Methods to Optimize Livestock Breeding Programs with Genotype by Environment Interaction and Genetic Heterogeneity of Environmental Variance

Herman Arend Mulder
Promotor: Prof. dr. ir. J.A.M. van Arendonk  
Hoogleraar Fokkerij en Genetica, Wageningen Universiteit

Co-promotoren:  
Dr. ir. P. Bijma  
Universitair docent, leerstoelgroep Fokkerij en Genetica,  
Wageningen Universiteit

Prof. dr. W.G. Hill  
Emeritus Professor of Animal Genetics, University of Edinburgh,  
Edinburgh, United Kingdom

Samenstelling promotiecommissie:  
Prof. dr. ir. J.C.M. Dekkers (Iowa State University, United States)  
Prof. dr. F.A. van Eeuwijk (Wageningen Universiteit)  
Dr. ir. J.W.M. Merks (Institute for Pig Genetics B.V., Beuningen)  
Prof. dr. A.J. van Noordwijk (Nederlands Instituut voor Ecologie, Heteren)

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Methods to Optimize Livestock Breeding Programs with Genotype by Environment Interaction and Genetic Heterogeneity of Environmental Variance

Herman Arend Mulder

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Methods to optimize livestock breeding programs with genotype by environment interaction and genetic heterogeneity of environmental variance

H.A. Mulder


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

With summaries in English and Dutch

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Abstract

Genotype by environment interaction (G × E) and genetic heterogeneity of environmental variance are both related to genetic variation in environmental sensitivity. Both phenomena can have consequences for livestock breeding programs. This thesis focuses on developing methods to optimize livestock breeding programs with G × E and genetic heterogeneity of environmental variance.

The first part of this thesis deals with G × E, which means that different genotypes respond differently to environmental changes. G × E causes reranking of genotypes when the genetic correlation between performances in different environments is smaller than one. G × E can exist, for example, between a selection environment (SLE) and a production environment (PDE). Recording of half-sibs or progeny in the PDE limits the loss in genetic gain. Due to the lower loss in genetic gain, progeny testing schemes rather than sib testing schemes are recommended when the genetic correlation between SLE and PDE is lower than 0.7 – 0.8. In dairy cattle, G × E limits the possibilities for cooperation of breeding programs operating in different environments. Long-term cooperation in the presence of G × E is possible when the genetic correlation is higher than 0.8 – 0.9. When breeding dairy cattle for two environments in the presence of G × E, it is optimal to run a single breeding program with progeny testing bulls in both environments when the genetic correlation is higher than 0.7 – 0.8. When the genetic correlation is lower than 0.7 – 0.8, two environment-specific breeding programs are optimal.

The second part of this thesis deals with genetic heterogeneity of environmental variance. Genetic heterogeneity of environmental variance means that genotypes differ in the magnitude of the environmental variance, for example, due to differences in environmental sensitivity. A multiple regression framework was developed to predict selection responses in mean and environmental variance. Although environmental variance can be considered as a trait with a low heritability, responses in environmental variance can be greater than 10% of the current mean environmental variance in some cases. Genetic heterogeneity of environmental variance can be exploited in livestock breeding programs to increase uniformity of animals by reducing environmental variance. This is especially of interest for traits where the current population mean is near an optimum value. Another application is to breed animals that are more robust against unpredictable environmental fluctuations.
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Chapter 1

General introduction

H. A. Mulder

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

Interactions between genetics and environments, and its implications for breeding

In animal breeding, we aim to improve animal performance by genetic selection. The performance of animals is the outcome of not only genetic merit, but also environmental factors. Furthermore, the expression of genetic merit depends on or interacts with environmental factors, leading to genotype by environment interaction (G × E). G × E may result in that the best genotype in one environment may not be the best genotype in another environment (Falconer and Mackay, 1996). In other words, G × E may result in reranking of genotypes, for example, the best Holstein bull in New Zealand may not be the best bull in the Netherlands.

G × E can exist between environments that are easy to identify, e.g. geographic region (e.g. Weigel et al., 2001) or organic versus conventional farming systems (e.g. Nauta et al., 2006). Within these environments, G × E can also exist due to fluctuations in weather, feed quality, etc. Some genotypes respond more to these environmental fluctuations than others do. In other words, genotypes differ in environmental sensitivity to these within-environment fluctuations, leading to genetic differences in environmental variance, so-called genetic heterogeneity of environmental variance. Genetic heterogeneity of environmental variance can be observed as heterogeneity of within-family variance, for example, half-sib progeny groups. Some studies have shown that selection of the best animals in a good environment increases environmental sensitivity (Falconer, 1990; Kolmodin et al., 2003; Van der Waa, 2004). Increased environmental sensitivity may lead to poor performance, when environmental conditions are unfavorable. Especially poor performance in terms of health and welfare traits (e.g. leg problems, infertility or even mortality) is not acceptable not only because of negative economic effects but also because of ethical reasons.

Both G × E and genetic heterogeneity of environmental variance have consequences for livestock breeding. Due to globalization of livestock breeding and differentiation of farming systems, G × E is getting more and more important in breeding programs. Furthermore, when genetic heterogeneity of environmental variance exists, it gives possibilities to select for increased uniformity and robustness of animals, which is of increasing importance. In the following sections, the extent of G × E and genetic heterogeneity of environmental variance in livestock will be briefly reviewed, as well as the existing literature on dealing with these phenomena in breeding programs. Finally, the objectives and the outline of the thesis are given.
The extent of $G \times E$ in livestock

In this section, the degree of $G \times E$ is given by the genetic correlation between environments as a measure of reranking of genotypes between environments (Falconer, 1952).

**Dairy cattle.** There is a large amount of literature on the degree of $G \times E$ for milk production traits in dairy cattle. Genetic correlations for yield traits tend to be above 0.8 between most environments indicating little $G \times E$ (Weigel et al., 2001; Kolmodin et al., 2002; Mulder et al., 2004). Lower genetic correlations (0.5 – 0.7) have been found between moderate and tropical environments (Cienfuegos-Rivas et al., 1999; Ojango and Pollott; 2002). For functional traits, genetic correlations tend to be lower than for production (0.3 – 1.0), indicating moderate to substantial $G \times E$ (Petersson et al., 2005; Calus et al., 2006; Interbull, 2007).

**Pigs.** In general, estimates of genetic correlations are scarcer than in dairy cattle. $G \times E$ exists in pigs between nucleus and commercial environments, for example, due to difference in hygiene level. Genetic correlations are in a wide range of 0.3 – 1.0 (Merks, 1988; Van Diepen and Kennedy, 1989; Cameron, 1993). The non-unity genetic correlation between purebred and crossbred performance lowers the genetic correlation between nucleus and commercial farms even more than only due to $G \times E$ (review by Wei and Van der Steen, 1991; Merks and Hanenberg, 1998).

**Poultry.** In poultry, the same issues apply as in pigs: $G \times E$ between nucleus and commercial environments and the non-unity genetic correlation between purebred and crossbred performance. In laying hens, genetic correlations between egg performance of purebred hens and crossbred hens in different housing systems range from 0.5 to 1.0 (Wei and Van der Werf, 1995; Besbes and Gibson, 1999). In broilers, genetic correlations for body weight and carcass traits between different environments range from 0.3 to 1.0 (Pakdel et al., 2005; Zerehdaran et al., 2005; Banos et al., 2006).

The extent of genetic heterogeneity of environmental variance

Some relatively old studies have shown the existence of variation between sires in within-family variance of progeny in dairy cattle (Van Vleck, 1968; Clay et al., 1979), which may indicate genetic variation in environmental variance. More recently, a limited number of studies have reported evidence for genetic heterogeneity of environmental variance in sheep, pigs, snails and broilers. The reported estimates of genetic variance are large relative to the mean environmental variance, indicating potential to change environmental variance by selection. The heritability, however, is low, between 0.02 and 0.05 (SanCristobal-Gaudy et al., 2001; Sorensen and Waagepetersen, 2003; Ros et al., 2004; Rowe et al., 2006; see review in Chapter 5). Probably the cleanest example is by Mackay and Lyman (2005) in an experiment with *Drosophila melanogaster*, who showed significant genetic variance in
environmental variance of bristle number by studying 300 iso-female lines, effectively clone lines. Furthermore, selection responses in phenotypic variance were observed with selection on high or low phenotypic variance in some selection experiments with *Drosophila melanogaster* and *Tribolium castaneum*, suggesting genetic variation in phenotypic variance (Rendel et al., 1966; Kaufman et al., 1977; Cardin and Minvielle, 1986).

**Breeding programs**

In animal breeding, the suggestion by Robertson (1959) that $G \times E$ is unimportant when the genetic correlation is higher than 0.8 is still used as a guideline for interpreting the importance of $G \times E$. A number of researchers have quantified the effects of $G \times E$ on genetic gain in some specific situations (James, 1961; Dickerson, 1962; Brascamp et al., 1985; Smith and Banos, 1991). Many questions, however, are unresolved. Examples are the sensitivity of genetic gain in closed nucleus breeding schemes to $G \times E$ between nucleus and commercial environments, the increase in genetic gain with selection across environments in the presence of $G \times E$, the optimal point to split a single breeding program into multiple breeding programs, and the optimization of breeding programs with both $G \times E$ and breeding goal differences between environments. In general, there is a need for methods and guidelines for optimization of breeding programs with $G \times E$ and breeding goal differences.

In the presence of genetic heterogeneity of environmental variance, selection may not only change the mean, but also the environmental variance of traits. Some studies have investigated the effects of specific types of selection (SanCristobal-Gaudy et al., 1998; Sorensen and Waagepetersen, 2003; Hill and Zhang, 2004). A general framework for prediction of selection responses in mean and environmental variance is lacking, however. Furthermore, it is unknown in which situations it would be desirable to change environmental variance and to which extent environmental variance can be changed by selection in livestock breeding programs.

**OBJECTIVES AND OUTLINE OF THIS THESIS**

The two main objectives of this Ph.D. research were:

- to optimize livestock breeding programs with $G \times E$ and breeding goal differences between environments (Chapter 2, 3, 4 and 7),
- to develop a framework for prediction of selection responses with genetic heterogeneity of environmental variance, and to investigate the use of such genetic heterogeneity in livestock breeding programs (Chapter 5, 6 and 7).
According to these objectives, the thesis can be split into two parts: Chapters 2, 3 and 4 deal with the optimization of breeding programs in the presence of G × E. Chapters 5 and 6 deal with prediction of selection responses and selection for uniformity in the presence of genetic heterogeneity of environmental variance.

Chapter 2: The effects of G × E between selection and production environment on genetic gain in sib-testing and progeny-testing schemes are quantified.

Chapter 3: The increase in genetic gain is quantified, when dairy cattle breeding programs cooperate by selection of animals across environments in the presence of G × E.

Chapter 4: Dairy cattle breeding programs are optimized when breeding simultaneously for two environments. The main topic is to develop guidelines for the question whether it is optimal to run one or two breeding programs.

Chapter 5: A multiple regression framework is developed to predict selection responses with genetic heterogeneity of environmental variance. Furthermore, a measure of heritability for genetic heterogeneity of environmental variance is proposed.

