Optimization of Dairy Cattle Breeding Programs for Different Environments with Genotype by Environment Interaction

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ABSTRACT

Dairy cattle breeding organizations tend to sell semen to breeders operating in different environments and genotype $\times$ environment interaction may play a role. The objective of this study was to investigate optimization of dairy cattle breeding programs for 2 environments with genotype $\times$ environment interaction. Breeding strategies differed in 1) including 1 or 2 environments in the breeding goal, 2) running either 1 or 2 breeding programs, and 3) progeny testing bulls in 1 or 2 environments. Breeding strategies were evaluated on average genetic gain of both environments, which was predicted by using a pseudo-BLUP selection index model.

When both environments were equally important and the genetic correlation was higher than 0.61, the highest average genetic gain was achieved with a single breeding program with progeny-testing all bulls in both environments. When the genetic correlation was lower than 0.61, it was optimal to have 2 environment-specific breeding programs progeny-testing an equal number of bulls in their own environment only. Breeding strategies differed by 2 to 12% in average genetic gain, when the genetic correlation ranged between 0.50 and 1.00. Ranking of breeding strategies, based on the highest average genetic gain, was relatively insensitive to heritability, number of progeny per bull, and the relative importance of both environments, but was very sensitive to selection intensity. With more intense selection, running 2 environment-specific breeding programs was optimal for genetic correlations up to 0.70–0.80, but this strategy was less appropriate for situations where 1 of the 2 environments had a relative importance less than 10 to 20%. Results of this study can be used as guidelines to optimize breeding programs when breeding dairy cattle for different parts of the world.

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

INTRODUCTION

Dairy cattle breeding is increasingly becoming an international business. Due to mergers, acquisitions, partnerships, or alliances, breeding organizations are continually selling a greater proportion of semen of proven bulls to different regions of the world. Consequently, phenotypes of daughters of these bulls are recorded in different environments. Genotype $\times$ environment interaction ($G \times E$) may play a role, indicated by genetic correlations lower than unity between countries. Genetic correlations are mostly between 0.85 and 1.00 for milk production traits between environments in North America and Western Europe (Weigel et al., 2001; Kearney et al., 2004; Mulder et al., 2004), but 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). Due to an increasing emphasis on functional traits in breeding goals, the correlation between total merit indices in different countries has decreased (Van der Beek, 2003). Note that genetic correlations between countries are less than unity not only because of $G \times E$, but also because of differences in trait definition or statistical methods used in breeding value estimation (Mark, 2004).

Knowing that genetic correlations between environments are less than unity, breeding organizations face the problem of how to optimize the breeding program when breeding for multiple environments. James (1961) proposed 3 strategies to breed for 2 environments: 1) selection and testing in 1 environment, 2) separate selection and testing in both environments, and 3) testing progeny in both environments and applying index selection to improve performance in both environments simultaneously. Considering only sire selection, he concluded that testing progeny in both environments and applying index selection was superior to separate selection and testing in both environments or selection and testing in 1 environment,

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when the genetic correlation was larger than 0.70. Vargas and van Arendonk (2004) compared genetic gain of a local progeny-testing scheme in Costa Rica with genetic gain of semen importation from the United States, and concluded that semen importation was justified (from a Costa Rican point of view) when the genetic correlation was higher than 0.75. From the perspective of 2 breeding programs in 2 environments, Smith and Banos (1991) and Mulder and Bijma (2006) investigated benefits of cooperation by selection of animals across environments. Both studies concluded that there was no extra genetic gain due to selection across environments when the genetic correlation was lower than 0.80 to 0.90.

So far, only James (1961) studied genetic gain in 2 environments comparing different breeding strategies. James (1961), however, did not investigate sensitivity of breeding strategies to heritability, selection intensity, and number of progeny per bull. Furthermore, Smith and Banos (1991) and Mulder and Bijma (2006) investigated only optimization within one of the strategies as proposed by James (1961). Due to internationalization of dairy cattle breeding organizations, there is a need for a more complete evaluation of different breeding strategies, including a sensitivity analysis, to optimize dairy cattle breeding programs when the objective is to improve performance in different environments in the presence of $G \times E$.

The objective of this study was to investigate optimization of dairy cattle breeding programs for multiple environments in the presence of $G \times E$. The optimal breeding strategy was determined given the relative importance of environments and the genetic correlation between environments. Furthermore, sensitivity of ranking of breeding strategies was investigated with respect to selection intensity, heritability, and number of progeny per bull.

MATERIALS AND METHODS

Breeding Objective

In this study, we considered a situation with a single dairy cattle breeding organization having 2 environments in its overall objective. For simplicity, genetic improvement was focused on higher milk yield in both environments. The aim of the breeding organization was to maximize genetic gain in the overall objective (ΔG) weighing genetic gain in each environment (ΔG_i) by the relative importance of that environment (w_i):

$$\Delta G = w_1 \Delta G_1 + w_2 \Delta G_2 \quad [1]$$

where $w_1 + w_2 = 1$. The relative importance of each environment can be a reflection of, for example, semen

sales, cow population size, or economic value of milk yield.

