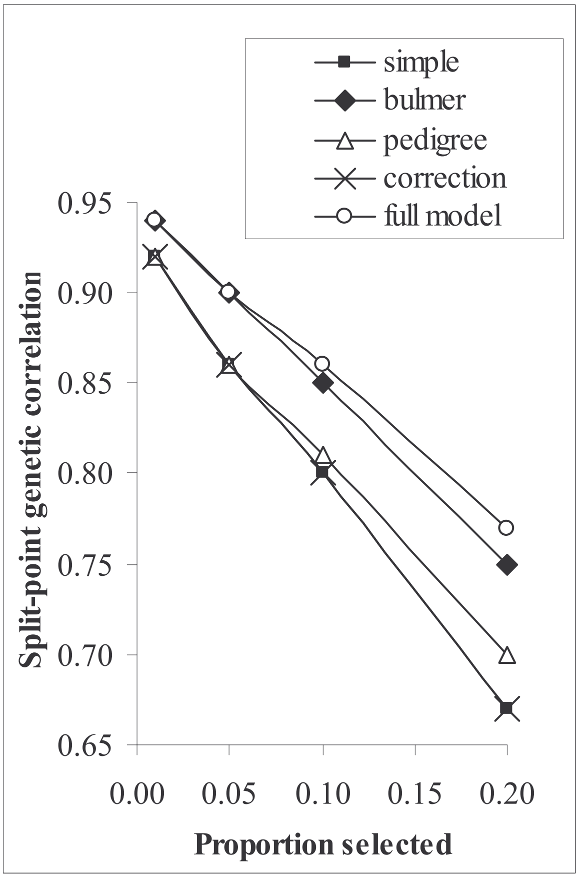

Figure 2. Split-point genetic correlation as a function of proportion of selected animals for different selection models ('simple': sires selected on progeny performance and dams selected on own performance; 'bulmer': as 'simple' but with Bulmer effect; 'pedigree': as 'simple' with including pedigree information in the index; 'correction': as 'simple' with correcting selection intensity for finite population size and correlated index values of relatives; 'full model': as 'simple' with including pedigree information, Bulmer effect, and correction of selection intensity for finite population size and correlated index values of relatives (= pseudo-BLUP selection index) (heritability = 0.3; phenotypic variance = 1.0; number of test-bulls per breeding program = 200 (total = 400); number of progeny per bull = 100; population size cows each environment = 1.0 million; proportion of selected SS = proportion of selected SD = proportion of selected DS = Proportion selected; proportion of selected DD = 0.80).

Short-term and long-term

So far, only equilibrium results were shown, but in some situations, equilibrium was reached after more than 100 generations of selection. In animal breeding a shorter time horizon is of more interest. Therefore, the split-point genetic correlation was determined as a function of generation number using the full pseudo-BLUP selection index model (Figure 3). To mimic a practical situation where both breeding programs had been mutually selecting each others sires and dams for many generations for the same breeding goal, first 20 generations were simulated to establish Bulmer equilibrium (Bulmer, 1971) and pedigree equilibrium (Dekkers, 1992). In generation 20 the genetic means were set to zero, so that both populations were genetically equal. Using generation 20 as starting point (considered as generation 0), the split-point genetic correlation was determined every generation as the highest value of the genetic correlation, where at least 99% of the selected animals in each selection path was selected within the own environment.

Figure 3 shows the split-point genetic correlation as a function of generation number for different values of proportion of selected animals. When generation number increased, the split-point genetic correlation increased rapidly the first 10 generations and reached the equilibrium asymptote after 60 generations of selection. Curves of different proportions of selected animals were rather similar and showed the same tendency as in Figure 2 that the split-point genetic correlation was decreasing with increasing proportion of selected animals. Using the practical set of proportions of selected animals as given in Table 1, showed the same pattern. In the first 5 generations sires and dams were selected in both environments, when the genetic correlation was higher than 0.60-0.75. After 5-10 generations sires and dams were only selected in both environments, when the genetic correlation was higher than 0.80. In the equilibrium, sires and dams were selected in both environments, when the genetic correlation was higher than 0.90.