Chapter 6: The framework of Chapter 5 is used to predict selection responses in mean and environmental variance in livestock breeding programs. Economic values for mean and variance are derived for some standard situations.

Chapter 7: In the general discussion, section 7.1 deals with models, experimental designs and genetic control of environmental sensitivity. Section 7.2 deals with optimization of breeding programs with genetic variation in environmental sensitivity and breeding goal differences between environments, extending on results in Chapter 4 and 6.

REFERENCES


Chapter 2

Effects of genotype by environment interaction on genetic gain in breeding programs

H. A. Mulder and P. Bijma

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

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Genetic gain with different environments

**ABSTRACT:** Genotype × environment interaction (G × E) is increasingly important, because breeding programs tend to be more internationally oriented. The aim of this theoretical study was to investigate the effects of G × E on genetic gain in sib-testing and progeny-testing schemes. Loss of genetic gain due to G × E was predicted for different values of heritability, number of progeny per dam, number of progeny per sire, proportion of selected sires, and population size in the selection environment. Two environments were considered: a selection environment (SLE) and a production environment (PDE). The breeding goal was only for performance in PDE. A pseudo-BLUP selection index was used to predict genetic gain.

Recording of half-sibs or progeny in PDE limited the loss in genetic gain in PDE due to G × E between SLE and PDE. Progeny-testing schemes had less loss in genetic gain than sib-testing schemes. Higher heritability increased the loss in genetic gain, whereas increasing the number of progeny per sire in PDE decreased the loss in genetic gain. The number of progeny per sire required to minimize loss in genetic gain due to G × E was greater for sib-testing schemes than for progeny-testing schemes. More progeny per dam slightly increased the loss in genetic gain. Genetic gains for sex-limited and carcass traits were less affected by G × E than traits measured on both sexes. Loss in genetic gain was due to decreased accuracy of selection in most situations, but it was due to decreased selection intensity in situations with small population size and a low proportion of selected sires. It was concluded that recording performance of relatives in PDE minimizes loss in genetic gain due to G × E, and that progeny-testing schemes rather than sib-testing schemes are preferable in situations with low to moderate heritability ($h^2 \leq 0.3$), relative short generation interval of progeny tested sires ($L_{\text{prog}} / L_{\text{Sib}} \leq 1.7$), and moderate to severe G × E interaction ($r_g \leq 0.8$).

**Keywords:** Genotype by Environment Interaction, Breeding Program, Genetic Gain, Progeny Testing, Sib Testing

**INTRODUCTION**

Livestock breeding programs are becoming more international, which means that the goals of such programs are to breed animals that can perform well in a variety of environments. As a consequence, knowledge of the effects of genotype × environment interaction (G × E) on genetic gain in breeding programs is increasingly important. Due to G × E, genetic rank of animals might change, so that the best animal in one environment might not be the best animal in another environment (Falconer and Mackay, 1996). The concept of a genetic correlation between performances in different environments can be used as a measure of ranking differences due to G × E (Falconer, 1952). In many situations, estimates of such
genetic correlations are less than unity (Merks, 1988; Wei and Van der Werf, 1995; Weigel et al., 2001), indicating that selection of parents in one environment may not optimize progeny performance in another environment.

Research has been carried out to optimize specific breeding programs of different species in the presence of $G \times E$ (e.g., Meuwissen and Woolliams, 1993, Bijma and Van Arendonk, 1998; Jiang and Groen, 1999). Based on these studies, however, it is difficult to identify the effects of $G \times E$ on genetic gain in combination with other parameters, such as heritability and number of progeny per sire. Furthermore, none of those studies compared sib-testing and progeny-testing schemes.

The objective of this study was to investigate the effects of $G \times E$ on genetic gain in sib-testing and progeny-testing schemes. Loss of genetic gain due to $G \times E$ was predicted for different values of heritability, number of progeny per dam, number of progeny per sire, proportions of selected sires, and population sizes of the selection environment. Furthermore, differences in breeding goal and differences between traits measured on both sexes, sex-limited traits, and carcass traits were investigated.

**MATERIALS AND METHODS**

**Breeding schemes**

In this study, two environments were considered: a selection environment (SLE), with all candidates for selection, and a production environment (PDE), with commercial animals, which were not eligible for selection. The breeding goal was performance in PDE. Different degrees of $G \times E$ between SLE and PDE were created by varying the genetic correlation (Falconer, 1952). Breeding schemes were based on either sib testing or progeny testing. Selection under sib testing was based on BLUP-EBV using the animals’ own performance, average performance of full-sibs and half-sibs, and pedigree information, whereas selection under progeny testing replaced sib performance with average performance of progeny. Own performance, average performance of full-sibs and half-sibs in SLE were always available, whereas average performance of half-sibs or progeny in PDE was optional. Progeny testing in SLE was not considered, because of the limited size of SLE.

Ultimately, three breeding schemes were designed: 1) selection environment sib testing (SEsib), 2) combined selection environment and production environment sib testing (CSPsib), and 3) combined selection environment and production environment progeny testing (CSPprog). With SEsib and CSPsib, sires and dams were sib-tested, whereas in CSPprog, sires were progeny-tested and dams were sib-tested. Sires and dams were selected by truncation on animal model BLUP-EBV. In SEsib, EBV were based only on records of relatives in SLE, whereas in CSPsib and CSPprog, EBV were based on records of relatives in SLE and PDE. In addition to records from SLE, in CSPsib, sires and dams had records of
half-sibs from PDE, whereas in CSPprog, sires had records of progeny from PDE and dams had records of half-sibs (same animals as progeny of sires) also from PDE (Table 1). A hierarchical mating structure was assumed and generations were discrete. Each generation $ns$ sires and $nd$ dams were selected in SLE. Each sire was mated to $nds (=nd/ns)$ dams. Each dam produced $noff$ offspring in SLE. The number of full-sibs ($nfs$) in SLE was equal to $noff−1$ (excluding individual). The number of half-sibs ($nhs$) in SLE was equal to $(nds−1)\times noff$ (excluding full-sibs and individual). Half-sibs ($nhs$) or progeny ($np$) in PDE were produced by $ndp$ dams born in PDE.

**Table 1.** Information used for calculation of pseudo-best linear unbiased prediction estimated breeding values for selection environment sib testing (SESib), combined selection environment and production environment sib testing (CSPsib), and combined selection environment and production environment progeny testing (CSPprog) for traits measured on both sexes in the selection environment (SLE) and production environment (PDE).

<table>
<thead>
<tr>
<th>Type of information</th>
<th>SESib</th>
<th></th>
<th></th>
<th>CSPsib</th>
<th></th>
<th></th>
<th>CSPprog</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>SLE m</td>
<td>PDE f</td>
<td></td>
<td>SLE m</td>
<td>PDE f</td>
<td></td>
<td>SLE m</td>
<td>PDE f</td>
</tr>
<tr>
<td>Own performance</td>
<td>+</td>
<td>+</td>
<td></td>
<td>+</td>
<td>+</td>
<td></td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Mean of full-sibs</td>
<td>+</td>
<td>+</td>
<td></td>
<td>+</td>
<td>+</td>
<td></td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Mean of paternal half-sibs</td>
<td>+</td>
<td>+</td>
<td></td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>EBV dam</td>
<td>+</td>
<td>+</td>
<td></td>
<td>+</td>
<td>+</td>
<td></td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>EBV sire</td>
<td>+</td>
<td>+</td>
<td></td>
<td>+</td>
<td>+</td>
<td></td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Mean EBV of dams half-sibs</td>
<td>+</td>
<td>+</td>
<td></td>
<td>+</td>
<td>+</td>
<td></td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Mean of progeny</td>
<td></td>
<td></td>
<td></td>
<td>+</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

$m =$ males and $f =$ females.

Values of parameters are listed in Table 2. The generation interval for sires in CSPprog schemes was set relative to the generation interval for sires and dams in SESib and CSPsib, so that one unit of time was equal to the generation interval for sires and dams in sib-testing schemes (SESib, CSPsib, and dams in CSPprog). Based on species-specific reproductive characteristics and time of measurement of trait, the relative generation interval for progeny-tested sires was between 1.3 and 1.8 (e.g., Merks, 1988; Meuwissen, 1989). The basic situation corresponded to a trait measured on both sexes before sexual maturity (e.g., growth rate). Reproductive characteristics corresponded to the situation in pigs or poultry or in dairy cattle with multiple ovulation and embryo transfer (MOET). Alternative situations were created by changing one parameter at a time, while keeping other parameters constant. Two
additional cases were formulated to illustrate the effects of $G \times E$ in other situations. In Case 1, the effect of $G \times E$ was investigated on other traits, such as sex-limited and carcass traits. Because of differences in the number of records in SLE, effects of $G \times E$ might be different for traits such as milk production or carcass quality. In Case 2, performance in SLE was included in the breeding goal.

Table 2. Values of parameters used in calculating genetic gain in sib-testing and progeny-testing schemes: basic parameters and range of values used in alternative breeding schemes.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Basic</th>
<th>Alternatives range</th>
<th>Increment</th>
</tr>
</thead>
<tbody>
<tr>
<td>Heritability ($h^2$)</td>
<td>0.3</td>
<td>0.05 to 0.6</td>
<td>0.05</td>
</tr>
<tr>
<td>Genetic correlation ($r_g$)</td>
<td>1.0</td>
<td>-1.0 to 1.0</td>
<td>0.1 / 0.01</td>
</tr>
<tr>
<td>Phenotypic variance ($\sigma^2_p$)</td>
<td>1.0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Proportion of selected sires ($p$)</td>
<td>0.05</td>
<td>0.01, 0.02, 0.10, 0.20</td>
<td></td>
</tr>
<tr>
<td>No. of progeny per dam SLE$^1$ ($noff$)</td>
<td>8</td>
<td>2 to 30</td>
<td>2</td>
</tr>
<tr>
<td>No. of animals in SLE</td>
<td>2,000</td>
<td>200 to 10,000</td>
<td>200</td>
</tr>
<tr>
<td>No. of progeny-tested sires (CSPprog)</td>
<td>400</td>
<td>100 to 1,000</td>
<td>100</td>
</tr>
<tr>
<td>No. of PDE progeny / half-sibs per sire ($np$)</td>
<td>100</td>
<td>10 to 500</td>
<td>10</td>
</tr>
<tr>
<td>No. of progeny per dam in PDE ($np / ndp$)$^2$</td>
<td>8</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Relative generation interval CSPprog sires$^3$</td>
<td>1.4</td>
<td>1.0 to 2.0</td>
<td>0.1</td>
</tr>
</tbody>
</table>

$^1$ SLE = selection environment; PDE = production environment; SESib = selection environment sib testing; CSPsib = combined selection environment and production environment sib testing; CSPprog = combined selection environment and production environment progeny testing; sires were progeny tested, whereas dams were sib tested like CSPsib.

$^2$ $ndp$ is number of dams of progeny in PDE.

$^3$ Relative generation interval SESib/CSPsib is 1.0.