Breeding Strategies

In a situation with progeny testing of bulls, the breeding organization would have different options to maximize genetic gain in the overall objective. In this study, we considered 1) including 1 or 2 environments in the breeding goal, 2) progeny testing part of the test-bulls in environment 1 and another part in environment 2, or 3) progeny testing all test-bulls either in a single or in both environments. Splitting up the population of test-bulls with testing part of the bulls in environment 1 and another part in environment 2 was considered as making 2 breeding programs. Hence, the term "breeding program(s)" was used to refer to the number of groups of test-bulls. Both breeding programs could have either the same breeding goal or different breeding goals. The breeding goal was defined as $H = \mathbf{v}'\mathbf{a}$, where $\mathbf{v}$ was a vector with economic values of environment 1 and 2, and $\mathbf{a}$ was a vector with true breeding values for milk yield in environment 1 and 2. Note that the breeding goal of a breeding program was not necessarily equal to the overall objective (equation [1]).

Based on the given options, the 4 most different strategies were chosen and simulated in this study: One environment breeding program with progeny testing bulls in 1 environment (**OE-1**), One joint breeding program with progeny testing bulls in 2 environments (**OJ-2**), 2 environment-specific breeding programs each with progeny testing bulls in 1 environment (**TE-1**), and 2 breeding programs with a joint breeding goal each with progeny testing bulls in 1 environment (**TJ-1**). Strategies are described below and summarized in Table 1.

OE-1. Strategy OE-1 consisted of 1 breeding program with progeny testing all bulls in environment 1. The breeding goal was to improve milk yield in environment 1; a zero economic value was given to milk yield in environment 2.

OJ-2. Strategy OJ-2 consisted of 1 breeding program with progeny testing all bulls in both environments. The breeding goal was to improve milk yield in both environments simultaneously. The economic values in the breeding goal were equal to the relative importances of both environments in the overall objective. The number of progeny per bull in each environment was equal to the relative importance of each environment multiplied by the total number of progeny per bull, which was nearly equal to the optimal distribution of progeny to maximize genetic gain in the overall objective (results not shown).

Table 1. Number of test-bulls, number of progeny per bull per environment, and economic values in the breeding goal per breeding program for strategy OE-1 (one environment breeding program), OJ-2 (one joint breeding program), TE-1 (2 environment-specific breeding programs) and TJ-1 (2 breeding programs with a joint breeding goal)

Strategy	No. of test-bulls	No. of progeny per bull		Breeding goal (economic values) ¹	
		E ₁ ²	E ₂	E ₁	E ₂
OE-1	400	100	0	1	0
OJ-2	400	$w_1 \cdot 100^3$	$w_2 \cdot 100$	w_1	w_2
TE-1 ⁴	$w_1 \cdot 400$	100	0	1	0
	$w_2 \cdot 400$	0	100	0	1
TJ-1 ⁴	$w_1 \cdot 400$	100	0	w_1	w_2
	$w_2 \cdot 400$	0	100	w_1	w_2

¹In strategy OJ-2 and TJ-1, the economic values are equal to the relative importance of both environments (w_i).

²E₁ is environment 1; E₂ is environment 2.

³In the basic situation (see Table 2): $w_1 = w_2 = 0.5$.

⁴Strategy TE-1 and TJ-1 consists of 2 breeding programs – each row is one breeding program.

TE-1. Strategy TE-1 contained 2 breeding programs, one for each environment. In breeding program 1, bulls were progeny tested in environment 1; in breeding program 2, bulls were progeny tested in environment 2. The breeding goal of breeding program 1 was to improve milk yield in environment 1; the breeding goal of breeding program 2 was to improve milk yield in environment 2. The number of bulls tested in each environment was equal to the relative importance of each environment multiplied by the total number of bulls tested, which was nearly equal to the optimal distribution of bulls to maximize genetic gain in the overall objective (results not shown). Strategy TE-1 was similar to the situation described in Mulder and Bijma (2006).

TJ-1. The structure of the breeding programs in strategy TJ-1 was identical to that in strategy TE-1. The only difference was that the breeding goal of both breeding programs was to improve milk yield in both environments simultaneously. The economic values in the breeding goal were equal to the relative importances of both environments.

Selection Paths. Four paths of selection were considered: sires to breed sons (**SS**), sires to breed daughters (**SD**), dams to breed sons (**DS**), and dams to breed daughters (**DD**). Breeding goals were equal for all selection paths. Performances in both environments were assumed to follow a multivariate normal distribution. Sires and dams were selected by truncation on an index weighing animal model BLUP-EBV for milk yield in both environments with the corresponding economic values, which were dependent on the breeding strategy. The EBV of bulls were based on average milk yield of progeny and pedigree information. The EBV of cows were based on own performance in first lactation in one environment and pedigree information. Se-

lection of SS and SD was by truncation across breeding programs in case of strategy TE-1 and TJ-1. Selection of DS was in all strategies by truncation across both environments, whereas DD were selected completely within their own environment. Generations were assumed discrete.

Parameter Values. Table 2 gives parameter values for the basic situation. In each strategy, 400 bulls were progeny tested each year with 100 daughters per bull to keep costs of testing bulls approximately equal for all strategies. The selected proportions represented practical dairy cattle breeding programs (Dekkers, 1992; Lohuis and Dekkers, 1998; Vargas and van Arendonk, 2004). In each breeding program, the best 20 bulls were selected as SS each year and the best 40 bulls were selected as SD each year out of 400 bulls in total ($p_{SS} = 0.05$; $p_{SD} = 0.10$). To produce 400 test-bulls, the best 1,000 cows were selected as DS 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% were 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 between environments (r_g) was varied between 0 and 1. The phenotypic variance was set to 1.0 in both environments. Alternative situations were created by changing one parameter at a time while keeping others constant. Parameter values in the basic situation were identical to those in Mulder and Bijma (2006).

