Benefits of Cooperation Between Breeding Programs in the Presence of Genotype by Environment Interaction

H. A. Mulder¹ and P. Bijma

Animal Breeding and Genetics Group, Wageningen University, PO Box 338, 6700 AH Wageningen, The Netherlands

ABSTRACT

Dairy cattle breeding programs and dairy farmers are selecting sires and dams across environments. Genotype $\times$ environment interaction ($G \times E$) limits the possibilities for cooperation between breeding programs operating in different environments. The objectives of this study were 2-fold: 1) to investigate the effects of heritability, selection intensity, number of progeny per bull, and size of breeding programs on possibilities for cooperation between dairy cattle breeding programs in the short and long term in the presence of $G \times E$, and 2) to quantify the effect of such cooperation on genetic gain. A dairy cattle situation with 2 breeding programs operating in 2 environments was simulated using a deterministic pseudo-BLUP selection index model. Long-term cooperation between the 2 breeding programs was possible in the presence of $G \times E$, when the genetic correlation was higher than 0.80 to 0.90, resulting in up to 15% extra genetic gain. In addition, in the initial generations of selection, the breeding programs could benefit from mutually selecting sires and dams from each other when the genetic correlation was as low as 0.40 to 0.60. With more intense selection, breeding programs were less likely to benefit from cooperation with breeding programs in other environments. Heritability and number of progeny per bull had little effect on possibilities for cooperation, unless the heritabilities and the number of progeny per bull were extremely different in the 2 environments. Small breeding programs benefited more from cooperation than did large breeding programs, and benefits were possible even at lower values (i.e., <0.80) of the genetic correlation. Possibilities for cooperation across environments would affect the optimal design of dairy cattle breeding programs considering genetic gain, inbreeding, and costs.

Key words: genotype $\times$ environment interaction, breeding program, dairy cattle, genetic gain

INTRODUCTION

Dairy cattle breeding programs and dairy farmers are currently selecting sires and dams from all over the world. Due to genotype $\times$ environment interaction ($G \times E$), indicated by genetic correlations between environments lower than unity, genetic rank of sires and dams differ among environments (Falconer and Mackay, 1996). Genetic correlations are in general between 0.80 and 1.00 for milk production traits either between different environments within countries (Hayes et al., 2003; Kearney et al., 2004; Mulder et al., 2004) or among countries in the northern hemisphere (Weigel et al., 2001; Zwald et al., 2003). Genetic correlations, however, are lower between milk production traits in North America or Western Europe and New Zealand, Australia, South America, or Africa (Costa et al., 2000; Ojango and Pollott, 2002; Zwald et al., 2003). Furthermore, genetic correlations are lower for functional traits than for milk production traits; for example, the average genetic correlation for longevity in different countries is 0.59 (Mark, 2004).

With little $G \times E$, breeding programs in different environments may successfully cooperate and select sires and dams worldwide, because 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), and lowers rate of inbreeding, at least in the short term. With substantial $G \times E$, however, long-term selection of sires and dams worldwide can be hampered, because populations in different environments tend to diversify, leading to separation of breeding programs in the long term (Smith and Banos, 1991). Banos and Smith (1991) mentioned that populations diverged quickly when the genetic correlation between countries was lower than 0.80. Smith and Banos (1991) concluded from their results that genetic correlations less than 0.80 to 0.90 would be large enough to remove benefits of worldwide selection.

A lot of research is dedicated to optimizing Interbull procedures (e.g., estimation of genetic correlations and breeding values across countries). However, effects of genetic correlations on short- and long-term possibilit-

Received July 15, 2005.

Accepted November 15, 2005.

¹Corresponding author: herman.mulder@wur.nl

ies for cooperation between dairy cattle breeding programs have received little attention, and effects of parameters characterizing breeding programs are largely unknown (e.g., heritability, selection intensity, size of breeding programs). Banos and Smith (1991) and Lohuis and Dekkers (1998) focused primarily on short-term benefits in genetic gain due to cooperation between dairy cattle breeding programs and allowed population size and $G \times E$ level to vary. In addition, Smith and Banos (1991) investigated long-term effects of different population sizes of males in combination with different levels of $G \times E$. Smith and Banos (1991), however, simulated mass selection of sires and dams with only selection of sires across environments, whereas in dairy cattle breeding, both sires and dams might be selected across environments using BLUP-EBV. Therefore, there is a need for a more complete evaluation of effects of different parameters, such as heritability, selection intensity, number of progeny per sire, and size of breeding programs in situations applicable to dairy cattle.

The objectives of this study were 2-fold: 1) to investigate the effects of heritability, selection intensity, number of progeny per bull, and size of breeding programs on possibilities for cooperation between dairy cattle breeding programs in the short and long term in the presence of $G \times E$, and 2) to quantify the effect of such cooperation on genetic gain.

MATERIALS AND METHODS

Cooperation Between Breeding Programs and Split-Point Genetic Correlation

In this study, we considered a situation with 2 dairy cattle breeding programs operating in 2 different environments. Most of the comparisons made and inferences drawn were based on selection behavior when both breeding programs were at equilibrium, or when genetic gain per generation was constant within each program. Selection of sires and dams was by truncation on EBV for the breeding objective of each given program. The breeding programs were considered to be "cooperating" when additional genetic gains could be obtained when selected sires and dams originated from both environments. In the presence of $G \times E$, populations can diverge in terms of genetic means, leading to individually operated (i.e., noncooperating) breeding programs at equilibrium. The highest value of the genetic correlation where breeding programs were operating individually at equilibrium was called the "split-point" genetic correlation in this study. Breeding programs cooperated when the genetic correlation was above this value; otherwise they operated individually because no additional gain could be obtained by selecting animals from the other environment.