**Case 1: Sex-limited and carcass traits.** Sex-limited traits were measured on females only (e.g., milk production or litter size). The number of full-sibs and half-sibs in SLE was half that for traits measured on both sexes. The number of progeny per sire in PDE was held constant at 100. Other values of parameters were equal to those in Table 2. Carcass traits were not measured on the selection candidates themselves. In SLE, the slaughter of animals decreased the number of candidates for selection and decreased selection intensity. In SLE, 20% of the animals were assumed to be slaughtered. The number of selected dams and sires was held constant compared with measuring traits on both sexes. All animals in PDE were slaughtered. Other values of parameters were as shown in Table 2.

**Case 2: Including SLE performance in breeding goal.** In practice, increased performance in SLE might be of economical interest. The economic value of performance in
SLE was varied between 0 and 1. The economic value of performance in PDE was equal to 1 minus the economic value of performance in SLE. Other values of parameters were as shown in Table 2.

Genetic gain, relative genetic gain and break-even genetic correlation

**Genetic gain per unit of time.** Genetic gain was calculated deterministically by approximating BLUP-selection under an animal model using a pseudo-BLUP selection index (Wray and Hill, 1989; Villanueva et al., 1993). Genetic gain in the breeding goal (performance in PDE) was predicted for sires and dams for each generation. To account for the longer generation interval for CSPprog sires, the formula of Dickerson and Hazel (1944) and Rendel and Robertson (1950) was modified to two selection paths (sires and dams) to calculate genetic gain per unit of time, which was equal to the generation interval of sib-testing schemes:

$$
\Delta G = \frac{R_s + R_d}{L_s + L_d} = \frac{(i_s r_{iii,s} + i_d r_{iii,d})\sigma_{ji}}{L_s + L_d}
$$  \hspace{1cm} (1)

where $\Delta G =$ genetic gain per unit of time in the breeding goal, $R_s$, $R_d =$ selection differentials for sires and dams, $L_s$, $L_d =$ generation interval for sires and dams relative to sib testing ($L_{sb} = 1$), $i_s$, $i_d =$ selection intensity for sires and dams, $r_{iii,s}$, $r_{iii,d} =$ $\sqrt{b^P b} / \sigma_{ji}^2 =$ accuracy of selection for sires and dams, $b =$ vector with selection index weights, $P =$ variance-covariance matrix of information sources used in the index, $\sigma_{ji}^2 =$ $v'Cv =$ genetic variance of the breeding goal, $v =$ vector with economic values, and $C =$ genetic variance-covariance matrix.

Results were based on genetic gain at equilibrium for the breeding goal per unit of time, accounting for build up of pedigree information (Dekkers, 1992) and reduction of genetic variance due to selection (Bulmer, 1971). Equilibrium was reached after 5 to 10 generations of selection. The matrices and vectors used to calculate accuracies of selection and the genetic variance of the breeding goal will be further described in the next section. In Case 2, the selection differential per generation for environment $j$ resulting from selection path $k$ (sires or dams) was:

$$
R_{j,k} = \frac{i_k \times b_k' g_{jk}}{\sigma_{j,k}}
$$  \hspace{1cm} (2)
where $g_{l,k}$ is a vector with covariances between information sources of selection path $k$ and the true breeding value for environment $j$ and $\sigma_{i,k}$ is the square root of the variance of the selection index for selection path $k$. The results of Equation 2 were substituted for $R_s$ and $R_d$ in Equation 1 to obtain genetic gain per unit of time for each environment.

Selection intensities ($i_s$ or $i_d$) were corrected for finite population size and correlated index values (Meuwissen, 1991a). The approximation of Burrows (1972) was used to correct selection intensity for finite population size. Correlations among index values of relatives in a finite population reduce the selection intensity because of a higher than random probability of selecting related selection candidates (Meuwissen, 1991a). As the correlation between index values of relatives increased, selection moves from within-family toward between-family selection. The method of Meuwissen (1991a), which is a three-dimensional application of the correction of Rawlings (1976), was used to correct selection intensities for correlated index values of candidates for selection. Correlations between index values of full-sibs and half-sibs were calculated as by De Boer and Van Arendonk (1991) and Bijma and Van Arendonk (1998). The corrected selection intensities ($i_s$ or $i_d$) were equal to $i_r(t_{i_j},t_{i_2})$ in the notation of Meuwissen (1991a).

Relative genetic gain. To measure loss in genetic gain due to $G \times E$ relative to no $G \times E$ ($r_g = 1$), relative genetic gain ($\Delta G_{rel}$) was calculated as:

$$
\Delta G_{rel} = \frac{\Delta G (r_g = x)}{\Delta G (r_g = 1)} = \frac{R_s(r_g = x) + R_d(r_g = x)}{R_s(r_g = 1) + R_d(r_g = 1)}
$$

Because the generation interval of sires and dams was constant within a scheme, the sum of generation intervals of sires and dams dropped out in Equation 3.

Break-even genetic correlation. The rank order of breeding schemes based on genetic gain changes with decreasing genetic correlation. Rank changes of breeding schemes will occur at the “break-even” genetic correlation (i.e., when genetic gains of breeding schemes are equal). In this study, break-even genetic correlations were calculated to compare CSPprog with CSPsib and SEsib.
Genetic gain with different environments

**Pseudo-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, which was available in the previous generation at selection. The advantages of using a pseudo-BLUP selection index were that genetic gain was predicted deterministically saving computation time and it provided insight on the effects of different parameters on the underlying components of genetic gain.

Construction of a selection index started with the breeding goal. The breeding goal contained two traits: performance in SLE and performance in PDE. Because the breeding goal was performance in PDE, a zero economic value was given to SLE performance. The breeding goal was $H = \mathbf{v}' \mathbf{a}$, where $\mathbf{a}$ is the vector of true breeding values for SLE and PDE performance. Each animal performed in one environment and was recorded one time. Phenotypic observations ($P$) are the sums of additive genetic effects ($A$) and environmental effects ($E$): $P = A + E$. The selection index $I$ in generation $t$ was:

$$I_{(t)} = \mathbf{b}^{'(t)} \mathbf{x}_{(t)}$$

where $\mathbf{b}_{(t)} = \mathbf{P}_{(t)}^{-1} \mathbf{G}_{(t)} \mathbf{v}$, where $\mathbf{P}_{(t)}$ = variance-covariance matrix of information sources in $\mathbf{x}_{(t)}$ in generation $t$, and $\mathbf{G}_{(t)}$ = covariance matrix between information sources in $\mathbf{x}_{(t)}$ in generation $t$ and true breeding values in $\mathbf{a}$, and $\mathbf{x}_{(t)}$ = vector of records in generation $t$. The potential records in $\mathbf{x}_{(t)}$ were: (1) own performance, (2) mean of full-sibs (excluding the individual), (3) mean of half-sibs in SLE or PDE (excluding full-sibs and the individual), (4) EBV dam, (5) EBV sire, (6) mean EBV of dams of half-sibs in SLE and (7) mean of progeny in PDE. The mean EBV of dams of half-sibs or progeny in PDE was not taken into account, because EBV were calculated only for animals in SLE. For pigs and poultry, EBV are usually not available for commercial animals because of incomplete dam pedigree. Information sources used with the three different breeding schemes are summarized in Table 1.

The EBV of sires and dams were used to include pedigree information. The EBV contained all information that was available in the previous generation. The mean EBV of dams of half-sibs in SLE was used to account for the genetic level of these dams. The EBV of sires and dams in generation $t$ were:

$$EBV_{j(t)} = \mathbf{b}_{j(t)}^{'(t)} \mathbf{x}_{(t)}$$
where $EBV_{j(t)}$ = estimated breeding value for trait $j$ in generation $t$, and $b_{j(t)} = P_{j(t)}^{-1}g_{j(t)}$, where $g_{j(t)}$ is the column of $G_{j(t)}$ corresponding to trait $j$ in generation $t$.

Variance-covariance matrix of information sources (P-matrix). The $P_{j(t)}$-matrix was partitioned into sub-matrices ($P_{y(t)}$) corresponding to two traits (SLE = 1 and PDE = 2):

$$P_{y(t)} = \begin{bmatrix}
P_{11(t)} & P_{12(t)} \\
P_{21(t)} & P_{22(t)}
\end{bmatrix}$$

with

$$P_{y(t)} = \begin{bmatrix}
OP_{y(t)} & PC1_{y(t)} & PC2_{y(t)} & D_{y(t)}/2 & S_{y(t)}/2 & 0 & PC4_{y(t)} \\
FS_{y(t)} & PC3_{y(t)} & D_{y(t)}/2 & S_{y(t)}/2 & 0 & PC5_{y(t)} \\
\text{symmetric} & \text{symmetric} & \text{symmetric} & \text{symmetric} & \text{symmetric} & \text{symmetric} & \text{symmetric}
\end{bmatrix}$$

in which the order of rows and columns corresponded to the order of the information sources in $x_{i(t)}$, where $OP_{y(t)} = C_{y(t)} + E_{y}$, where $C_{y(t)}$ is the $ij$th element of the genetic variance-covariance matrix in generation $t$ and $E_{y}$ is the $ij$th element of the environmental variance-covariance matrix. $PC1_{y(t)} = Cs_{y(t)} + Cd_{y(t)}$, where $Cs_{y(t)}$ is the $ij$th element of the sire genetic variance-covariance matrix in generation $t$, and $Cd_{y(t)}$ is the $ij$th element of the dam genetic variance-covariance matrix in generation $t$. $FS_{y(t)} = Cs_{y(t)} + Cd_{y(t)} + (Cms_{y(t-0)} + E_{y})/nfs$, where $Cms_{y(t-0)}$ is the $ij$th element of the genetic variance-covariance matrix of Mendelian sampling terms. $PC2_{y(t)} = PC3_{y(t)} = Cs_{y(t)}$; $\overline{FS}_{y(t)} = Cs_{y(t)} + (Cd_{y(t)})/(nfs - 1) + (Cms_{y(t-0)} + E_{y})/nhs$; $PC4_{y(t)} = \frac{1}{2}C_{y(t)}$; $PC5_{y(t)} = \frac{1}{2}Cs_{y(t)} + \frac{1}{2}Cd_{y(t)}$; $PC6_{y(t)} = \frac{1}{2}Cs_{y(t)}$; $\overline{PG}_{y(t)} = \frac{1}{2}C_{y(t)} + (\frac{1}{2}C_{y(t)})/ndp + (Cms_{y(t-0)} + E_{y})/np$; and $D_{y(t)}$, $S_{y(t)}$ see below.