Evaluation of Breeding Strategies Genetic Gain. Genetic gains in both environments (ΔG_1 and

Table 2. Values for genetic correlation, heritability, phenotypic variance, number of test-bulls, number of progeny per sire, number of cows in each environment, relative importance of environment 1 and selected proportions 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	0.05, 0.1, 0.3 and 0.6
Phenotypic variance (σ_p^2)	1.0	
Number of test-bulls	400	
Number of progeny per bull	100	10, 20, 100, 1,000
Population size cows per environment	1,000,000	
Relative importance ¹ of environment 1 (w_1)	0.5	0.5–1.0
Selected proportion sires to breed bulls (p_{SS})	0.05	0.01, 0.02, 0.05, 0.10, 0.20
Selected proportion sires to breed cows (p_{SD})	0.10	0.01, 0.02, 0.05, 0.10, 0.20
Selected proportion dams to breed bulls (p_{DS})	0.005	0.01, 0.02, 0.05, 0.10, 0.20
Selected proportion dams to breed cows (p_{DD})	0.80	

¹ $w_2 = 1 - w_1$.

ΔG_2) were predicted per generation per breeding program for all strategies, by deterministic simulation approximating BLUP-selection under an animal model using a pseudo-BLUP selection index (Wray and Hill, 1989; Villanueva et al., 1993). The pseudo-BLUP selection index model is described in the next section. Results presented refer to genetic gain at equilibrium accounting for build-up of pedigree information (Dekkers, 1992) and reduction of genetic variance due to selection (Bulmer, 1971). Genetic gain in the overall objective (ΔG) was calculated using equation [1]. In strategy TE-1, however, genetic gain was different for both breeding programs. Therefore, ΔG was calculated using genetic gain in environment 1 of breeding program 1 (ΔG_1) and genetic gain in environment 2 of breeding program 2 (ΔG_2).

Break-Even Genetic Correlation. The optimum breeding strategy with respect to ΔG depended on the genetic correlation. Rankings changed only between strategy TE-1 and the other strategies OE-1, OJ-2, and TJ-1. Break-even genetic correlations were defined as the genetic correlations where ΔG of strategy TE-1 was equal to ΔG of strategy OE-1, OJ-2, or TJ-1.

Pseudo-BLUP Selection Index Model

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 include all information available in the previous generation. Iteration on the selection index resulted in a build-up of pedigree information (Dekkers, 1992). Details of the selection indices are explained in Appendix 1.

Variance Reduction due to Selection. The genetic and EBV variance-covariance matrices were 2×2 matrices (milk yield in both environments as different

traits). Genetic variances and covariances changed not only due to linkage disequilibrium caused by selection (Bulmer, 1971), but also due to selection of SS, SD, and DS across breeding programs/environments with different genetic means (Mueller and James, 1983). The calculation of genetic and EBV (co)variances is explained in Appendix 2.

Selection Intensity. In strategies TE-1 and TJ-1, SS and SD were selected by truncation across breeding programs, whereas DS were selected across environments in all strategies. A common truncation point was determined using Ridders' Method (Press et al., 1992). Subsequently, the common truncation point (x) was translated into selected proportions (p) within each breeding program/environment using properties of the normal distribution (Abramowitz and Stegun, 1968). Finally, selection intensities were calculated using the method of Burrows (1972), to correct for finite population size, and the method of Meuwissen (1991) to correct for correlated index values of relatives.

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

$$R_{i,k,r(t)} = \frac{i_{k(t)} \times \mathbf{b}_{I,k(t)}' \mathbf{g}_{i,k(t)}}{\sigma_{I,k(t)}}$$

where $i_{k(t)}$ is the selection intensity, $\mathbf{b}_{I,k(t)}$ is the vector with selection index weights, $\mathbf{g}_{i,k(t)}$ is the vector with covariances between phenotypic information sources and the breeding goal and $\sigma_{I,k(t)}$ is the standard deviation of the selection index I (see also Appendix 1). The genetic mean of selected animals was

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

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

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

where $f_{k,r(t)}$ is the fraction of selected animals originating from environment k for selection path r in generation t ($\sum_k f_{k,r(t)} = 1$). The genetic mean of newborn bulls

was calculated as $\frac{1}{2} \bar{\mu}_{i,SS(t)}^* + \frac{1}{2} \bar{\mu}_{i,DS(t)}^*$, whereas the ge-

netic mean of newborn cows was $\frac{1}{2} \mu_{i,SD(t)}^* + \frac{1}{2} \mu_{i,DD(t)}^*$.

Genetic means were zero in both environments in generation zero. In strategy OE-1 and strategy OJ-2, equations to calculate genetic means and genetic selection differentials contained only a single group of bulls. 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 subsequent generations changed less than 1.0×10^{-10} . Equilibrium was reached after 10 to 15 generations of selection, although occasionally it could take longer in strategy TE-1 (Mulder and Bijma, 2006).

RESULTS

Behavior of Strategies

Figures 1A and 1B show genetic gain in environments 1 and 2, respectively, as a function of the genetic correlation for all strategies in the basic situation (Table 2).

The OE-1-strategy was designed to maximize genetic gain in environment 1. Genetic gain in environment 1 was nearly constant (Figure 1A), whereas genetic gain in environment 2 was purely a correlated response (Figure 1B), as expected. The DS were mainly selected from environment 1, but with higher values of the genetic correlation, some DS were also selected from environment 2, resulting in a small increase in genetic gain in environment 1 when the genetic correlation was higher than 0.70 (Figure 1A).