Breeding Programs

Possibilities for cooperation between the 2 breeding programs were investigated by deterministic simulation using a pseudo-BLUP selection index. The breeding objective of breeding program 1 was milk yield in environment 1; the breeding objective 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. Performance in both environments was assumed to follow a multivariate normal distribution. Sires and dams were selected by truncation on animal model BLUP-EBV, approximated by a pseudo-BLUP selection index. The EBV of sires were based on average performance of progeny and pedigree information; EBV of dams were based on own performance in first lactation in one environment and pedigree information. Four selection paths were considered: sires to breed sons (SS), sires to breed daughters (SD), dams to breed sons (DS), and dams to breed daughters (DD). Selection of SS, SD, and DS was by truncation across environments, whereas DD were completely selected within their own environment. Generations were assumed to be discrete.

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. Selected fractions were chosen to represent practical dairy cattle breeding programs and were similar to those of 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 ($p_{SS} = 0.05$), whereas the best 40 SD were selected out of 400 bulls in total ($p_{SD} = 0.10$). To produce 400 test bulls, 1,000 DS were selected each year out of 200,000 cows in the 2 environments together ($p_{DS} = 0.005$). Each dam population consisted of 1 million cows, of which 10% were considered as potential DS. Other dams were excluded for various reasons not directly related to the breeding objective. The 80% best cows were selected as DD each year within their own environment to produce female replacements using AI ($p_{DD} = 0.80$). The heritability (h^2) of milk yield was 0.3 in both environments and the genetic correlation between both environments (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.

Pseudo-BLUP Selection Index

For reasons of computing time, selection on animal model BLUP-EBV was approximated using a pseudo-

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

Parameter	Basic	Alternative range
Genetic correlation (r_g)	0 to 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 to 300 (sum always 400)
Number of progeny per bull (np)	100	10 to 100
Population size cows per environment	1,000,000	
Selected fraction sires to breed sons (p_{SS})	0.05	0.01, 0.05, 0.10, 0.20
Selected fraction sires to breed daughters (p_{SD})	0.10	0.01, 0.05, 0.10, 0.20
Selected fraction dams to breed sons (p_{DS})	0.005	0.01, 0.05, 0.10, 0.20
Selected fraction dams to breed daughters (p_{DD})	0.80	

BLUP selection index. A pseudo-BLUP selection index approximates BLUP-selection by including pedigree information using the EBV of sires and dams as sources of information in the selection index (Wray and Hill, 1989; Villanueva et al., 1993). These EBV of sires and dams include all information that was available in the previous generation at the time of selection. Iteration on the selection index resulted in a build-up of pedigree information (Dekkers, 1992). A pseudo-BLUP selection index assumes that fixed effects are known without error. The construction of the selection indices is explained in Appendix 1. Table 2 summarizes the notation used.

Variance Reduction Due To Selection. The genetic variance-covariance matrices and variance-covariance matrices of EBV were 2×2 matrices (milk yield in environment 1 and 2 as different traits). Genetic (co)variances and (co)variances of EBV changed not only 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). The calculation of the genetic variance-covariance matrices and variance-covariance matrices of EBV is explained in Appendix 2.

Selected Fraction and Selection Intensity. Sires and dams in the selection paths SS, SD, and DS were selected across environments on EBV. A common truncation point was determined by using Ridders' Method (Press et al., 1992) based on the total number of selected animals in a certain selection path, the genetic mean and variance of EBV of the subpopulations for the breeding program of interest, and the distribution of animals across environments. Subsequently, the common truncation point (x) was translated into selected fractions (p) within each environment using properties

of the normal distribution (Abramowitz and Stegun, 1968). Selection intensities were corrected for finite population size using the method of Burrows (1972) and for correlated EBV using the method of Meuwissen (1991).

Genetic Mean and Genetic Gain. Genetic selection differentials for performance in environment i $R_{i,kl,r(t)}$ were calculated for animals selected for breeding program l within environment k and selection path r in generation t as

$$\frac{i_{kl(t)} \times \mathbf{b}_{m,kl(t)}' \mathbf{g}_{i,k(t)}}{\sigma_{EBV,m,kl(t)}}$$

(Cameron, 1997), where $i_{kl(t)}$ is the selection intensity, $\mathbf{b}_{m,kl(t)}$ is the vector with selection index weights for breeding objective m , $\mathbf{g}_{i,k(t)}$ is the vector with covariances between phenotypic information sources and the breeding objective m and $\sigma_{EBV,m,kl(t)}$ is the standard deviation of the EBV for breeding objective m (see Appendices 1 and 2 for construction of $\mathbf{g}_{i,k(t)}$ and calculation of $b_{m,kl(t)}$ and $\sigma_{EBV,m,kl(t)}$). The genetic mean of selected animals in one environment was

$$\mu_{i,kl,r(t)}^* = \mu_{i,k,r(t)} + R_{i,kl,r(t)},$$

where $\mu_{i,k,r(t)}$ is the genetic mean before selection. The average genetic mean of all selected animals was

$$\bar{\mu}_{i,l,r(t)}^* = \sum_{k=1}^2 f_{kl,r(t)} \mu_{i,kl,r(t)}^*,$$

where $f_{kl,r(t)}$ is the proportion of selected animals originating from environment k for selection path r in gener-

Table 2. Notation used

Notation	Definition
h^2, r_g	Heritability, genetic correlation between environments
σ_p^2, np	Phenotypic variance, number of progeny per bull
f	Proportion of selected animals
R	Genetic selection differential
μ, μ^*	Genetic mean, genetic mean of selected animals
$p_{SS}, p_{SD}, p_{DS}, p_{DD}$	Selected fraction of sires to breed sons (SS), sires to breed daughters (SD), dams to breed sons (DS), dams to breed daughters (DD)
i, k, x	Selection intensity, variance reduction coefficient, truncation point
$\mathbf{b}, \mathbf{x}$	Selection index weights, vector with information
$\mathbf{P}, \mathbf{P}_{ij}, \mathbf{Pm}_{ij}, \mathbf{Pf}_{ij}$	Variance-covariance (sub)matrix of information sources for males and females
$\mathbf{g}_j, \mathbf{g}_{ij}, \mathbf{gm}_{ij}, \mathbf{gf}_{ij}$	Covariance vector between information source and true breeding value for males and females
$\overline{PG}_{ij}, OP_{ij}$	Covariance of mean of progeny, covariance of own performance
S_{ij}, D_{ij}, M_{ij}	Covariance between EBV of sire, dam or mean EBV of dams of progeny
$C_{ij}, Cs_{ij}, Cd_{ij}, Cms_{ij}$	Genetic, sire genetic, dam genetic and Mendelian sampling covariance
σ_{EBV}^2	Variance of EBV
A	True breeding value
Subscripts i, j	Performance environment 1 or 2
Subscripts k, l	Environment of selection, number of breeding program
Subscript m	Breeding objective