The elements corresponding to half-sibs or progeny in PDE were not always used dependent on breeding scheme (see Table 1).
Covariances between selection index and breeding goal (G-matrix). The $G_{(i)}$-matrix was partitioned in vectors $g_{(i)}$ or $g_{(j)}$, where $i$ is the trait of information in the selection index and $j$ is the trait in the breeding goal:

$$G_{(i)} = \begin{bmatrix} g_{11(i)} & g_{12(i)} \\ g_{21(i)} & g_{22(i)} \end{bmatrix} \text{ with: } g_{(i)} = \begin{bmatrix} C_{(i)} \\ C_{(i)} + C_{D_{(i)}} \\ C_{(i)} \\ D_{(i)} / 2 \\ S_{(i)} / 2 \\ C_{(i)} / 2 \end{bmatrix} \text{ and } g_{(j)} = \begin{bmatrix} g_{1(j)} \\ g_{2(j)} \end{bmatrix}$$

Genetic variance-covariance matrix (C-matrix). The $C_{(i)}$-matrix was a $2 \times 2$ matrix. The genetic (co)variance in generation $t$ was partitioned into:

$$C_{(i)} = C_{S_{(i)}} + C_{D_{(i)}} + C_{s_{(i-0)}}$$

where $C_{(i)}$ = genetic covariance between traits $i$ and $j$ in generation $t$, $C_{S_{(i)}}$ = genetic sire covariance between traits $i$ and $j$ in generation $t$, $C_{D_{(i)}}$ = genetic dam covariance between traits $i$ and $j$ in generation $t$, and $C_{s_{(i-0)}} = \frac{1}{2} C_{s_{(i-0)}}$ = genetic Mendelian sampling covariance between traits $i$ and $j$, which is half of the initial genetic covariance in generation 0.

Genetic parameters change due to linkage disequilibrium caused by selection (Bulmer, 1971). The $C_{S_{(i)}}$-matrix and $C_{D_{(i)}}$-matrix, therefore, were updated each generation according to Cochran (1951). For instance, for an element $C_{S_{(i)}}$ in generation $t$:

$$C_{S_{(i)}} = \frac{1}{4} \left[ C_{S_{(i-1)}} - \frac{\text{Cov}(A_{i}, I)_{t-1}}{\sigma_{i(t-1)}^2} \right]$$

where $\text{Cov}(A_{i}, I)_{t-1} = b_{i(t-1)}' g_{(i-1)}$; $\sigma_{i(t-1)}^2 = b_{i(t-1)}' P_{(i-1)} b_{i(t-1)}$ = variance of the selection index, $I$, in generation $t - 1$, and $k_s = i_s (i_s - x_s)$, where $i_s$ is the selection intensity for sires and $x_s$ is the standardized truncation point for sires. The variance-covariance matrix $C_{D_{(i)}}$
was calculated similarly, but $k_d$ was used instead of $k_s$. After 5-10 generations of selection the genetic variance-covariance matrix reached Bulmer equilibrium (Bulmer, 1971).

**Variance-covariance matrix of EBV (S-matrix and D-matrix).** The $S_{(\theta)}$-matrix contains the variances and covariances between EBV of sires; the $D_{(\theta)}$-matrix contains the variances and covariances between EBV of dams. In multivariate analysis the elements of $S_{(\theta)}$ and $D_{(\theta)}$ are equal to the covariances between the true additive genetic effects and the EBV (Villanueva et al., 1993). Elements of $S_{(\theta)}$-matrix and $D_{(\theta)}$-matrix change due to selection so these were updated each generation, e.g. for an element $S_{\gamma(t)}$ in generation $t$:

$$S_{\gamma(t)} = \text{Cov}(A_{\gamma}, EBV_{j})_{t-1} - \frac{\text{Cov}(A_{\gamma}, I)_{t-1} \text{Cov}(EBV_{j}, I)_{t-1}}{\sigma^2_{(t-1)}} k_s$$

where $\text{Cov}(A_{\gamma}, EBV_{j})_{t-1} = b_{j(t-1)}' g_{(t-1)}$; $\text{Cov}(A_{\gamma}, I)_{t-1} = b_{j(t-1)}' g_{(t-1)}$; and $\text{Cov}(EBV_{j}, I)_{t-1} = b_{j(t-1)}' G_{(t-1)} v$.

**RESULTS**

**General**

Figure 1 shows genetic gain per unit of time as a function of genetic correlation for SEsib, CSPsib, and CSPprog. Genetic gain increased as genetic correlation approached unity or minus unity, for which genetic gain was similar for the three breeding schemes. For a genetic correlation of unity, genetic gains with CSPsib and SEsib were similar because the extra information from half-sibs in PDE included in CSPsib added little to the accuracy of selection. The genetic gain with CSPprog was similar to the genetic gains with SEsib and CSPsib.

For these breeding schemes, genetic gains were different for correlations close to zero (Figure 1). Because the largest differences occurred when the genetic correlation was zero, relative genetic gains will be presented for a genetic correlation of zero in Figures 2, 3, 4, and 5, and Table 3. In Figure 1, the largest effect of the genetic correlation on genetic gain was for SEsib and the smallest for CSPprog. With SEsib, genetic gain in PDE was purely a correlated response (straight lines), and the relative genetic gain was equal to the genetic correlation (not shown). Genetic gains with SEsib were therefore not included in every figure or table. The curves for CSPprog and CSPsib in Figure 1 showed that including information of relatives in PDE in the index resulted in a substantial genetic gain for every value of the genetic correlation and thus reduced the loss in genetic gain due to $G \times E$. 

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Genetic gain with different environments

Figure 1. Genetic gain per unit of time as a function of genetic correlation for selection environment sib testing (SEsib), combined selection environment and production environment sib testing (CSPsib) and combined selection environment and production environment progeny testing (CSPprog). Heritability = 0.3; phenotypic variance = 1.0; proportion of selected sires = 0.05; number of progeny per dam = 8; number of animals in selection environment = 2,000; number of progeny-tested sires (CSPprog) = 400; number of progeny per sire in production environment = 100; and relative generation interval CSPprog sires = 1.4.

Table 3 shows the effect of G × E on the underlying components of genetic gain. Decrease in accuracy \(r_{hi}\) was the main source of loss in genetic gain due to G × E. A decrease in accuracy resulted in an increase in the equilibrium genetic variance of the breeding goal \(\sigma^2_{HI}\). Selection intensity \(i\) was lower with a genetic correlation \(r_g\) of zero due to a higher correlation between index values of relatives, depending on the breeding scheme. The proportion of genetic gain contributed by each selection path \(\Delta G_{prop}\) changed for CSPprog as the genetic correlation decreased from unity to zero, because accuracy of sires was hardly affected, whereas accuracy of dams was affected considerably by G × E.
Table 3. Components of genetic gain for sire and dam selection path for selection environment sib testing (SEsib), combined selection environment and production environment sib testing (CSPsib) and combined selection environment and production environment progeny testing (CSPprog) with a genetic correlation \( r_g \) of 1 or 0\(^1\).

<table>
<thead>
<tr>
<th>Breeding scheme</th>
<th>Selection path</th>
<th>( r_g )</th>
<th>( i )</th>
<th>( r_{II} )</th>
<th>( \sigma_H )</th>
<th>( \Delta G )</th>
<th>( \Delta G_{prop} ) (^3)</th>
</tr>
</thead>
<tbody>
<tr>
<td>SEsib sire</td>
<td>1</td>
<td>2.045</td>
<td>0.601</td>
<td>0.482</td>
<td>0.593</td>
<td>0.618</td>
<td></td>
</tr>
<tr>
<td></td>
<td>0</td>
<td>2.045</td>
<td>0.000</td>
<td>0.548</td>
<td>0.000</td>
<td>NP(^5)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>rel(^4)</td>
<td>1.000</td>
<td>0.000</td>
<td>1.137</td>
<td>0.000</td>
<td></td>
<td></td>
</tr>
<tr>
<td>dam</td>
<td>1</td>
<td>1.264</td>
<td>0.601</td>
<td>0.482</td>
<td>0.366</td>
<td>0.382</td>
<td></td>
</tr>
<tr>
<td></td>
<td>0</td>
<td>1.264</td>
<td>0.000</td>
<td>0.548</td>
<td>0.000</td>
<td>NP</td>
<td></td>
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<tr>
<td></td>
<td>rel(^4)</td>
<td>1.000</td>
<td>0.000</td>
<td>1.137</td>
<td>0.000</td>
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<td></td>
</tr>
<tr>
<td>CSPsib sire</td>
<td>1</td>
<td>2.045</td>
<td>0.611</td>
<td>0.480</td>
<td>0.600</td>
<td>0.618</td>
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</tr>
<tr>
<td></td>
<td>0</td>
<td>1.997</td>
<td>0.427</td>
<td>0.511</td>
<td>0.436</td>
<td>0.615</td>
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</tr>
<tr>
<td></td>
<td>rel(^4)</td>
<td>0.977</td>
<td>0.698</td>
<td>1.065</td>
<td>0.726</td>
<td></td>
<td></td>
</tr>
<tr>
<td>dam</td>
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<td>1.264</td>
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<tr>
<td></td>
<td>0</td>
<td>1.252</td>
<td>0.427</td>
<td>0.511</td>
<td>0.273</td>
<td>0.385</td>
<td></td>
</tr>
<tr>
<td></td>
<td>rel(^4)</td>
<td>0.991</td>
<td>0.698</td>
<td>1.065</td>
<td>0.737</td>
<td></td>
<td></td>
</tr>
<tr>
<td>CSPprog sire</td>
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<td>0.904</td>
<td>0.452</td>
<td>0.837</td>
<td>0.728</td>
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<tr>
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<td>0</td>
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<tr>
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<td>rel(^4)</td>
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<td>dam</td>
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<td>0.133</td>
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<td>rel(^4)</td>
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<td>0.420</td>
<td>1.035</td>
<td>0.423</td>
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</tr>
</tbody>
</table>

\(^1\) Heritability = 0.3; phenotypic variance = 1.0; proportion of selected sires = 0.05; number of progeny per dam = 8; number of animals in selection environment = 2,000; number of progeny-tested sires (CSPprog) = 400; number of progeny per sire in production environment = 100; relative generation interval CSPprog sires = 1.4.

\(^2\) \( \Delta G = i \times r_{II} \times \sigma_H \), where \( \Delta G \) = genetic gain in the breeding goal per generation, \( i \) is the selection intensity corrected for finite population size and correlated index values, \( r_{II} = \) accuracy of selection and \( \sigma_H \) = square root of genetic variance of the breeding goal.

\(^3\) \( \Delta G_{prop} \) = proportion of genetic gain for sire or dam selection path of the overall genetic gain per unit of time.

\(^4\) rel = relative value = \( \frac{\text{value} [ r_g = 0 ]}{\text{value} [ r_g = 1 ]} \)

\(^5\) NP = not predictable.
Figure 2. Relative genetic gain \((\Delta G_{r_g = x}/\Delta G_{r_g = 1})\); \(r_g\) = genetic correlation) as a function of heritability for combined selection environment and production environment sib testing (CSPsib) and combined selection environment and production environment progeny testing (CSPprog), with \(r_g = 0.5\) and \(0\). Phenotypic variance = 1.0; proportion of selected sires = 0.05; number of progeny per dam = 8; number of animals in selection environment = 2,000; number of progeny-tested sires (CSPprog) = 400; number of progeny per sire in production environment = 100; and relative generation interval for CSPprog sires = 1.4.