The OJ-2 strategy was designed to simultaneously improve milk yield in environments 1 and 2. When the genetic correlation decreased, genetic gain in both environments decreased linearly (Figures 1A and 1B). Equal numbers of DS were selected from each environment.

Strategy TE-1 was designed to have substantial genetic gain in each environment regardless of the genetic correlation. When the genetic correlation was higher than 0.90, genetic gain in both environments

increased because both environments contributed to the selected parents in SS, SD, and DS [Figure 1A and 1B; see also Mulder and Bijma (2006)]. When the genetic correlation was 0.90 or lower, only a single environment contributed to the selected parents in SS, SD and DS, resulting in reduced selection intensity due to selection of the same number of animals from a lower number of selection candidates.

In strategy TJ-1, 2 breeding programs were operating with a joint breeding goal to improve milk yield in both environments simultaneously. When the genetic correlation decreased, genetic gain in both environments decreased linearly (Figures 1A and 1B). Both environments always contributed to the selected parents in SS, SD, and DS, in contrast to strategy TE-1.

Comparison of Strategies

Genetic Gain. Strategy OE-1 had the highest genetic gain in environment 1 (ΔG_1), which was nearly constant across the different genetic correlations simulated (Figure 1A). When the genetic correlation was smaller than 0.90, strategy TE-1 had a lower but constant ΔG_1 , due to reduced selection intensity. Strategies OJ-2 and TJ-1 both had higher ΔG_1 than TE-1, when the genetic correlation was higher than 0.61 and 0.70, respectively. Strategy OJ-2 always had a higher ΔG_1 than strategy TJ-1. When the genetic correlation was unity, ΔG_1 of all strategies was equal.

Strategy OE-1 had the lowest genetic gain in environment 2 (ΔG_2) for nearly all values of the genetic correlation (Figure 1B). The curves of strategies OJ-2, TE-1, and TJ-1 were identical to the curves of these strategies in Figure 1A, due to equal weighing of both environments in the breeding goal (OJ-2 and TJ-1), the balanced distribution of bulls (TE-1 and TJ-1) or progeny (OJ-2) across environments.

Figure 2 shows genetic gain in the overall objective (ΔG) in the basic situation as a function of the genetic correlation. The ranking of the curves was similar to that in Figure 1B. When the genetic correlation was higher than 0.61, strategy OJ-2 had the highest ΔG . When the genetic correlation was lower, strategy TE-1 had the highest ΔG . Strategy TJ-1 had higher ΔG than strategy TE-1 when the genetic correlation was higher than 0.70, whereas strategy OE-1 had higher ΔG than strategy TE-1 when the genetic correlation was higher than 0.75.

Genetic Gain Relative to OJ-2. Table 3 shows ΔG_1 , ΔG_2 , and ΔG , absolute and relative to strategy OJ-2 in the basic situation for different values of the genetic correlation. Strategy OJ-2 was used as a reference because it was the strategy with the highest ΔG

Figure 1. Genetic gain in environment 1 (A) and environment 2 (B) as a function of the genetic correlation for strategy OE-1 (1 environment breeding program), OJ-2 (1 joint breeding program), TE-1 (2 environment-specific breeding programs), and TJ-1 (2 breeding programs with a joint breeding goal) in the basic situation (see Table 2).

when the genetic correlation was higher than 0.61. Within strategy, ΔG_1 , ΔG_2 , and ΔG were equal among strategy OJ-2, TE-1, and TJ-1, but were different for strategy OE-1. Strategy OE-1 had a 2 to 18% higher ΔG_1 and a 6 to 41% lower ΔG_2 , resulting in 2 to 12%

lower ΔG compared with strategy OJ-2. Strategy TE-1 had 10% lower ΔG than strategy OJ-2 when the genetic correlation was 0.90, but 5% higher ΔG when the genetic correlation was 0.5. Strategy TJ-1 had 2 to 6% lower ΔG than strategy OJ-2.

Figure 2. Genetic gain in the overall objective (average genetic gain in both environments weighted by the relative importance of both environments) as a function of genetic correlation for strategy OE-1 (1 environment breeding program), OJ-2 (1 joint breeding program), TE-1 (2 environment-specific breeding programs), and TJ-1 (2 breeding programs with a joint breeding goal) in the basic situation (see Table 2).

Break-Even Genetic Correlations

It is clear from Figure 2, that ranking of strategies OE-1, OJ-2, and TJ-1 is not affected by the genetic correlation. However, the ranking with strategy TE-1 was dependent on the genetic correlation, as indicated by the points of intersection (= break-even genetic correlation). In the next section, break-even genetic correlations are presented of strategies OE-1, OJ-2, and TJ-1 with strategy TE-1 as functions of relative importances of environments, selection intensity, heritability, and number of progeny per bull.

Relative Importances of Environments. Figure 3A shows break-even genetic correlations as a function of the relative importance of environment 1 (w_1), using the basic parameter values (Table 2). In strategy OJ-2, each of the 400 bulls had 50 progeny in environment 1 and 50 progeny in environment 2, whereas in strategy TE-1 and TJ-1, 200 bulls were progeny tested with 100 daughters each in environment 1 and the remaining 200 bulls were progeny tested with 100 daughters each in environment 2, regardless of the value of w_1 . When w_1 increased, break-even genetic correlations of TE-1 with OE-1 and OJ-2 decreased.