ation $t \left(\sum_1^2 f_{kl,r(t)} = 1 \right)$. The genetic mean of newborn bull calves was calculated as $\frac{1}{2}\bar{\mu}_{i,l,ss(t)}^* + \frac{1}{2}\bar{\mu}_{i,l,ds(t)}^*$, whereas the genetic mean of newborn heifer calves was $\frac{1}{2}\bar{\mu}_{i,l,sd(t)}^* + \frac{1}{2}\bar{\mu}_{i,l,dd(t)}^*$. Genetic means in generation zero were equal in both environments and set to zero. Genetic gain was calculated as the difference in genetic mean in generation t and generation $t - 1$. Equilibrium was reached when genetic gain in both breeding programs changed less than 1.0×10^{-10} in subsequent generations. Equilibrium was usually reached after 10 to 20 generations of selection, although exceptions to this rule were observed. Results were based on equilibrium values, unless otherwise indicated.

RESULTS

Genetic Gain and Proportion of Animals Selected Within Own Environment

Figure 1A shows equilibrium genetic gain in environment 1 for breeding programs 1 and 2, as a function of the genetic correlation between environment 1 and 2.

The figure could be divided up into 2 parts: 1) genetic gains of 2 individually operated breeding programs when the genetic correlation was ≤ 0.90 (the split-point genetic correlation), and 2) genetic gains of 2 cooperating breeding programs when the genetic correlation was > 0.90 . When the genetic correlation was ≤ 0.90 , 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 , genetic gains of both breeding programs were equal, and increased curvilinearly with the genetic correlation, because breeding programs were cooperating, resulting in higher selection intensity.

Figure 1B shows the equilibrium proportion of animals selected (f) for breeding program 1 within environment 1 for the selection paths SS, SD, and DS as a function of the genetic correlation. When the genetic correlation was 0.90 or below, sires and dams for breeding program 1 were completely selected within environment 1 ($f = 1.00$), indicating that breeding programs were operating individually. When the genetic correlation was > 0.90 , sires and dams were selected in both environments. When the genetic correlation was unity, 50% of the sires and dams were selected within environ-

Figure 1. Cooperation between breeding programs in the presence of genotype × environment interaction. A) Genetic gain in environment 1 from breeding program 1 and 2 (bp1, bp2) as a function of the genetic correlation. B) Proportion of animals selected for breeding program 1 within environment 1 as a function of the genetic correlation for the selection paths sires to breed sons (SS), sires to breed daughters (SD), and dams to breed sons (DS). C) Ratio of genetic gain in environment 1 of breeding programs 2 and 1 as a function of generation number, for different values of the genetic correlation (rg). D) Proportion of SS selected for breeding program 1 within environment 1 as a function of generation number for different values of the genetic correlation (rg). 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; selected fraction SS = 0.05; selected fraction SD = 0.10; selected fraction DS = 0.005; selected fraction DD = 0.80.

ment 1, because the traits in both environments were essentially the same and population sizes of bulls and cows were equal in both environments.

Figure 1C shows the ratio of genetic gain in environment 1 of breeding programs 2 and 1 as a function of generation number, for different values of the genetic correlation near the split-point genetic correlation. When the genetic correlation was higher than the split-

point genetic correlation (0.95 or 0.91), the ratio approached 1.00 after some generations and breeding programs cooperated. When the genetic correlation was equal to the split-point genetic correlation of 0.90, the ratio increased first close to 1.00 and after 30 generations of selection the ratio decreased to the ratio of a correlated response and a direct response (= genetic correlation), indicating that breeding programs were

separated. When the genetic correlation was 0.85, the ratio decreased the first 20 generations to the ratio of a correlated response and a direct response. After 60 and 15 generations of selection for, respectively, a genetic correlation of 0.90 and 0.85, there was a small dip in the ratio caused by establishing a new equilibrium with respect to reduction of genetic variance due to selection and build-up of pedigree information after complete separation of both breeding programs.

Figure 1D shows the proportion of SS selected for breeding program 1 within environment 1 as a function of generation number, for different values of the genetic correlation near the split-point genetic correlation. Results in SD and DS were similar to those in SS. When the genetic correlation was 0.95 and 0.91, the proportion of sires selected for breeding program 1 within environment 1 stabilized to 0.58 and 0.73, respectively. Both breeding programs were selecting sires and dams in both environments, indicating cooperation between both breeding programs. When the genetic correlation was 0.90 or 0.85, the proportion of SS selected for breeding program 1 within environment 1 increased toward 1.00, indicating that sires were only selected within the own environment at equilibrium. In other words, breeding programs cooperated in the initial generations, but eventually separated to operate individually, due to differences in trait means between the 2 programs.

Selection Intensity

Figure 2 shows the split-point genetic correlation as a function of the selected fraction of SS, for 2 sets of selected fractions of sires and dams in SD and DS. In the situation “equal,” the selected fractions in SD and DS were equal to the selected fraction of SS, whereas DD were always selected within their own population with a selected fraction of 0.80. In the situation “practical,” the selected fractions of SD, DS, and DD were fixed to the basic parameter values listed in Table 1 and only the selected fraction of SS was varied. For both situations, the split-point genetic correlation decreased with increasing selected fraction of SS. The decrease was larger with equal selected fractions of SS, SD, and DS (“equal”) than with fixed selected fractions of SD and DS (“practical”). In summary, breeding programs cooperate more with less intense selection.