Heritability

Figure 2 shows relative genetic gain (Equation 3) as a function of heritability for CSPsib and CSPprog at genetic correlations of 0.5 and 0. Relative genetic gain was higher for CSPprog than for CSPsib, indicating less sensitivity for CSPprog to G \(\times\) E. Relative genetic gain decreased as heritability increased. At high heritabilities and a genetic correlation of unity, own performance in SLE is an important information source, but it is of no importance with a genetic correlation of zero. At high heritabilities, the denominator of the relative genetic gain equation (Equation 3) increases more than the numerator, which explains the lower relative genetic gain in Figure 2. The decrease in relative genetic gain was smaller for CSPprog than for CSPsib for both values of the genetic correlation because only the dam selection path contributed to losses in genetic gain (Table 3).
Figure 3. Relative genetic gain ($\Delta G[r_g = x]/\Delta G[r_g = 1]$; $r_g$ = genetic correlation) as a function of number of progeny per dam in the selection environment for combined selection environment and production environment sib testing (CSPsib) and combined selection environment and production environment progeny testing (CSPprog) with a genetic correlation of zero and heritabilities ($h^2$) of 0.1, 0.3 and 0.5. Phenotypic variance = 1.0; proportion of selected sires = 0.05; number of animals in selection environment = 2,000; number of progeny-tested sires (CSPprog) = 400; number of progeny per sire in production environment = 100; relative generation interval for CSPprog sires = 1.4.

Number of progeny per dam in SLE

Figure 3 shows relative genetic gain as a function of the number of progeny per dam in SLE for CSPsib and CSPprog at different heritabilities and with a genetic correlation of zero. The relative genetic gain was less for higher heritability, as was also shown in Figure 2. Relative genetic gain with CSPprog decreased exponentially as number of progeny per dam increased. The contribution of the dam selection path to the total genetic gain increased with more progeny per dam (higher selection intensity), and the dam selection path was the only source of losses in genetic gain due to $G \times E$ with CSPprog (Table 3). The effect of the dam selection path on relative genetic gain was marginal with a small number of progeny per dam but substantial with a large number of progeny. Relative genetic gain with CSPsib decreased marginally as the number of progeny per dam increased because of only small changes in selection intensity, accuracy, and variance in the breeding goal, which partly counteracted each other.
Figure 4. Relative selection intensity of sires for combined selection environment and production environment sib-testing schemes (CSPsib) \( (i \ [r_g = 0]/i \ [r_g = 1]; i = \text{selection intensity}, r_g = \text{genetic correlation}) \) as a function of population size of the selection environment (SLE) for different proportions of selected sires (\( p = 0.01, 0.02, 0.05, 0.10, \text{and} 0.20 \)). Heritability = 0.3; phenotypic variance = 1.0; number of progeny per dam = 8; number of progeny per sire in production environment = 100.

Proportion of selected sires and SLE population size

Changing the SLE population size, or the proportion of selected sires, had little effect on relative genetic gain with CSPsib and CSPprog when the proportion of selected sires was at least 0.05 and the SLE population size was at least 2,000 animals (not shown). Relative genetic gain with CSPsib, however, was less if the proportions of selected males and SLE population sizes were smaller due to corrections to the selection intensity for correlated index values and finite population size. Figure 4 shows that the relative selection intensity was substantially decreased with a genetic correlation of zero for small population sizes (0 to 2,000 animals) and small proportions of selected sires (\( p = 0.01 \) to 0.05). The correlation between index values increased from 0.69 to 1.00 for full-sibs and from 0.43 to 0.94 for half-sibs, as the genetic correlation decreased from 1.00 to 0.00. With a genetic correlation of zero, selection was mainly between sire families. With CSPprog relative genetic gain and relative selection intensity were fairly stable, as the proportion of selected sires and the number of progeny-tested sires were varied (not shown). With progeny testing the correlation between index values of related sires changed very little (full-sibs = 0.41 to 0.43; half-sibs = 0.20 to 0.21), when the genetic correlation decreased from 1.00 to 0.00.
Figure 5. Relative genetic gain \((\Delta G[r_g = x]/\Delta G[r_g = 1])\); \(r_g\) = genetic correlation) as a function of number of half-sibs per sire in production environment (PDE) for combined selection environment and production environment sib testing (CSPsib) and relative genetic gain as a function of number of PDE progeny per sire for combined selection environment and production environment progeny testing (CSPprog) with a genetic correlation of zero and heritabilities \((h^2)\) of 0.1, 0.3 and 0.5. Pherotypic variance = 1.0; proportion of selected sires = 0.05; number of progeny per dam = 8; number of animals in selection environment = 2,000; number of progeny-tested sires (CSPprog) = 400; relative generation interval for CSPprog sires = 1.4).

Number of PDE progeny per sire

Figure 5 shows relative genetic gain with a genetic correlation of zero as a function of number of half-sibs per sire in PDE with CSPsib and as a function of number of progeny per sire in PDE with CSPprog. Relative genetic gain was higher with CSPprog than with CSPsib. Relative genetic gain increased asymptotically as number of progeny/half-sibs per sire increased. The required number of half-sibs/progeny per sire to reach the asymptote was higher with CSPsib than with CSPprog. With CSPsib, the genetic gain at a genetic correlation of zero increased considerably as the number of half-sibs per sire increased, whereas genetic gain at a genetic correlation of unity increased marginally, resulting in an increasing relative genetic gain. With CSPprog, however, genetic gain increased similarly at both values of the
genetic correlation, resulting in a fairly stable relative genetic gain, as the number of progeny per sire was larger than 50. More half-sibs/progeny per sire were necessary to reach the asymptote for a low heritability of 0.1 for CSPsib and CSPprog.

Figure 6. Break-even genetic correlation as a function of generation interval of sires with combined selection environment and production environment progeny testing (CSPprog) relative to the generation interval of selection environment sib testing (SEsib) or combined selection environment and production environment sib testing (CSPsib) comparing genetic gain of CSPprog with genetic gain of CSPsib or SEsib for heritabilities ($h^2$) of 0.1, 0.3 and 0.5. Phenotypic variance = 1.0; proportion of selected sires = 0.05; number of progeny per dam = 8; number of animals in selection environment = 2,000; number of progeny-tested sires (CSPprog) = 400; number of progeny per sire in production environment = 100.

Generation interval

When generation interval of sires in CSPprog was varied, absolute genetic gain changed in the opposite direction, but relative genetic gain was unaffected because it is independent of the sum of the generation intervals (see Equation 3). However, when the absolute genetic gain
of CSPprog was compared with genetic gain of CSPsib or SEsib, the generation interval of sires in CSPprog played an important role.

Figure 6 shows the break-even genetic correlation as a function of the generation interval of sires of CSPprog comparing CSPprog with SEsib or CSPsib. When the genetic correlation (0 to 1) was less than the break-even genetic correlation, the genetic gain of CSPprog was higher than the genetic gain of SEsib or CSPsib, and vice versa. When the relative generation interval of CSPprog sires was short (e.g., 1.2), the break-even genetic correlation was 1.00, indicating that genetic gain of CSPprog was higher than genetic gain of CSPsib or SEsib. When the relative generation interval of CSPprog sires was more than 1.8, however, genetic gain of CSPprog was less than the genetic gain of CSPsib. When the relative generation interval of CSPprog sires was between 1.2 and 1.8 or 2.0, the break-even genetic correlation decreased as the generation interval of sires of CSPprog increased relative to CSPsib and SEsib. The effect was larger for CSPprog relative to CSPsib than relative to SEsib. The break-even genetic correlation decreased as heritability increased. Sib-testing schemes, therefore, are relatively better than progeny-testing schemes at high heritabilities \( h^2 \geq 0.3 \) and small \( G \times E \) interactions \( r_g \geq 0.8 \), whereas progeny-testing schemes are better than sib-testing schemes at low heritabilities \( h^2 \leq 0.3 \) and moderate to severe \( G \times E \) interactions \( r_g \leq 0.8 \).

Cases

Case 1: Sex-limited and carcass traits. Table 4 shows absolute and relative genetic gains for traits measured on both sexes, sex-limited to female, and carcass traits. Absolute genetic gains were larger for traits measured on both sexes than for sex-limited and carcass traits. Differences were larger among trait types for high genetic correlations, whereas differences were small with a genetic correlation of zero. Genetic gains were larger for CSPprog than for CSPsib and SEsib for sex-limited and carcass traits for all values of the genetic correlation. Relative genetic gain with SEsib was unaffected by trait type, whereas relative genetic gain for sex-limited and carcass traits with CSPsib and CSPprog was larger than for traits measured on both sexes. Sex-limited and carcass traits had fewer records of relatives in SLE than traits measured on both sexes; thus, less genetic gains were achieved at high genetic correlations. The denominator of the equation for relative genetic gain (Equation 3) was smaller resulting in a larger relative genetic gain. In summary, with CSPsib and CSPprog genetic gains for sex-limited and carcass traits were less affected by \( G \times E \) than genetic gains for traits measured on both sexes.
Table 4. Genetic gain for selection environment sib testing (SEsib), combined selection environment and production environment sib testing (CSPsib) and combined selection environment and production environment progeny testing (CSPprog) for traits measured on both sexes, sex-limited to female traits and carcass traits (20% of selection environment animals slaughtered) for different values of the genetic correlation ($r_g$) (Case 1).

<table>
<thead>
<tr>
<th>Trait type</th>
<th>$r_g$</th>
<th>Genetic gain per unit of time</th>
<th>Relative genetic gain $^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>SEsib</td>
<td>CSPsib</td>
</tr>
<tr>
<td>Both sexes</td>
<td>1</td>
<td>0.479</td>
<td>0.485</td>
</tr>
<tr>
<td></td>
<td>0.8</td>
<td>0.384</td>
<td>0.437</td>
</tr>
<tr>
<td></td>
<td>0.6</td>
<td>0.288</td>
<td>0.402</td>
</tr>
<tr>
<td></td>
<td>0.4</td>
<td>0.192</td>
<td>0.377</td>
</tr>
<tr>
<td></td>
<td>0.2</td>
<td>0.096</td>
<td>0.361</td>
</tr>
<tr>
<td></td>
<td>0</td>
<td>0.000</td>
<td>0.354</td>
</tr>
<tr>
<td>Sex-limited</td>
<td>1</td>
<td>0.398</td>
<td>0.425</td>
</tr>
<tr>
<td></td>
<td>0.8</td>
<td>0.319</td>
<td>0.400</td>
</tr>
<tr>
<td></td>
<td>0.6</td>
<td>0.239</td>
<td>0.382</td>
</tr>
<tr>
<td></td>
<td>0.4</td>
<td>0.159</td>
<td>0.369</td>
</tr>
<tr>
<td></td>
<td>0.2</td>
<td>0.080</td>
<td>0.361</td>
</tr>
<tr>
<td></td>
<td>0</td>
<td>0.000</td>
<td>0.359</td>
</tr>
<tr>
<td>Carcass</td>
<td>1</td>
<td>0.284</td>
<td>0.351</td>
</tr>
<tr>
<td></td>
<td>0.8</td>
<td>0.227</td>
<td>0.343</td>
</tr>
<tr>
<td></td>
<td>0.6</td>
<td>0.170</td>
<td>0.338</td>
</tr>
<tr>
<td></td>
<td>0.4</td>
<td>0.113</td>
<td>0.335</td>
</tr>
<tr>
<td></td>
<td>0.2</td>
<td>0.057</td>
<td>0.333</td>
</tr>
<tr>
<td></td>
<td>0</td>
<td>0.000</td>
<td>0.332</td>
</tr>
</tbody>
</table>

$^1$ Heritability = 0.3; phenotypic variance = 1.0; proportion of selected sires = 0.05; number of progeny per dam = 8; number of animals in selection environment = 2,000; number of progeny-tested sires (CSPprog) = 400; number of progeny per sire in production environment = 100; relative generation interval CSPprog sires = 1.4.