Table 3. Genetic gain in environment 1 (ΔG_1), environment 2 (ΔG_2), and the overall objective¹ (ΔG) for strategy OE-1 (1 environment breeding program), OJ-2 (1 joint breeding program), TE-1 (2 environment-specific breeding programs), and TJ-1 (2 breeding programs with a joint breeding goal), absolute and relative to strategy OJ-2 for different values of the genetic correlation in the basic situation²

Trait	r_g	Genetic gain						
		Absolute				Relative to OJ-2		
		OE-1	OJ-2	TE-1	TJ-1	OE-1	TE-1	TJ-1
ΔG_1	0.90	0.58	0.57	0.51	0.56	1.02	0.90	0.98
	0.70	0.58	0.53	0.51	0.51	1.09	0.97	0.96
	0.50	0.58	0.49	0.51	0.46	1.18	1.05	0.94
ΔG_2	0.90	0.54	0.57	0.51	0.56	0.94	0.90	0.98
	0.70	0.41	0.53	0.51	0.51	0.77	0.97	0.96
	0.50	0.29	0.49	0.51	0.46	0.59	1.05	0.94
ΔG^1	0.90	0.56	0.57	0.51	0.56	0.98	0.90	0.98
	0.70	0.49	0.53	0.51	0.51	0.93	0.97	0.96
	0.50	0.43	0.49	0.51	0.46	0.88	1.05	0.94

¹Genetic gain in the overall objective was calculated as $\Delta G = w_1\Delta G_1 + w_2\Delta G_2$, where ΔG_i is genetic gain in environment i and w_i is relative importance of environment i ($w_1 = w_2 = 0.5$).

²Heritability = 0.3; phenotypic variance = 1.0; number of test-bulls = 400; number of progeny per bull = 100; cow population size per environment = 1.0 million; selected proportion SS = 0.05; selected proportion SD = 0.10; selected proportion DS = 0.005; selected proportion DD = 0.80.

This indicates that with increasing difference in relative importance of both environments, it is better to have only 1 breeding program, unless the genetic correlation is very low. When w_1 was 0.9, break-even genetic correlations of TE-1 with OE-1 and OJ-2 were zero or close to zero, indicating that a separate breeding program in environment 2 (TE-1) resulted in lower

ΔG than the other strategies, regardless of the genetic correlation. The break-even genetic correlation of TE-1 with TJ-1 was less sensitive to w_1 , because the structure of bull testing was the same.

Figure 3B shows break-even genetic correlations as a function of relative importance of environment 1, when testing optimal proportions of progeny (OJ-2) or

Figure 3. Break-even genetic correlation based on genetic gain in the overall objective, as a function of relative importance of environment 1 (E1) comparing strategy TE-1 (2 environment-specific breeding programs) with OE-1 (1 environment breeding program), OJ-2 (1 joint breeding program), and TJ-1 (2 breeding programs with a joint breeding goal). A) In OJ-2, the number of progeny per bull in each environment is 50 (total = 100); in TE-1 and TJ-1, the number of bulls tested in each environment is equal to 200 (total = 400). B) In OJ-2, the number of progeny per bull in environment i is equal to the relative importance of environment i (w_i) times 100; in TE-1 and TJ-1, the number of bulls tested in environment i is equal to w_i times 400. Other input parameters are equal to the basic situation (Table 2).

Figure 4. Break-even genetic correlation, based on genetic gain in the overall objective, as a function of selected proportion comparing strategy TE-1 (2 environment-specific breeding programs) with OE-1 (1 environment breeding program), OJ-2 (1 joint breeding program), and TJ-1 (2 breeding programs with a joint breeding goal). Selected proportion SS = selected proportion SD = selected proportion DS = selected proportion x-axis; other input parameters are equal to the basic situation (Table 2).

bulls (TE-1/TJ-1) in each environment. In strategy OJ-2, the number of progeny per bull per environment was equal to the relative importance times 100, whereas in strategy TE-1 and TJ-1 the number of bulls tested in each environment was equal to the relative importance times 400. These distributions of progeny or bulls were very close to the optimum distributions of progeny or bulls to maximize ΔG (results not shown). Compared with 50%–50% distributions of progeny or bulls (Figure 3A), break-even genetic correlations of TE-1 with OE-1 and OJ-2 were less sensitive to w_1 . Roughly, it can be concluded that establishing a separate breeding program (TE-1) in a less important environment is justified when the number of bulls tested in this environment is a reflection of the relative importance of that environment and when the genetic correlation is lower than 0.50 to 0.60.

Selection Intensity. Figure 4 shows break-even genetic correlations as a function of the selected proportion in SS, SD, and DS, which were equal in this figure. The selected proportion in DD and other parameters were equal to the basic parameter values (Table 2). For all comparisons, break-even genetic correlations decreased with increasing selected proportions. The largest decrease in break-even genetic correlation was between strategy TE-1 and OJ-2, while the smallest

was found between strategy TE-1 and OE-1. When the selected proportion increased (lower selection intensity), strategy TE-1 became less and less competitive to strategies OE-1, OJ-2, and TJ-1 and was only best with low genetic correlations (≤ 0.50). In contrast, when the selected proportion decreased (higher selection intensity), having 2 environment-specific breeding programs (TE-1) was optimal even with genetic correlations up to 0.70 to 0.80.