Heritability and Number of Progeny per Bull

Table 3 shows the split-point genetic correlation for different heritabilities and numbers of progeny per bull. Note that each bull was progeny tested in only one environment. When heritability and the number of

Figure 2. The split-point genetic correlation as a function of the selected fraction sires to breed sons (SS) for 2 sets of selected fractions of SS, sires to breed daughters (SD), and dams to breed sons (DS) (“equal”: selected fraction SD = selected fraction DS = selected fraction SS, selected fraction DD = 0.8; “practical”: selected fraction SD = 0.1, selected fraction DS = 0.005, selected fraction DD = 0.8). 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.

progeny per bull were equal in both environments, the split-point genetic correlation hardly changed, because differences in accuracy of selection between animals in environment 1 or 2 were solely determined by the genetic correlation.

When heritability and number of progeny per bull were different in both environments, the split-point genetic correlation decreased, especially when either the heritability was low in one environment (0.10 vs. 0.30) or the number of progeny per bull was low in one environment (10 vs. 100 progeny). When both heritability and number of progeny were different in both environments, the split-point genetic correlation decreased substantially. Differences in accuracy of selection between animals in environment 1 or 2 were affected not only by the genetic correlation, but also by differences in heritability or number of progeny per bull. The breeding program with the lowest heritability or the lowest number of progeny had the largest benefits of selection of sires and dams across both environments even with a moderate genetic correlation between environments.

In summary, heritability and number of progeny per bull had negligible effects on the split-point genetic correlation, unless heritability and number of progeny per bull were extremely different in the 2 environments.

Table 3. Effect of heritability and number of progeny per bull on the split-point genetic correlation¹

Changed parameter	Heritability ²		Number of progeny ³		Split-point genetic correlation
	h_1^2	h_2^2	np_1	np_2	
Basic situation	0.3	0.3	100	100	0.90
Equal heritability	0.1	0.1	100	100	0.89
	0.5	0.5	100	100	0.91
	0.1	0.3	100	100	0.84
Different heritability	0.5	0.3	100	100	0.89
	0.3	0.3	10	10	0.90
	0.3	0.3	50	50	0.90
Equal number of progeny	0.3	0.3	10	100	0.86
	0.3	0.3	50	100	0.90
	0.1	0.3	10	100	0.60
Different h^2 and $np^{2,3}$	0.1	0.3	50	100	0.78

¹Phenotypic variance = 1.0; number of test bulls per breeding program = 200 (total = 400); cow population size per environment = 1.0 million; selected fraction SS = 0.05; selected fraction SD = 0.10; selected fraction DS = 0.005; selected fraction DD = 0.80.

² h_i^2 = Heritability in environment i .

³ np_l = Number of progeny per bull of breeding program l in environment i ($i = l$).

Number of Bulls Tested per Breeding Program

Figure 3A shows the proportion of SS selected for breeding program 1 within environment 1 as a function of the genetic correlation for different numbers of bulls tested in environments 1 and 2. The total number of bulls tested was always equal to 400 and the number of selected sires in SS and SD in each breeding program was always constant. When the number of bulls tested

in breeding program 1 decreased from 200 to 100, the split-point genetic correlation decreased from 0.90 to 0.79. When the genetic correlation was unity, the proportion of SS selected for breeding program 1 within environment 1 was exactly equal to the proportion of total number of bulls tested in breeding program 1, as expected. These patterns were also observed for selection paths SD and DS in breeding program 1 and for selection paths SS, SD, and DS in breeding program

Figure 3. Results for breeding programs with different numbers of test bulls. A) Proportion of sires to breed sons (SS) selected for breeding program 1 (SS11) within environment 1 as a function of the genetic correlation for different numbers of bulls tested in breeding programs 1 and 2 [e.g., 100 to 300: 100 in breeding program 1 and 300 in environment 2 (total number of test bulls = 400)]. B) Increase in genetic gain (%) relative to individually operated breeding programs as a function of genetic correlation, when 100 bulls are tested in breeding program 1 (bp1) and 300 bulls in breeding program 2 (bp2). Heritability = 0.3; phenotypic variance = 1.0; number of progeny per bull = 100; population size cows each environment = 1.0 million; selected fraction SS = 0.05; selected fraction SD = 0.10; selected fraction DS = 0.005; selected fraction DD = 0.80.

2 (results not shown). Split-point genetic correlations were, however, not always exactly equal for all selection paths and for both breeding programs; the lowest split-point genetic correlation was considered as most important.

Figure 3B shows that the percentage increase in genetic gain due to cooperation, relative to individually operated breeding programs, was much larger for a small breeding program with 100 bulls tested (breeding program 1) than for a large breeding program with 300 bulls tested (breeding program 2). The advantage of cooperation was up to 34% for a breeding program of 100 test bulls (breeding program 1), whereas the advantage of cooperation was only up to 7% for a breeding program with 300 test bulls (breeding program 2). In the curve of breeding program 1, 2 parts could be distinguished in the percentage increase in genetic gain: 1) when the genetic correlation was between 0.80 and 0.85, and 2) when genetic correlation was higher than 0.85. This was due to a difference in split-point genetic correlation between the 2 breeding programs (result not shown).

It can be concluded that the split-point genetic correlation decreased with the increase in asymmetry in number of bulls tested per environment and small breeding programs had a larger benefit from cooperation than did large breeding programs.

Short Term vs. Long Term

With the exception of Figure 1C and 1D, which showed all generations, only equilibrium results have been shown so far, but in some situations, equilibrium was reached only 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 (Figure 4A) and the increase in genetic gain relative to individually operated breeding programs was determined as a function of generation number for different values of the genetic correlation (Figure 4B). To mimic a practical situation where both breeding programs had been selecting sires and dams across the 2 environments for many generations, the first 20 generations were simulated to establish Bulmer equilibrium (Bulmer, 1971) and pedigree equilibrium (Dekkers, 1992). In generation 20, genetic means of both populations were set to zero, so that genetic means were again equal. Using generation 20 as starting point (considered as generation 0), the split-point genetic correlation was determined in every generation as the highest value of the genetic correlation, where more than 99% of the selected animals in each selection path originated from the own environment.