$^2$ Relative genetic gain was calculated as follows: $\Delta G(r_g = x) / \Delta G(r_g = 1)$.

**Case 2: Including SLE performance in the breeding goal.** Figure 7 shows genetic gain for each environment as a function of the economic value of SLE in the breeding goal with a genetic correlation of 0.5. With SEsib, genetic gain was not affected by increasing the economic value of SLE because information was available only from SLE. The straight lines for SEsib were the upper (0.48) and lower limits (0.24) of genetic gains with CSPsib and CSPprog. Genetic gain in SLE increased as economic value of SLE increased with CSPsib.
and CSPprog, whereas genetic gain in PDE decreased as economic value of SLE increased. Genetic gain in SLE was greater with CSPsib than with CSPprog, whereas genetic gain in PDE was greater with CSPprog than with CSPsib. The increase in genetic gain in SLE was greater with CSPsib (from 0.31 to 0.48) than with CSPprog (from 0.28 to 0.42). With CSPprog, progeny information in PDE was the major determinant of genetic gain, making the scheme less flexible for increasing genetic gain in SLE when changing the breeding goal.

![Genetic gain in SLE and PDE](image)

**Figure 7.** Genetic gain in each environment (SLE = selection environment; PDE = production environment) as a function of the economic value of performance in SLE in the breeding goal (economic value\(_{PDE} = 1 - \) economic value\(_{SLE}\)) with a genetic correlation of 0.5 for selection environment sib testing (SE\(_{sib}\)), combined selection environment and production environment sib testing (CSPsib), and combined selection environment and production environment progeny testing (CSPprog) (Case 2). Heritability = 0.3; phenotypic variance = 1.0; proportion of selected sires = 0.05; number of progeny per dam = 8; number of animals in selection environment = 2,000; number of progeny-tested sires (CSPprog) = 400; number of progeny per sire in production environment = 100; relative generation interval for CSPprog sires = 1.4.
DISCUSSION

Methodology and results

In this study, genetic gain was predicted for sib-testing and progeny-testing schemes with varying degrees of $G \times E$ between SLE and PDE. Selection index theory was used to predict genetic gain from BLUP-selection with an animal model. Reduction of genetic variance due to selection linkage disequilibrium and reduction of selection intensity due to finite population size and correlated index values were accounted for. Wray and Hill (1989) showed that selection index theory can be used to approximate selection on BLUP-EBV accurately.

Without $G \times E$, sib-testing schemes resulted in a slightly higher genetic gain than progeny-testing schemes, which agrees with studies on MOET in dairy cattle (Nicholas and Smith, 1983; Bovenhuis et al., 1989; Meuwissen, 1991b). Nicholas and Smith (1983) found an increase of 30% in genetic gain comparing sib-testing with progeny-testing schemes, which is much larger than that reported here. Nicholas and Smith (1983) did not account for decreased genetic variance due to selection (Bulmer, 1971) and decreased selection intensity due to finite population size and correlated index values (Meuwissen, 1991a), leading to an overestimation of the advantage of sib testing over progeny testing.

With $G \times E$ no study was found comparing sib-testing and progeny-testing schemes. As in Wei and Van der Werf (1994), Bijma and Van Arendonk (1998), and Jiang and Groen (1999), including information of half-sib performance in the production environment in the selection index resulted in a higher genetic gain, especially when the genetic correlation between performance in selection and production environment was low. Progeny-testing schemes were rather robust for $G \times E$ between selection and production environment, which is in agreement with Meuwissen and Woolliams (1993), who simulated an open nucleus in dairy cattle. The above studies are all species specific. The uniqueness of this study is that effects of $G \times E$ on genetic gain were investigated in sib-testing and progeny-testing schemes using parameter values that represented pig, poultry and dairy cattle breeding schemes.

Effects of $G \times E$ on genetic gain

The $G \times E$ affected accuracy of selection, selection intensity, and the genetic variance of the breeding goal. Loss in genetic gain was determined mainly by loss in accuracy of selection.

Accuracy of selection. Accuracy of selection is affected by the genetic correlation as a measure of $G \times E$, heritability, type of information (own, sib, or progeny performance) and the number of records of certain information sources (number of sibs; number of progeny). As the genetic correlation decreased, the importance of SLE information in the index decreased and the importance of PDE information increased because performance in PDE was the breeding goal. An increase in the number of half-sibs or progeny in PDE replaced SLE
information by PDE information, which limited the loss in genetic gain due to \( G \times E \). In the absence of \( G \times E \) (\( r_g = 1 \)), importance of own performance in SLE increased with heritability, as expected, whereas with maximum \( G \times E \) (\( r_g = 0 \)) own performance in SLE did not contribute to accuracy of selection for PDE at all. Consequently, relative loss of genetic gain due to \( G \times E \) increased with heritability. Progeny performance in PDE was an important information source regardless of the breeding goal and the genetic correlation. Therefore, progeny-testing schemes guarantee high genetic gain in PDE, but they are less flexible for increasing performance in SLE, unless progeny testing is possible in SLE.

**Selection intensity.** Selection intensity is a function of the proportion selected and is reduced with small population size (Burrows, 1972) or correlated index values of relatives (Meuwissen, 1991a). Within a breeding scheme, \( G \times E \) would not be expected to change the selection intensity very much, because the proportion of animals selected and the population size remain the same. With a small proportion of selected sires (<0.05) or a small population size (<2,000), however, selection intensity was decreased with CSPsib due to a higher correlation between index values of relatives. With a genetic correlation of zero, selection was mainly between sire families, and the number of sire families was small (e.g., five families for 1% selected from 500 males). The selection intensity of sires with CSPprog was hardly affected by \( G \times E \).

**Genetic variance of the breeding goal.** The genetic variance of the breeding goal in this study was equal to the genetic variance for performance in PDE. Due to selection linkage disequilibrium, genetic variance decreased. The magnitude of the decrease was determined by the accuracy of selection and selection intensity (Bulmer, 1971). Due to \( G \times E \), the accuracy of selection decreased, which resulted in an increase in genetic variance of the breeding goal. The increase in genetic variance was largest with SESib and smallest with CSPprog. The increase in genetic variance compensated partly for the decreases in accuracy and selection intensity.

**Dealing with \( G \times E \) in livestock breeding programs**

When \( G \times E \) interaction plays a role in breeding schemes, different strategies can be used to deal with this interaction. Strategies can be classified into aspects related to environment, trait definition, statistical models used in breeding value estimation and aspects related to breeding schemes. Environmental strategies attempt to decrease \( G \times E \) by choosing a selection environment as similar as possible to commercial environments with respect to feeding regimen, housing system, and health status (Webb and Curran, 1986). Measurements of traits should be standardized between environments to avoid \( G \times E \) as a consequence of differences in trait definition. When breeding value estimation is done separately in different countries, \( G \times E \) might arise from use of different statistical models. The goal of organizations
such as Interbull (Uppsala, Sweden) is to harmonize statistical models and trait definitions in different countries (Van der Linde and De Jong, 2002).

In many situations, however, $G \times E$ cannot be avoided because it is beyond the control of breeders and statisticians. In these situations, breeding schemes need to be optimized to limit the loss in genetic gain in the presence of $G \times E$. Robertson (1959) suggested as a guideline that a genetic correlation of 0.8 or higher could be interpreted as $G \times E$ with little biological importance. Assuming a genetic correlation of 0.8 between SLE and PDE, however, would mean that 20% of the genetic gain might be sacrificed if no records were available on relatives performing in PDE. Recording of half-sibs can limit the loss in genetic gain to 10% and recording of progeny can limit the loss to 4%. Brascamp et al. (1985), Webb and Curran (1986), and Hartmann (1990) considered testing of half-sibs under commercial situations as a good option to maintain genetic gain in the presence of $G \times E$. Merks and De Vries (2002) proposed efficient use of large amounts of commercial information on pigs stored by farmers and slaughterhouses. In poultry breeding, however, commercial information is difficult to use because recording of pedigrees is difficult under commercial circumstances. Recurrent testing of crossbred offspring of purebred selection candidates is used in layer breeding programs to maintain genetic gain under commercial conditions (Albers et al., 2002). Cold and normal conditions are used in broiler breeding programs to increase ascites resistance (Albers et al., 2002). In dairy cattle, sires are selected based on progeny records performing in different commercial dairy farms, whereas dams are selected partly in a nucleus herd. Meuwissen and Woolliams (1993) concluded that open MOET nucleus breeding schemes with progeny testing are robust even with significant $G \times E$. In environments where no progeny are tested, loss in genetic gain might be larger because genetic gain in that environment is a correlated response.

Breeding schemes differ in loss in genetic gain due to $G \times E$. Based on results in this study, progeny-testing schemes have less loss in genetic gain than sib-testing schemes and tend to have greater genetic gain when the genetic correlation is low to moderate ($r_g \leq 0.8$). Progeny-testing schemes are preferable in situations with low to moderate heritability ($h^2 \leq 0.3$), relatively short generation interval for progeny-tested sires ($L_{prog} / L_{sib} \leq 1.7$), and moderate to severe $G \times E$ interaction ($r_g \leq 0.8$). The concept of break-even genetic correlation (the value of the genetic correlation when genetic gain with different breeding schemes is equal) can be used to determine whether sib testing or progeny testing is preferable. Costs of the breeding program and rate of inbreeding are other criteria to consider in deciding whether sib testing or progeny testing is preferable. Progeny-testing schemes are more expensive than sib-testing schemes because more progeny need to be produced and recorded and because housing costs for sires are more due to the longer generation interval. Rates of inbreeding will favor progeny testing, even in situations without $G \times E$ (Bovenhuis et al., 1989). With increasing $G \times E$, however, the advantage of progeny testing could increase.
even more because the correlation between index values of relatives is fairly stable with progeny testing, whereas the correlation increases with sib testing. The higher correlation between index values of relatives with sib testing causes a higher rate of inbreeding (Burrows, 1984; Bijma et al., 2001). Economic aspects of the breeding program and rate of inbreeding must be considered when optimizing a specific breeding program.