The reason for the large effect of the selected proportion on the break-even genetic correlation is that the difference in selection intensity between 1 large breeding program (OE-1, OJ-2, and TJ-1) and 2 smaller breeding programs (TE-1) was increasing with increasing selected proportion (Falconer and Mackay, 1996). Consequently, the difference between ΔG of strategy OJ-2, OE-1, and TJ-1 at a genetic correlation of unity and the horizontal part of the curve of ΔG of strategy TE-1 was increasing with increased selected proportion (see also Figure 2). The points of intersection of the curves of strategies OE-1, OJ-2, and TJ-1 with the curve of strategy TE-1 moved to the left, leading to lower break-even genetic correlations when the selected proportion increased.

Heritability and Number of Progeny per Bull.

Table 4 shows break-even genetic correlations for different values of the heritability and numbers of progeny per bull in combination with w_1 equal to 0.5 and 0.8. The distribution of progeny (OJ-2) or bulls (TE-1/TJ-1) over environment 1 and 2 was proportional to the relative importance of each environment. The effect of w_1 was larger than that of different values of the heritability or number of progeny per bull. Break-even genetic correlations were more sensitive to heritability and number of progeny per bull when w_1 was 0.8. Break-even genetic correlations comparing TE-1 with OE-1 increased with increasing heritability, but were less variable comparing TE-1 with OJ-2 or TJ-1. Break-even genetic correlations decreased with increasing number of progeny per bull, especially comparing TE-1 with OJ-2. Especially with small numbers of progeny and lower values of the genetic correlation, strategy OJ-2 was less competitive, because of lower accuracy of selection. In conclusion, the ranking of strategies was not very sensitive to changes in heritability or number of progeny per bull.

DISCUSSION

Methodology and Results

In this study, breeding strategies for dairy cattle were compared in the presence of $G \times E$. The 3 strategies proposed by James (1961) served as starting point. In contrast to James (1961), 4 paths of selection were

Table 4. Break-even genetic correlations¹ comparing strategy TE-1 (2 environment-specific breeding programs) with OE-1 (1 environment breeding program), OJ-2 (1 joint breeding program), and TJ-1 (2 breeding programs with a joint breeding goal) for different values of the heritability (h^2) and number of progeny per bull in combination with 2 values of relative importance of environment 1 (w_1)²

Parameter	Value	Break-even genetic correlations ¹					
		TE-1 – OE-1		TE-1 – OJ-2		TE-1 – TJ-1	
		w_1		w_1		w_1	
		0.5	0.8	0.5	0.8	0.5	0.8
h^2	0.05	0.73	0.53	0.63	0.55	0.70	0.62
	0.10	0.74	0.54	0.61	0.53	0.70	0.63
	0.30	0.75	0.57	0.61	0.53	0.70	0.64
	0.60	0.77	0.61	0.63	0.56	0.72	0.67
Progeny / bull	10	0.77	0.62	0.69	0.63	0.72	0.67
	20	0.77	0.60	0.66	0.59	0.71	0.66
	100	0.75	0.57	0.61	0.53	0.70	0.64
	1000	0.75	0.56	0.58	0.50	0.70	0.64

¹Genetic correlation where genetic gain in the overall objective (ΔG) is equal for 2 strategies ($\Delta G = w_1\Delta G_1 + w_2\Delta G_2$, where ΔG_i is genetic gain in environment i and w_i is relative importance of environment i ; $w_2 = 1 - w_1$).

²Phenotypic variance = 1.0; number of test-bulls = 400; cow population size per environment = 1.0 million; selected proportion SS = 0.05; selected proportion SD = 0.10; selected proportion DS = 0.005; selected proportion DD = 0.80. Number of bulls environment i (TE/TJ-1) = $w_i \times 400$; number of progeny per bull environment i (OJ-2) = $w_i \times$ progeny / bull.

considered to represent practical dairy cattle breeding programs. Furthermore, a pseudo-BLUP selection index model was used to predict genetic gain of true BLUP-selection under an animal model (Wray and Hill, 1989; Villanueva et al., 1993). Nevertheless, in agreement with James (1961), 1 breeding program with progeny testing all bulls in both environments (OJ-2) was superior to 2 environment-specific breeding programs with separate progeny testing of bulls (TE-1) for higher values of the genetic correlation. The break-even genetic correlation was, however, slightly different: 0.61 in this study vs. 0.70 in James (1961). In agreement with Vargas and van Arendonk (2004), 2 environment-specific breeding programs (TE-1) had a higher average genetic gain in both environments than 1 large environment-specific breeding program (OE-1), when the genetic correlation was lower than 0.75. Results of 2 environment-specific breeding programs (TE-1) were discussed in more detail in Mulder and Bijma (2006). In contrast to previous studies, sensitivity of ranking of breeding strategies was investigated for different input parameters. Break-even genetic correlations were used to illustrate sensitivity of ranking of breeding strategies.

Heritability, number of progeny per bull and the relative importance of both environments had only small effects on ranking of breeding strategies. Heterogeneity of heritability between both environments may affect the optimal distribution of progeny over both environments (Van Vleck, 1987) in strategy OJ-2 or the optimal distribution of bulls tested in each environment in strategy TE-1 or TJ-1. Given the results in

Table 4, the ranking of breeding strategies will be little affected by heterogeneity of heritability within reasonable ranges. In contrast to Mulder and Bijma (2006), the effect of generation number was small and the equilibrium break-even genetic correlation was quickly reached (results not shown). Selection intensity, however, had a very large effect on break-even genetic correlations. With increasing selection intensity, break-even genetic correlations increased, indicating increased competitiveness of 2 environment-specific breeding programs (strategy TE-1) compared with the other strategies (OE-1, OJ-2, and TJ-1). When comparing breeding strategies, it is therefore crucial to use selection intensities that represent the practical values.