Figure 4A shows the split-point genetic correlation as a function of generation number. When generation number increased, the split-point genetic correlation increased rapidly in the first 10 generations and reached the equilibrium asymptote after 60 generations of selection. In the first 5 generations, sires and dams were selected in both environments, when the genetic correlation was greater than 0.60 to 0.75. After 5 to 10 generations, sires and dams were only selected across environments, when the genetic correlation was >0.80 . At equilibrium, sires and dams were selected in both environments, when the genetic correlation was >0.90 . Curves of the split-point genetic correlation as a function of generation number were similar for other values of selected fractions (results not shown).

Figure 4B shows the percentage increase in genetic gain due to cooperation relative to individually operated breeding programs. When the genetic correlation was 0.95 or 1.00, which were both higher than the equilibrium split-point genetic correlation, genetic gain increased by, respectively, 12 and 15%. The percentage increase in genetic gain was constant with increasing generation number. When the genetic correlation was 0.90 or below, genetic gain increased in the first 10 generations by up to 8%. After more generations of selection, the increase in genetic gain disappeared, because breeding programs separated. In conclusion, cooperation between breeding programs operating in different environments can increase genetic gain, but cooperation is only possible in the long-term when the genetic correlation is higher than 0.90.

DISCUSSION

This study investigated cooperation between dairy cattle breeding programs in the presence of $G \times E$. Possibilities for cooperation in the long-term were mainly dependent on the value of the genetic correlation. A pseudo-BLUP selection index model was used to predict genetic gain and to derive split-point genetic correlations. Previous studies used a simpler selection index model (Banos and Smith, 1991; Smith and Banos, 1991; Lohuis and Dekkers, 1998). To show the relevance of using a more sophisticated model, split-point genetic correlations were calculated in the basic situation (Table 1) with a simple selection index model and with the pseudo-BLUP selection index model. The split-point genetic correlation was higher with a pseudo-BLUP selection index model (0.90 vs. 0.87), mainly as a consequence of accounting for reduction of genetic (co)variance because of linkage disequilibrium due to selection (Bulmer, 1971). Due to selection, the genetic correlation between environments decreased (Villanueva and Kennedy, 1990), resulting in slightly less opportunity for

Figure 4. Short- and long-term effects of cooperation between breeding programs. A) Split-point genetic correlation as a function of generation number (split-point genetic correlation was determined as the highest genetic correlation, where more than 99% of the selected animals in each selection path originated from the own environment). B) Increase in genetic gain (%) due to cooperation relative to individually operated breeding programs as a function of generation number for different values of the genetic correlation (rg). 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; selected fraction sires to breed sons (SS) = 0.05; selected fraction sires to breed daughters (SD) = 0.10; selected fraction dams to breed sons (DS) = 0.005; selected fraction dams to breed daughters (DD) = 0.80.

breeding programs to cooperate with breeding programs in other environments. Split-point genetic correlations were, nevertheless, in the same range as in Banos and Smith (1991) and Smith and Banos (1991). Banos and Smith (1991) predicted a split-point genetic correlation of 0.80, but investigated only the first 5 generations, whereas Smith and Banos (1991) predicted equilibrium split-point genetic correlations in the range of 0.80 to 0.90, depending on population size of males. Benefits of cooperation and effects of unequal sizes of both breeding programs were very similar as in Banos and Smith (1991), Smith and Banos (1991), and Lohuis and Dekkers (1998). In addition to effects of unequal sizes of breeding programs, we also investigated effects of heritability, selection intensity, and number of progeny per sire, which had not been previously investigated.

This study did not account for inbreeding. Banos and Smith (1991) and Lohuis and Dekkers (1998) accounted for inbreeding by using predicted rates of inbreeding depending only on the number of selected sires and dams (Falconer and Mackay, 1996). As a consequence, Banos and Smith (1991) found almost constant optimal numbers of selected sires when maximizing a function of genetic gain minus costs of inbreeding depression. In this study and in that of Smith and Banos (1991),

fixed numbers of selected sires and dams were used, resulting in fixed rates of inbreeding when using prediction formulas as given in Falconer and Mackay (1996). Even with more sophisticated models to predict rate of inbreeding (e.g., Bijma et al., 2001), variation in rate of inbreeding would be small due to selection of fixed numbers of selected sires and dams, and small differences in probability of coselection of relatives. Therefore, effects on split-point genetic correlation and benefits of cooperation would likely be small when accounting for inbreeding.

In practice, several Holstein-Friesian breeding programs are operating in different areas of the world. In principle, each breeding program can select sires and dams from all over the world. With more breeding programs and environments, a larger proportion of selection candidates is located in other environments than in the domestic environment. Consequently, selecting sires and dams across environments will probably increase benefits of cooperation between breeding programs even more (Smith and Banos, 1991), depending on genetic correlations and genetic means of different environments. For a given country, the current system is comparable to the situation with a small breeding program and a large breeding program (see Figure 3), because the breeding programs of all other countries

can be considered together as one large breeding program. With multiple environments and breeding programs, sires and dams may be selected across environments even at lower values of the genetic correlation than in the situation with 2 environments and 2 breeding programs.

In real life, different breeding programs often have different breeding goals. This means that not only $G \times E$ on a trait-by-trait level but also differences in breeding goal play a role in possibilities for cooperation between breeding programs. Differences in economic weights do not affect the accuracy of EBV of animals in other environments, whereas $G \times E$ on a trait-by-trait level does affect the accuracy of EBV of animals in other environments. In reality, $G \times E$ on a trait-by-trait level and differences in breeding goals are usually occurring simultaneously (Goddard, 1992). Therefore, the results in this study may serve as a guideline by interpreting single-trait selection as selection on an index combining different traits, replacing the genetic correlation between single-trait performances in different environments by the genetic correlation between breeding goals. Because of breeding goal differences, the genetic correlation between breeding goals is expected to be less than the genetic correlation between single-trait performances in different environments. Due to broadening of breeding goals in different countries, the genetic correlation between breeding goals has decreased in the last 5 to 10 yr, leading to fewer animals in common among top bull listings across various countries (Miglior et al., 2005).