**IMPLICATIONS**

This study showed that the genotype × environment interaction between selection environment and production environment decreased genetic gain under commercial conditions. Recording of half-sibs or progeny under commercial conditions limited the loss in genetic gain. Progeny-testing schemes had less loss in genetic gain than sib-testing schemes. Higher heritability resulted in substantially more loss in genetic gain, but increasing the number of progeny per sire in the production environment limited the loss. Progeny-testing schemes were preferable in situations with low heritability, relatively short generation interval of progeny-tested sires, and moderate to severe genotype × environment interaction. The break-even genetic correlation (the value of genetic correlation when the genetic gain of different breeding schemes is equal) is useful for determining whether sib testing or progeny testing is preferable.

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**REFERENCES**


Genetic gain with different environments


Meuwissen, T. H. E. 1991a. Reduction of selection differentials in finite populations with a

Meuwissen, T. H. E. 1991b. The use of increased female reproductive rates in dairy cattle


Nicholas, F. W., and C. Smith. 1983. Increased rates of genetic change in dairy cattle by

Rawlings, J. O. 1976. Order statistics for a special class of unequally correlated multinormal


Robertson, A. 1959. The sampling variance of the genetic correlation coefficient. Biometrics
15:469–485.

Interbull meeting, Interlaaken, Switzerland. Interbull Bull. 29:55–60.

response from selection on multiple traits using univariate and multivariate best linear


Wei, M., and J. H. J. Van der Werf. 1995. Genetic correlation and heritabilities for purebred

evaluation of dairy sires using a multiple-trait model with individual animal performance

Chapter 3

Benefits of cooperation between breeding programs in the presence of genotype by environment interaction

H. A. Mulder and P. Bijma

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

Selection within and across environments

**ABSTRACT:** Dairy cattle breeding programs and dairy farmers are selecting sires and dams across environments. Genotype × environment interaction (G × E) limits the possibilities for cooperation between breeding programs operating in different environments. The objectives of this study were twofold: 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 × 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 × 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.

**Keywords:** genotype × environment interaction, breeding program, dairy cattle, genetic gain

**Abbreviation key:** DD = dams to breed daughters, DS = dams to breed sons, G × E = genotype by environment interaction, SD = sires to breed daughters, SS = sires to breed sons,

**INTRODUCTION**

Dairy cattle breeding programs and dairy farmers are currently selecting sires and dams from all over the world. Due to genotype × environment interaction (G × 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 × 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 × 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 possibilities 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 × 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 × 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 twofold: 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 × E, and 2) to quantify the effect of such cooperation on genetic gain.
MATERIAL 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 × E, populations can diverge in terms of genetic means, leading to individually operated (i.e., non-cooperating) 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.

**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.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Basic</th>
<th>Alternative range</th>
</tr>
</thead>
<tbody>
<tr>
<td>Genetic correlation (( r_g ))</td>
<td>0 – 1</td>
<td></td>
</tr>
<tr>
<td>Heritability (( h^2 ))</td>
<td>0.3</td>
<td>0.1, 0.3 and 0.5</td>
</tr>
<tr>
<td>Phenotypic variance (( \sigma_p^2 ))</td>
<td>1.0</td>
<td></td>
</tr>
<tr>
<td>Number of test bulls per breeding program</td>
<td>200</td>
<td>100-300 (sum always 400)</td>
</tr>
<tr>
<td>Number of progeny per bull (( np ))</td>
<td>100</td>
<td>10-100</td>
</tr>
<tr>
<td>Population size cows per environment</td>
<td>1,000,000</td>
<td></td>
</tr>
<tr>
<td>Selected fraction sires to breed sons (( p_{SS} ))</td>
<td>0.05</td>
<td>0.01, 0.05, 0.10, 0.20</td>
</tr>
<tr>
<td>Selected fraction sires to breed daughters (( p_{SD} ))</td>
<td>0.10</td>
<td>0.01, 0.05, 0.10, 0.20</td>
</tr>
<tr>
<td>Selected fraction dams to breed sons (( p_{DS} ))</td>
<td>0.005</td>
<td>0.01, 0.05, 0.10, 0.20</td>
</tr>
<tr>
<td>Selected fraction dams to breed daughters (( p_{DD} ))</td>
<td>0.80</td>
<td></td>
</tr>
</tbody>
</table>

**Pseudo-BLUP selection index**

For reasons of computing time, selection on animal model BLUP-EBV was approximated using a pseudo-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 \( i \) \( R_{i,k,r(t)} \) were calculated for animals selected for breeding program \( l \) within environment \( k \) and selection path \( r \) in generation \( t \) as \( \frac{i_{k(t)} \times b_{m,k(t)}^* g_{i,k(t)}}{\sigma_{EBV,m,k(t)}} \) (Cameron, 1997), where \( i_{k(t)} \) is the selection intensity, \( b_{m,k(t)}^* \) is the vector with selection index weights for breeding objective \( m \), \( g_{i,k(t)} \) is the vector with covariances between phenotypic information sources and the breeding objective \( m \) and \( \sigma_{EBV,m,k(t)} \) is the standard deviation of the EBV for breeding objective \( m \) (see Appendix 1 and 2 for construction of \( g_{i,k(t)} \) and calculation of \( b_{m,k(t)}^* \) and \( \sigma_{EBV,m,k(t)} \)). The genetic mean of selected animals in one environment 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 \( \bar{\mu}_{i,k,r(t)} = \sum_{i=1}^{2} f_{i,k,r(t)} \mu_{i,k,r(t)}^* \), where \( f_{i,k,r(t)} \) is the proportion of selected animals originating from environment \( k \) for selection path \( r \) in generation \( t \) \( (\sum_{i=1}^{2} f_{i,k,r(t)} = 1) \). The genetic mean of newborn bull calves was calculated as
\[ \frac{1}{2} \mu_{l,t,se(t)} + \frac{1}{2} \mu_{l,t,de(t)} \], whereas the genetic mean of newborn heifer calves was
\[ \frac{1}{2} \mu_{l,t,se(t)} + \frac{1}{2} \mu_{l,t,de(t)} \]. 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 \( 1.0 \times 10^{-10} \) 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.

Table 2. Notation used.

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>( h^2 ), ( r_g )</td>
<td>Heritability, genetic correlation between environments</td>
</tr>
<tr>
<td>( \sigma_p^2 ), ( np )</td>
<td>Phenotypic variance, number of progeny per bull</td>
</tr>
<tr>
<td>( f )</td>
<td>Proportion of selected animals</td>
</tr>
<tr>
<td>( R )</td>
<td>Genetic selection differential</td>
</tr>
<tr>
<td>( \mu, \mu^* )</td>
<td>Genetic mean, genetic mean of selected animals</td>
</tr>
<tr>
<td>( p_{SS}, p_{SD}, p_{DS}, p_{DD} )</td>
<td>Selected fraction of sires to breed sons (SS), sires to breed daughters (SD), dams to breed sons (DS), dams to breed daughters (DD)</td>
</tr>
<tr>
<td>( i, k, x )</td>
<td>Selection intensity, variance reduction coefficient, truncation point</td>
</tr>
<tr>
<td>( b, x )</td>
<td>Selection index weights, vector with information</td>
</tr>
<tr>
<td>( P, P_y, P_m, P_f )</td>
<td>Variance-covariance (sub)matrix of information sources for males and females</td>
</tr>
<tr>
<td>( g_j, g_{ij}, g_m, g_f )</td>
<td>Covariance vector between information source and true breeding value for males and females</td>
</tr>
<tr>
<td>( \overline{PG}<em>{ij}, OP</em>{ij} )</td>
<td>Covariance of mean of progeny, covariance of own performance</td>
</tr>
<tr>
<td>( S_{ij}, D_{ij}, M_{ij} )</td>
<td>Covariance between EBV of sire, dam or mean EBV of dams of progeny</td>
</tr>
<tr>
<td>( C_{ij}, C_{sij}, Cd_{ij}, Cms_{ij} )</td>
<td>Genetic, sire genetic, dam genetic and Mendelian sampling covariance</td>
</tr>
<tr>
<td>( \sigma_{EBV}^2 )</td>
<td>Variance of EBV</td>
</tr>
<tr>
<td>( A )</td>
<td>True breeding value</td>
</tr>
<tr>
<td>Subscripts ( i, j )</td>
<td>Performance environment 1 or 2</td>
</tr>
<tr>
<td>Subscripts ( k, l )</td>
<td>Environment of selection, number of breeding program</td>
</tr>
<tr>
<td>Subscript ( m )</td>
<td>Breeding objective</td>
</tr>
</tbody>
</table>
Selection within and across environments

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 environment 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 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. 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.
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.

![Figure 2](image.png)

**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 dams to breed daughters (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.

**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.

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

<table>
<thead>
<tr>
<th>Changed parameter</th>
<th>Heritability $^2$</th>
<th>Number of progeny $^3$</th>
<th>Split-point genetic correlation</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$h_i^2$</td>
<td>$h_j^2$</td>
<td>$n_{p_i}$</td>
</tr>
<tr>
<td>Basic situation</td>
<td>0.3</td>
<td>0.3</td>
<td>100</td>
</tr>
<tr>
<td>Equal heritability</td>
<td>0.1</td>
<td>0.1</td>
<td>100</td>
</tr>
<tr>
<td></td>
<td>0.5</td>
<td>0.5</td>
<td>100</td>
</tr>
<tr>
<td>Different heritability</td>
<td>0.1</td>
<td>0.3</td>
<td>100</td>
</tr>
<tr>
<td></td>
<td>0.5</td>
<td>0.3</td>
<td>100</td>
</tr>
<tr>
<td>Equal number of progeny</td>
<td>0.3</td>
<td>0.3</td>
<td>10</td>
</tr>
<tr>
<td></td>
<td>0.3</td>
<td>0.3</td>
<td>50</td>
</tr>
<tr>
<td>Different number of progeny</td>
<td>0.3</td>
<td>0.3</td>
<td>10</td>
</tr>
<tr>
<td></td>
<td>0.3</td>
<td>0.3</td>
<td>50</td>
</tr>
<tr>
<td>Different $h^2$ and $np$</td>
<td>0.1</td>
<td>0.3</td>
<td>10</td>
</tr>
<tr>
<td></td>
<td>0.1</td>
<td>0.3</td>
<td>50</td>
</tr>
</tbody>
</table>

1 Phenotypic 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 $n_{p_i}$ = number of progeny per bull of breeding program $i$ in environment $i$ ($i = l$).

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 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.

**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 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.
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 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.

Short-term versus 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.

\[\text{Figure 4.} \text{ Short- and long-term effects of cooperation between breeding programs. A) Split-point genetic correlation as a function of generation number (split-point genetic correlation was determined as the highest genetic correlation, where more than 99% of the selected animals in each selection path originated from the own environment). B) Increase in genetic gain (%) due to cooperation relative to individually operated breeding programs as a function of generation number for different values of the genetic correlation (rg). Heritability = 0.3; phenotypic variance = 1.0; number of test bulls per breeding program = 200 (total = 400); number of progeny per bull = 100; population size cows each environment = 1.0 million; selected fraction sires to breed sons (SS) = 0.05; selected fraction sires to breed dams (SD) = 0.10; selected fraction dams to breed sons (DS) = 0.005; selected fraction dams to breed daughters (DD) = 0.80.}\]

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 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
Selection within and across environments

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.