In this study, inbreeding was ignored. Breeding strategies are ideally compared at equal rates of inbreeding (Bijma, 2000). In all strategies, the same numbers of sires and dams were selected resulting in equal rates of inbreeding assuming that rate of inbreeding is only a function of the numbers of selected sires and dams (Falconer and Mackay, 1996). The rate of inbreeding is, however, also a function of selection intensity (Robertson, 1961; Bijma et al., 2000). Even though equal numbers of sires and dams were selected, selection intensity was lower in strategy TE-1 (e.g., selection of 20 SS from 200 bulls instead of 400 bulls). Comparing at equal rates of inbreeding would have favored strategy TE-1 resulting in slightly higher break-even genetic correlations.

In this study, discrete generations were simulated, whereas overlapping generations would better repre-

sent the dairy cattle situation. Considering overlapping generations would have an effect on selection intensity, because there are more selection candidates available than assumed in this study. Furthermore, overlapping generations would have an effect on the accuracy of selection; for example, cows with more lactations or bulls with second-crop daughters. Bulls may have second-crop daughters in both environments, even though they were initially tested in one environment. Assuming that effects on selection intensity would be small (Figure 4) and given that differences in accuracy had small effects on break-even genetic correlations (Table 4), effects on break-even genetic correlations would be small when considering overlapping generations.

Implications for Breeding in Practice

The question for breeding organizations is whether different environments in the world can be supplied with one optimum global genotype or that specialized genotypes need to be developed for each environment. Breeding an optimal global genotype would require breeding for general adaptability, creating generalists, whereas breeding specialized genotypes for each environment would require breeding for special adaptability, creating specialists (Dickerson, 1962; Olesen et al., 2000). Improving general adaptability can be achieved with a single breeding program progeny testing all bulls in all environments and applying index selection to simultaneously improve performance in all environments (e.g., strategy OJ-2), whereas improving special adaptability can be achieved with environment-specific breeding programs (e.g., strategy TE-1). In this study, only 2 environments were considered; nevertheless, we may extrapolate results in this study toward situations with several environments, when assuming that selected proportions in environment-specific breeding programs are roughly twice as high as selected proportions in a single breeding program and comparable to the basic situation in this study. When genetic correlations between environments are higher than 0.50 to 0.70, a single breeding program with progeny testing bulls in different environments and applying index selection to simultaneously improve performance in different environments (e.g., strategy OJ-2) would be optimal to breed for general adaptability. When genetic correlations between environments are lower than 0.50 to 0.70, environment-specific breeding programs (e.g., strategy TE-1) are necessary to breed for special adaptability. It is, however, hard to justify specific breeding programs for environments of low importance; for example, those in which only a very small amount of the semen is

sold. As long as the genetic correlation is higher than 0.75, it is genetically optimal to import semen from large environment-specific breeding programs to these niche markets (Goddard, 1992; Vargas and van Arendonk, 2004; strategy OE-1 in this study).

It should be noted that, from a global genetic diversity point of view, strategy TE-1 would help to maintain global genetic diversity more than the other strategies, because different lines are developed specialized for different environments (Lin and Togashi, 2002). Even when different breeding programs cooperate when the genetic correlation is higher than the split-point genetic correlation (Mulder and Bijma, 2006), $G \times E$ and breeding goal differences result in a larger number of selected sires and dams worldwide (Goddard, 1992).

In practice, not only $G \times E$, but also breeding goal differences are reasons for optimizing breeding programs for different environments. Results in this study may serve as a guideline for 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. Note that 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 (Goddard, 1992). In the last 5 to 10 yr, breeding goals in many countries have broadened through changes in selection indices, shifting the focus on production to a more balanced breeding goal of improving production, longevity, udder health, conformation, and reproduction. Consequently, similarities of top bull listings across the various countries have decreased because of lower genetic correlations between total merit indices (Van der Beek, 2003; Miglior et al., 2005). Development of global or subglobal ranking scales (Powell and Van Raden, 2002), which is methodically equal to strategy TJ-1 in this study, and harmonization of trait and breeding goal definitions to increase genetic correlations between countries can help to increase benefits from worldwide selection of sires and dams (Mulder et al., 2005).

When breeding for different environments, conflicts may arise between goals of farmers and those of the breeding organization (Bichard, 2002). Farmers in environment 1 are only interested in performance in environment 1, so that strategy OE-1 is best. However, this is not the best strategy for the breeding organization, when environment 2 is also very important; for example, in semen sales. Although farmers may not see the advantage of strategy TE-1 or OJ-2, there may be indirect advantages for them. When farmers are

the owners of a cooperative breeding organization, strategy TE-1 or OJ-2 can lead to lower semen prices due to increased overall market share of the breeding organization.