Differences in breeding goals or $G \times E$ on a trait-by-trait level can increase the global effective population size due to selection of different sires and dams in different breeding programs (Goddard, 1992). Therefore, the rate of inbreeding in the global population would be lower than if all breeding programs were selecting the same sires and dams. When the genetic correlation is lower or equal to the split-point genetic correlation, breeding programs are not selecting each other's sires and dams. Consequently, rates of inbreeding will probably increase within environments, because selection of less-related animals in other environments is not possible to achieve optimal genetic gain. However, genetic diversity of the whole breed will increase due to emergence of isolated strains. Goddard (1992), however, suggested that inbreeding effects and the large size of the world population would prevent complete isolation.

Optimization of breeding programs is usually aimed at maximization of genetic gain with constrained inbreeding (Bijma, 2000). Cooperation with other breeding programs is an opportunity to either increase genetic gain substantially without extra investment in testing more bulls, or reducing the number of test bulls

while maintaining genetic gain. Furthermore, it is a way to select less-related animals, thus reducing inbreeding rate. The increase of the split-point genetic correlation with a lower selected fraction indicates a trade-off between selection intensity and possibilities for cooperation. Possibilities for cooperation across environments would affect, therefore, the optimal design of dairy cattle breeding programs considering genetic gain, inbreeding, and costs.

CONCLUSIONS

Cooperation between 2 breeding programs was possible in the long term, when the genetic correlation between performance in both environments was higher than 0.80 to 0.90, resulting in up to 15% extra genetic gain with equal-sized breeding programs. On the contrary, in the first generations, cooperation was possible when the genetic correlation was as low as 0.40 to 0.60. With more intense selection, breeding programs were less likely to benefit from cooperation with breeding programs in other environments. Heritability and number of progeny per bull had little effect on possibilities for cooperation, unless heritability and number of progeny were extremely different in the 2 environments. Small breeding programs benefited more from cooperation than did large breeding programs, and cooperation was possible at lower values of the genetic correlation. Possibilities for cooperation across environments would affect the optimal design of dairy cattle breeding programs considering genetic gain, inbreeding, and costs.

ACKNOWLEDGMENTS

The authors thank Johan van Arendonk, Roel Veerkamp, and Bart Ducro for helpful suggestions and comments on earlier versions of the manuscript, and for fruitful discussions about this study. The authors would like to thank two anonymous reviewers for valuable comments.

REFERENCES

- Abramowitz, M., and I. A. Stegun. 1968. Handbook of mathematical functions. 5th ed. Dover Publications, Inc., New York, NY.
- Banos, G., and C. Smith. 1991. Selecting bulls across countries to maximize genetic improvement in dairy cattle. *J. Anim. Breed. Genet.* 108:174–181.
- Bijma, P. 2000. Long-term genetic contributions: Prediction of rates of inbreeding and genetic gain in selected populations. PhD Thesis, Wageningen University, Wageningen, The Netherlands.
- Bijma, P., J. A. M. van Arendonk, and J. A. Woolliams. 2001. Predicting rates of inbreeding for livestock improvement schemes. *J. Anim. Sci.* 79:840–853.
- Bulmer, M. G. 1971. The effect of selection on genetic variability. *Am. Nat.* 105:201–211.
- Burrows, P. M. 1972. Expected selection differentials for directional selection. *Biometrics* 28:1091–1100.

- Cameron, N. D. 1997. Selection indices and prediction of genetic merit in animal breeding. CAB International, Wallingford, UK.
- Costa, C. N., R. W. Blake, E. J. Pollak, P. A. Oltenacu, R. L. Quaas, and S. R. Searle. 2000. Genetic analysis of Holstein Cattle populations in Brazil and the United States. *J. Dairy Sci.* 83:2963–2974.
- Dekkers, J. C. M. 1992. Asymptotic response to selection on best linear unbiased predictors of breeding values. *Anim. Prod.* 54:351–360.
- Falconer, D. S., and T. F. C. Mackay. 1996. Introduction to quantitative genetics. 4th ed. Pearson Education Limited, Essex, UK.
- Goddard, M. E. 1992. Optimal effective population size for the global population of black and white dairy cattle. *J. Dairy Sci.* 75:2902–2911.
- Hayes, B. J., M. Carrick, P. J. Bowman, and M. E. Goddard. 2003. Genotype $\times$ environment interaction for milk production of daughters of Australian dairy sires from test-day records. *J. Dairy Sci.* 86:3736–3744.
- Kearney, J. F., M. M. Schutz, P. J. Boettcher, and K. A. Weigel. 2004. Genotype $\times$ environment interaction for grazing versus confinement. I. Production traits. *J. Dairy Sci.* 87:501–509.
- Lohuis, M. M., and J. C. M. Dekkers. 1998. Merits of borderless evaluations. *Proc. 6th World Congr. Genet. Appl. Livest. Prod., Armidale, Australia* 26:169–172.
- Mark, T. 2004. Applied genetic evaluations for production and functional traits in dairy cattle. *J. Dairy Sci.* 87:2641–2652.
- Meuwissen, T. H. E. 1991. Reduction of selection differentials in finite populations with a nested full-half sib family structure. *Biometrics* 47:195–203.
- Miglior, F., B. L. Muir, and B. J. Van Doormaal. 2005. Selection indices in Holstein cattle of various countries. *J. Dairy Sci.* 88:1255–1263.
- Mueller, J. P., and J. W. James. 1983. Effects of reduced variance due to selection in open nucleus breeding systems. *Aust. J. Agric. Res.* 34:53–62.
- Mulder, H. A., A. F. Groen, G. De Jong, and P. Bijma. 2004. Genotype $\times$ environment interaction for yield and somatic cell score with automatic and conventional milking systems. *J. Dairy Sci.* 87:1487–1495.
- Ojango, J. M. K., and G. E. Pollott. 2002. The relationship between Holstein bull breeding values for milk yield derived in both the UK and Kenya. *Livest. Prod. Sci.* 74:1–12.
- Press, W. H., S. A. Teukolsky, W. T. Vetterling, and B. P. Flannery. 1992. Numerical recipes in FORTRAN: The art of scientific computing. Cambridge University Press, Cambridge, UK.
- Smith, C., and G. Banos. 1991. Selection within and across populations in livestock improvement. *J. Anim. Sci.* 69:2387–2394.
- Vargas, B., and J. A. M. van Arendonk. 2004. Genetic comparison of breeding schemes based on semen importation and local breeding schemes: Framework and application to Costa Rica. *J. Dairy Sci.* 87:1496–1505.
- Villanueva, B., and B. W. Kennedy. 1990. Effect of selection on genetic parameters of correlated traits. *Theor. Appl. Genet.* 80:746–752.
- Villanueva, B., N. R. Wray, and R. Thompson. 1993. Prediction of asymptotic rates of response from selection on multiple traits using univariate and multivariate best linear unbiased predictors. *Anim. Prod.* 57:1–13.
- Weigel, K. A., R. Rekaya, N. R. Zwald, and W. F. Fikse. 2001. International genetic evaluation of dairy sires using multiple-trait model with individual animal performance records. *J. Dairy Sci.* 84:2789–2795.
- Wray, N. R., and W. G. Hill. 1989. Asymptotic rates of response from index selection. *Anim. Prod.* 49:217–227.
- Zwald, N. R., K. A. Weigel, W. F. Fikse, and R. Rekaya. 2003. Application of a multiple-trait herd cluster model for genetic evaluation of dairy sires from seventeen countries. *J. Dairy Sci.* 86:376–382.