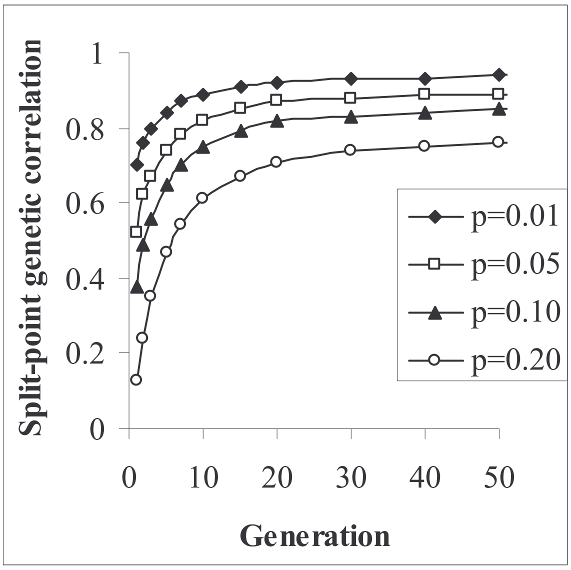

Figure 3. Split-point genetic correlation as a function of generation number for different proportions of selected animals (p) (heritability = 0.3; phenotypic variance = 1.0; number of test-bulls per breeding program = 200 (total = 400); number of progeny per bull = 100; population size cows each environment = 1.0 million; proportion of selected SS = proportion of selected SD = proportion of selected DS = p; proportion of selected DD = 0.80).

Other parameters

Other parameters such as heritability and number of progeny per bull were also varied. In general, the effect at the equilibrium split-point genetic correlation was negligible, when values were equal in both environments. When values were unequal in both environments, however, the equilibrium split-point genetic correlation decreased to 0.84-0.86.

Asymmetry in number of progeny tested bulls in each environment had also a decreasing effect at the split-point genetic correlation. When 100 bulls were tested in environment 1 and 300 bulls were tested in environment 2, the split-point genetic correlation decreased to 0.79. The small breeding program in environment 1 had a large benefit from collaboration with up to 34% more genetic gain, while the big breeding program in environment 2 had a much smaller benefit from collaboration with at maximum only 7% more genetic gain.

DISCUSSION

This study compared different models in prediction of collaboration of breeding programs in the presence of G × E. Furthermore, factors were identified affecting collaboration or separation of breeding programs. Collaboration was possible in the equilibrium, when genetic gain for a particular environment was equal for both breeding programs in the equilibrium. This condition of equal genetic gain was mathematically presented in Mulder and Bijma (2005). When the genetic correlation was lower than the split-point genetic correlation, breeding programs were eventually separated, because the condition of equal genetic gain was never reached. As a consequence, genetic means diverged resulting in that less and less animals were selected across environments. Finally, the difference in genetic means was so large that animals were only selected within the domestic environment and breeding programs were completely separated (Smith and Banos, 1991).

It was found that proportion of selected animals was one of the major parameters determining the split-point genetic correlation. With increasing proportion of selected animals (lower selection intensity), the split-point genetic correlation decreased resulting in more opportunity for collaboration of breeding programs in the presence of G × E. Also Smith and Banos (1991) reported larger benefits from collaboration of breeding programs with less intense selection. They reported implicitly split-point genetic correlations and found also that the equilibrium was sometimes reached after many generations of selection. In agreement with Smith and Banos (1991) and Banos and Smith (1991), smaller breeding programs had larger benefits from collaboration than large breeding programs. However, it should be noted that Smith and Banos (1991) and Banos and Smith (1991) used simple selection index theory, which over predicts possibilities of collaboration (see Figure 2) because of neglecting reduction of genetic variance due to selection (Bulmer, 1971). Both studies did not study in detail the effects of different parameters at split-point genetic correlations.

In practice, not only G × E on a trait-by-trait level plays a role in collaboration or separation of breeding programs, but also the differences in breeding goal. Due to broadening of breeding goals in different countries, the genetic correlation between breeding goals has decreased in the last 5-10 years. As a consequence, dairy cattle breeding programs tend to select more domestic sires (Miglior et al., 2005; Van der Beek, 2003). Collaboration of breeding programs is, however, an opportunity to increase genetic gain substantially without extra investment in testing more bulls. Furthermore, it is a way to select less related animals in other environments reducing inbreeding rate. To enhance possibilities for collaboration of breeding programs, development of a global breeding goal was suggested in Mulder et al. (2005).

CONCLUSION

Collaboration of two breeding programs was possible in the long-term, when the genetic correlation between performances in both environments was higher than 0.80-0.90, resulting in at maximum 15% extra genetic gain with equal sized breeding programs. On the contrary, in the first generations collaboration was possible when the genetic correlation was higher than 0.40-0.60. With more intense selection (lower proportion of selected animals), breeding programs are less likely to benefit from collaboration with breeding programs in other environments. Small breeding programs had larger benefits from collaboration than large breeding programs and collaboration was possible with lower values of the genetic correlation. A simple selection index overestimated the possibilities of collaboration as a consequence of neglecting reduction of genetic variances and covariances due to selection.

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