CONCLUSIONS

When breeding for different environments, an important question is whether different environments can be supplied with genetic material from one or several breeding program(s). In this study, different breeding strategies were compared with respect to optimizing genetic gain in 2 environments with $G \times E$. When both environments were equally important and the genetic correlation was higher than 0.61, the highest average genetic gain of both environments was achieved with a single breeding program progeny testing all bulls in both environments and applying index selection to simultaneously improve performance in both environments. When the genetic correlation was lower than 0.61, it was optimal to have 2 environment-specific breeding programs progeny testing an equal number of bulls in their own environment only. When the genetic correlation was higher than 0.70, 2 environment-specific breeding programs could increase genetic gain by changing their breeding goals to one joint breeding goal improving performance in both environments simultaneously. Breeding strategies differed 2 to 12% in average genetic gain, but differed more when considering a single environment. Break-even genetic correlations, which were the values of the genetic correlation where the ranking of breeding strategies changed, were relatively insensitive to heritability, number of progeny per bull and the relative importance of both environments, but were very sensitive to selection intensity. With more intense selection, running 2 environment-specific breeding programs was optimal for genetic correlations up to 0.70 to 0.80, but this strategy was less appropriate for situations where 1 of the 2 environments had a relative importance less than 10 to 20%. Results of this study can be used as guidelines to optimize breeding programs when breeding dairy cattle for different parts of the world.

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APPENDIX 1

Pseudo-BLUP Selection Index

Selection indices were constructed in generation t as $I_{(t)} = \mathbf{v}'\mathbf{EBV}_{(t)}$ for all bulls and cows being selection candidates, where $\mathbf{EBV}_{(t)}$ is a vector with $EBV_{j(t)}$ of environment j . In strategy TE-1, each bull and cow had 2 index values: 1 for each breeding program. In other strategies, bulls and cows had only 1 index value, because of 1 breeding goal. All bulls and cows had EBV for both environments, which were calculated as $EBV_{j(t)} = \mathbf{b}'_{j(t)}\mathbf{x}_{(t)}$ with $\mathbf{b}_{j(t)} = \mathbf{P}_{(t)}^{-1}\mathbf{g}_{j(t)}$, 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 . With multivariate breeding value estimation, the selection index could be equivalently calculated as $I_{(t)} = \mathbf{b}'_{I(t)}\mathbf{x}_{(t)}$ with $\mathbf{b}_{I(t)} = \mathbf{P}_{(t)}^{-1}\mathbf{G}_{(t)}\mathbf{v} = \mathbf{B}'_{(t)}\mathbf{v}$, where $\mathbf{B}_{(t)}$ is a matrix of both $\mathbf{b}_{j(t)}$ -vectors. The matrix $\mathbf{G}_{(t)}$ consists of both $\mathbf{g}_{j(t)}$ vectors. The vector $\mathbf{b}_{I(t)}$ was used in calculation of the genetic selection differentials $R_{(t)}$ and in calculation of the variance of the selection index $\sigma^2_{I(t)} = \mathbf{b}'_{I(t)}\mathbf{P}_{(t)}\mathbf{b}_{I(t)}$.

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. The EBV of sires and dams were used to include pedigree information and contained all information that was available in the previous generation. The $\mathbf{P}_{(t)}$ -matrix and the $\mathbf{g}_{j(t)}$ -vector were essentially the same as in Mulder and Bijma (2006).

APPENDIX 2

Variance Reduction due to Selection

The methodology followed Mulder and Bijma (2006) to a large extent. The difference was mainly that the selection criterion in Mulder and Bijma (2006) was the EBV of a particular environment, whereas in this study the selection criterion was an index I combining EBV of both environments. Consequently, the formulas to update sire and dam genetic variance-covariance matrices ($\mathbf{C}_{s(t)}$ and $\mathbf{C}_{d(t)}$) and variance-covariance matrices of sire and dam EBV ($\mathbf{S}_{(t)}$ and $\mathbf{D}_{(t)}$) were slightly different and given below.

The $\mathbf{C}_{s(t)}$ -matrix and $\mathbf{C}_{d(t)}$ -matrix were updated each generation according to Bijma et al. (2001); for example, for an element $Cs_{ij,l(t)}$ of breeding program l (strategy TE-1) in generation t :

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

where

- $C_{ij,k(t-1)}$ = genetic variance between trait i and j in environment k in generation $t - 1$,
- $\text{Cov}(A_i, I_{kl})_{(t-1)} = b'_{I,kl(t-1)}\mathbf{g}_{i,k(t-1)}$,
- I_{kl} = selection criterion of animals selected for breeding program l within environment k 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 the 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 $k_{s,kl(t-1)}$.

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 (strategy TE-1) in generation t :

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

where

$EBV_{j,kl}$ = EBV for performance in environment j for an animal selected for breeding program l within environment k ,

$\text{Cov}(A_i, EBV_{j,kl})_{(t-1)} = \mathbf{b}_{j,kl(t-1)}' \mathbf{g}_{i,k(t-1)}$, and

$\text{Cov}(EBV_{j,kl}, I_{kl})_{(t-1)} = \mathbf{b}_{j,kl(t-1)}' \mathbf{G}_{kl(t-1)} \mathbf{v}$.

The given formulas were appropriate for strategy TE-1 and TJ-1. In strategy OE-1 and OJ-2, the given formulas for the $\mathbf{Cs}_{(t)}$ -matrix and $\mathbf{S}_{(t)}$ -matrix were reduced to the formulas given in Mulder and Bijma (2005), because there was only one group of bulls. The formulas for the $\mathbf{Cd}_{(t)}$ -matrix and $\mathbf{D}_{(t)}$ -matrix were still applicable in its complicated form, because DS were selected in both environments.