APPENDIX 1

Pseudo-BLUP Selection Index

Selection indices or EBV of environment j in generation t ($EBV_{j(t)} = \mathbf{b}_{j(t)}'\mathbf{x}_{(t)}$) were constructed for all bulls and cows being selection candidates for both breeding programs. Each bull and cow had 2 EBV: one for each environment. The selection index weights $\mathbf{b}_{j(t)}$ were calculated as $\mathbf{P}_{(t)}^{-1}\mathbf{g}_{j(t)}$, where $\mathbf{P}_{(t)}$ is the variance-covariance matrix of information sources in $\mathbf{x}_{(t)}$ and $\mathbf{g}_{j(t)}$ is the covariance vector between information sources in $\mathbf{x}_{(t)}$ and the true breeding value of environment j . The information sources in $\mathbf{x}_{(t)}$ of bulls were (1) mean performance of progeny, (2) mean EBV of dams of progeny, (3) EBV dam, and (4) EBV sire. The information sources in $\mathbf{x}_{(t)}$ of cows were: (1) own performance of first lactation, (2) EBV dam, and (3) EBV sire. The mean EBV of dams of progeny was used to increase accuracy of selection. Dams of progeny were assumed unselected due to random use of test bulls on first-lactation cows. The EBV of sires and dams were used to include pedigree information and contained all information that was available in the previous generation at selection.

The $\mathbf{P}_{(t)}$ -matrix was formed with submatrices ($\mathbf{P}_{ij(t)}$) for each combination of traits i and j (environment 1 and 2):

$$\mathbf{P}_{(t)} = \begin{bmatrix} \mathbf{P}_{11(t)} & \mathbf{P}_{12(t)} \\ \mathbf{P}_{21(t)} & \mathbf{P}_{22(t)} \end{bmatrix}$$

with different submatrices $\mathbf{Pm}_{ij(t)}$ and $\mathbf{Pf}_{ij(t)}$, for males and females, respectively, following the given order of information sources:

$$\mathbf{Pm}_{ij} = \begin{bmatrix} \overline{PG}_{ij(t)} & M_{ij(t)}/2np & D_{ij(t)}/4 & S_{ij(t)}/4 \\ & M_{ij(t)}/np & 0 & 0 \\ & & D_{ij(t)} & 0 \\ & & & S_{ij(t)} \end{bmatrix}$$

$$\mathbf{Pf}_{ij} = \begin{bmatrix} OP_{ij(t)} & D_{ij(t)}/2 & S_{ij(t)}/2 \\ & D_{ij(t)} & 0 \\ & & S_{ij(t)} \end{bmatrix}$$

where $\overline{PG}_{ij(t)} = (\text{co})\text{variance of mean performance of progeny between trait } i \text{ and } j \text{ in generation } t = \frac{1}{4}C_{ij(t)} + \left(\frac{1}{4}C_{ij(t)} + Cms_{ij(t=0)} + E_{ij}\right)/np$, where $C_{ij(t)}$ is element of the genetic variance-covariance matrix, $Cms_{ij(t=0)}$ is element of the genetic variance-covariance matrix of Mendelian sampling term, E_{ij} is element of the environmental variance-covariance matrix and np is number of progeny, $OP_{ij(t)} = (\text{co})\text{variance of own performance between trait } i \text{ and } j \text{ in generation } t = C_{ij(t)} + E_{ij}$, $M_{ij(t)} = (\text{co})\text{variance of mean EBV of dams of progeny between trait } i \text{ and } j \text{ in generation } t = \text{element of } \mathbf{b}'_{j(t-1)}\mathbf{P}_{(t-1)}\mathbf{b}_{j(t-1)}$, because dams of progeny were assumed to be not selected due to random use of test bulls on cows in first lactation, and $D_{ij(t)}, S_{ij(t)} = (\text{co})\text{variance of EBV dam/sire between trait } i \text{ and } j \text{ in generation } t$, see under “variance reduction due to selection”.

The $\mathbf{g}_{j(t)}$ vector was partitioned into $\mathbf{g}_{ij(t)}$, where i is the trait of information in the selection index and j is the trait that the EBV corresponds to:

$$\mathbf{g}_{j(t)} = \begin{bmatrix} \mathbf{g}_{1j(t)} \\ \mathbf{g}_{2j(t)} \end{bmatrix}$$

with different vectors $\mathbf{g}_{ij(t)}$, $\mathbf{gm}_{ij(t)}$ and $\mathbf{gf}_{ij(t)}$, for bulls and cows, following the given order of information sources:

$$\mathbf{gm}_{ij(t)} = \begin{bmatrix} C_{ij(t)}/2 \\ 0 \\ D_{ij(t)}/2 \\ S_{ij(t)}/2 \end{bmatrix} \quad \mathbf{gf}_{ij(t)} = \begin{bmatrix} C_{ij(t)} \\ D_{ij(t)}/2 \\ S_{ij(t)}/2 \end{bmatrix}.$$

APPENDIX 2

Variance Reduction Due To Selection

Due to differences in selected fractions between the selection paths SS and DS as parents of bulls and the selection paths SD and DD as parents of cows, each breeding program had 2 genetic variance-covariance matrices because of different Bulmer equilibria. Therefore, each breeding program had 2 sire and dam genetic variance-covariance matrices ($\mathbf{Cs}_{(t)}$ and $\mathbf{Cd}_{(t)}$). A genetic (co)variance ($C_{ij(t)}$) was partitioned into:

$$C_{ij(t)} = \frac{1}{4}Cs_{ij(t)} + \frac{1}{4}Cd_{ij(t)} + Cms_{ij(t=0)}$$

where $Cms_{ij(t=0)} = \frac{1}{2}C_{ij(t=0)}$ = genetic Mendelian sampling (co)variance between traits i and j , which is half of the initial genetic (co)variance.

The $\mathbf{Cs}_{(t)}$ -matrix and $\mathbf{Cd}_{(t)}$ -matrix were updated each generation according to Bijma et al. (2001); for example, for an element $Cs_{ij,l(t)}$ of breeding program l in generation t :

$$Cs_{ij,l(t)} = \sum_1^k \left\{ f_{kl(t-1)} \left[C_{ij,k(t-1)} - \frac{\text{Cov}(A_i, EBV_{m,kl})_{(t-1)} \text{Cov}(A_j, EBV_{m,kl})_{(t-1)}}{\sigma_{EBV,m,kl(t-1)}^2} k_{s,kl(t-1)} \right] \right\} \\ + \sum_1^k \{ f_{kl(t-1)} [\mu_{i,kl(t-1)}^* - \bar{\mu}_{i,l(t-1)}^*] [\mu_{j,kl(t-1)}^* - \bar{\mu}_{j,l(t-1)}^*] \}$$

where $\text{Cov}(A_i, EBV_{m,kl})_{(t-1)} = \mathbf{b}'_{m,kl(t-1)}\mathbf{g}_{i,kl(t-1)}$, $EBV_{m,kl}$ = selection criterion of animals selected for breeding objective m of breeding program l within environment k in generation $t - 1$, $\sigma_{EBV,m,kl(t-1)}^2 = \mathbf{b}'_{m,kl(t-1)}\mathbf{P}_{k(t-1)}\mathbf{b}_{m,kl(t-1)}$ = variance of $EBV_{m,kl}$ in generation $t - 1$, and $k_{s,kl(t-1)} = i_{s,kl(t-1)}(i_{s,kl(t-1)} - x_{s,kl(t-1)})$ = variance reduction coefficient, where $i_{s,kl(t-1)}$ is selection intensity of sires selected for breeding program l within environment k in generation

$t - 1$ and $x_{s,kl(t-1)}$ is the corresponding standardized truncation point. The $\mathbf{Cd}_{(t)}$ -matrix was calculated similarly using $k_{d,kl(t-1)}$ instead of $k_{s,kl(t-1)}$.

Due to differences in selected fractions between the selection paths SS and DS as parents of bulls and the selection paths SD and DD as parents of cows, each breeding program had 2 variance-covariance matrices of sire EBV ($\mathbf{S}_{(t)}$) and dam EBV ($\mathbf{D}_{(t)}$) because of different Bulmer equilibria. In multivariate analysis the elements of $\mathbf{S}_{(t)}$ and $\mathbf{D}_{(t)}$ are equal to the covariances between the true additive genetic effects and the EBV (Villanueva et al., 1993). Elements of $\mathbf{S}_{(t)}$ -matrix and $\mathbf{D}_{(t)}$ -matrix were updated each generation, e.g., for an element $S_{ij,l(t)}$ of breeding program l in generation t :

$$S_{ij,l(t)} = \sum_1^k \left\{ f_{kl(t-1)} \left[\text{Cov}(A_i, EBV_{j,kl}(t-1)) - \frac{\text{Cov}(A_i, EBV_{m,kl}(t-1)) \text{Cov}(EBV_{j,kl}, EBV_{m,kl}(t-1))}{\sigma_{EBV,m,kl(t-1)}^2} k_{s,kl(t-1)} \right] \right\} \\ + \sum_1^k \{ f_{kl(t-1)} [\mu_{i,kl(t-1)}^* - \bar{\mu}_{i,l(t-1)}^*] [\mu_{j,kl(t-1)}^* - \bar{\mu}_{j,l(t-1)}^*] \}$$

where $EBV_{j,kl}$ = EBV for performance in environment j for an animal selected for breeding program l within environment k , $\text{Cov}(A_i, EBV_{j,kl}(t-1)) = \mathbf{b}'_{j,kl(t-1)} \mathbf{g}_{m,kl(t-1)}$, and $\text{Cov}(EBV_{j,kl}, EBV_{m,kl}(t-1)) = \mathbf{b}'_{j,kl(t-1)} \mathbf{g}_{m,kl(t-1)}$.