CONCLUSION

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.
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REFERENCES


Cameron, N. D. 1997. Selection indices and prediction of genetic merit in animal breeding. CAB international, Wallingford, United Kingdom.


Selection within and across environments


APPENDIX 1

Pseudo-BLUP selection index

Selection indices or EBV of environment \( j \) in generation \( t \) (\( \text{EBV}_{j(t)} = b_j^{*t} x_{i(t)} \)) 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 \( b_{j(t)} \) were calculated as \( P_{i(t)}^{-1} g_{j(t)} \), where \( P_{i(t)} \) is the variance-covariance matrix of information sources in \( x_{i(t)} \) and \( g_{j(t)} \) is the covariance vector between information sources in \( x_{i(t)} \) and the true breeding value of environment \( j \). The information sources in \( x_{i(t)} \) 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 \( x_{i(t)} \) 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 to be 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 \( P_{i(t)} \)-matrix was formed with sub-matrices (\( P_{j(t)} \)) for each combination of traits \( i \) and \( j \) (environment 1 and 2):

\[
P_{i(t)} = \begin{bmatrix} P_{11(t)} & P_{12(t)} \\ P_{21(t)} & P_{22(t)} \end{bmatrix}
\]

with different sub-matrices \( P_{m_{j(t)}} \) and \( P_{f_{j(t)}} \), for males and females, respectively, following the given order of information sources:

\[
P_{m_{j(t)}} = \begin{bmatrix} \bar{P} G_{j(t)} & \frac{M_{j(t)}}{2np} & \frac{D_{j(t)}}{4} & \frac{S_{j(t)}}{4} \\ \frac{M_{j(t)}}{np} & 0 & 0 & D_{j(t)} \\ \frac{D_{j(t)}}{4} & 0 & 0 & S_{j(t)} \\ \frac{S_{j(t)}}{4} & S_{j(t)} & S_{j(t)} & S_{j(t)} \end{bmatrix}
\]

\[
P_{f_{j(t)}} = \begin{bmatrix} \bar{O} P_{j(t)} & \frac{D_{j(t)}}{2} & \frac{S_{j(t)}}{2} \\ \frac{D_{j(t)}}{2} & 0 & S_{j(t)} \\ \frac{S_{j(t)}}{2} & S_{j(t)} & S_{j(t)} \end{bmatrix}
\]

56
where $\overline{PG}_{g(i)} = (\text{co})\text{variance of mean performance of progeny between trait } i \text{ and } j \text{ in generation } t = \frac{1}{4} C_{g(i)} + \frac{1}{4} C_{g(i)} + C_{ms_{g(i-1)}} + E_{g(i)}/np$, where $C_{g(i)}$ is element of the genetic variance-covariance matrix, $C_{ms_{g(i-1)}}$ is element of the genetic variance-covariance matrix of Mendelian sampling terms, $E_{g(i)}$ is element of the environmental variance-covariance matrix and $np$ is number of progeny; $OP_{g(i)} = (\text{co})\text{variance of own performance between trait } i \text{ and } j \text{ in generation } t = C_{g(i)} + E_{g(i)}$; $M_{g(i)} = (\text{co})\text{variance of mean EBV of dams of progeny between trait } i \text{ and } j \text{ in generation } t$, see under “variance reduction due to selection”).

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

$$g_{j(i)} = \begin{bmatrix} g_{1j(i)} \\ g_{2j(i)} \end{bmatrix}$$

with for different vectors $g_{j(i)}$, $gm_{j(i)}$ and $gf_{j(i)}$, for bulls and cows, following the given order of information sources:

$$gm_{j(i)} = \begin{bmatrix} C_{g(i)}/2 \\ 0 \\ D_{j(i)}/2 \\ S_{j(i)}/2 \end{bmatrix} \quad \quad \quad \quad gf_{j(i)} = \begin{bmatrix} C_{g(i)} \\ D_{g(i)}/2 \\ S_{j(i)}/2 \end{bmatrix}$$

**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 two genetic variance-covariance matrices as a consequence of different Bulmer-equilibria. Therefore, each breeding program had two sire and dam genetic variance-covariance matrices ($Cs_{s(i)}$ and $Cd_{d(i)}$). A genetic (co)variance ($C_{g(i)}$) was partitioned into:
Selection within and across environments

\[ C_{y(t)} = \frac{1}{4} C_{s_y(t)} + \frac{1}{4} C_{d_y(t)} + C_{ms_y(t-0)} \]

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

The \( C_s_{(t)} \) -matrix and \( C_d_{(t)} \) -matrix were updated each generation according to Bijma et al. (2001), e.g. for an element \( C_{s_{y,j}(t)} \) of breeding program \( l \) in generation \( t \) :

\[
C_{s_{y,j}(t)} = \sum_k \left\{ f_{k(t-1)} \left[ C_{s_{y,j}(t-1)} - \frac{\text{Cov}(A_i, EBV_{m,k,l})_{(t-1)} \text{Cov}(A_j, EBV_{m,k,l})_{(t-1)}}{\sigma^2_{EBV,m,k,l(t-1)}} k_{s,k,l(t-1)} \right] \right. \\
+ \sum_k \left\{ f_{k(t-1)} \left[ \mu_{i,k,l(t-1)} - \mu_{i,j,l(t-1)} \right] \left[ \mu_{j,k,l(t-1)} - \mu_{j,j,l(t-1)} \right] \right. \\
\]

where \( \text{Cov}(A_i, EBV_{m,k,l})_{(t-1)} = b'_m,k,l(t-1) b_{m,k,l(t-1)} \), \( EBV_{m,k,l} \) = selection criterion of animals selected for breeding objective \( m \) of breeding program \( l \) within environment \( k \) in generation \( t-1 \), \( \sigma^2_{EBV,m,k,l(t-1)} = b'_m,k,l(t-1) b_{m,k,l(t-1)} \) = variance of \( EBV_{m,k,l} \) in generation \( t-1 \), and \( k_{s,k,l(t-1)} = i_{s,k,l(t-1)} x_{s,k,l(t-1)} \) = variance reduction coefficient, where \( i_{s,k,l(t-1)} \) is selection intensity of sires selected for breeding program \( l \) within environment \( k \) in generation \( t-1 \) and \( x_{s,k,l(t-1)} \) is the corresponding standardized truncation point. The \( C_d_{(t)} \) -matrix was calculated similarly using \( k_{d,k,l(t-1)} \) instead of \( k_{s,k,l(t-1)} \).

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 (\( S_{(o)} \)) and dam EBV (\( D_{(o)} \)) as a consequence of different Bulmer-equilibria. In multivariate analysis the elements of \( S_{(o)} \) and \( D_{(o)} \) are equal to the covariances between the true additive genetic effects and the EBV (Villanueva et al., 1993). Elements of \( S_{(o)} \) -matrix and \( D_{(o)} \) -matrix were updated each generation, e.g., for an element \( S_{y,j,(t)} \) of breeding program \( l \) in generation \( t \) :

\[
S_{y,j,(t)} = \sum_k \left\{ f_{k(t-1)} \left[ \text{Cov}(A_i, EBV_{j,k,l})_{(t-1)} - \frac{\text{Cov}(A_i, EBV_{j,k,l})_{(t-1)} \text{Cov}(EBV_{j,k,l}, EBV_{m,k,l})_{(t-1)}}{\sigma^2_{EBV,m,k,l(t-1)}} k_{s,k,l(t-1)} \right] \right. \\
+ \sum_k \left\{ f_{k(t-1)} \left[ \mu_{i,k,l(t-1)} - \mu_{i,j,l(t-1)} \right] \left[ \mu_{j,k,l(t-1)} - \mu_{j,j,l(t-1)} \right] \right. \\
\]
where \( EBV_{j,kl} \) = EBV for performance in environment \( j \) for an animal selected for breeding program \( l \) within environment \( k \), \( Cov(A_t, EBV_{j,kl})_{(t-1)} = b'_{j,kl(t-1)} g_{t,kl(t-1)} \), and
\[ Cov(EBV_{j,kl}, EBV_{m,kl})_{(t-1)} = b'_{j,kl(t-1)} g_{m,kl(t-1)} \cdot \]
Chapter 4

Optimization of dairy cattle breeding programs for different environments with genotype by environment interaction

H. A. Mulder¹, R. F. Veerkamp², B. J. Ducro¹, J. A. M. van Arendonk¹, P. Bijma¹

¹Animal Breeding and Genetics Group, Wageningen University, PO Box 338, 6700 AH Wageningen, The Netherlands.
²Animal Sciences Group, Division Animal Resources Development, PO Box 65, 8200 AB Lelystad, The Netherlands.

ABSTRACT: Dairy cattle breeding organizations tend to sell more semen to different environments and genotype × 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 × environment interaction. Breeding strategies differed in 1) including one or two environments in the breeding goal, 2) running either one or two 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.

Keywords: genetic gain, dairy cattle, breeding program, genotype × environment interaction

Abbreviation key: DD = dams to breed daughters, DS = dams to breed sons, G × E = genotype × environment interaction, OE-1 = one environment breeding program with progeny testing bulls in 1 environment, OJ-2 = one joint breeding program with progeny testing bulls in 2 environments, SD = sires to breed daughters, SS = sires to breed sons, TE-1 = two environment-specific breeding programs with progeny testing each bull in 1 environment, TJ-1 = two breeding programs with a joint breeding goal with progeny testing each bull in 1 environment.

INTRODUCTION

Dairy cattle breeding is becoming increasingly 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 ×
environment interaction (G × 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 et al., 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 × 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 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, 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 two 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 × E.
Breeding for different environments

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.

MATERIAL AND METHODS

Breeding objective

In this study, we considered a situation with a single dairy cattle breeding organization having two 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 ($\Delta G$) weighing genetic gain in each environment ($\Delta G_i$) by the relative importance of that environment ($w_i$):

$$\Delta G = w_1\Delta G_1 + w_2\Delta G_2$$  \hspace{1cm} (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 two 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 four 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 (ES-1).
(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.

**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 (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).

<table>
<thead>
<tr>
<th>Strategy</th>
<th>Number of test-bulls</th>
<th>Number of progeny per bull</th>
<th>Breeding goal (economic values)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>E₁^2</td>
<td>E₁</td>
</tr>
<tr>
<td>OE-1</td>
<td>400</td>
<td>100</td>
<td>0</td>
</tr>
<tr>
<td>OJ-2</td>
<td>400</td>
<td>w₁ * 100 ^3</td>
<td>w₁</td>
</tr>
<tr>
<td>TE-1</td>
<td>w₁ * 400</td>
<td>100</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>w₂ * 400</td>
<td>0</td>
<td>100</td>
</tr>
<tr>
<td>TJ-1</td>
<td>w₁ * 400</td>
<td>100</td>
<td>w₁</td>
</tr>
<tr>
<td></td>
<td>w₂ * 400</td>
<td>0</td>
<td>100</td>
</tr>
</tbody>
</table>

- In strategy OJ-2 and TJ-1, the economic values are equal to the relative importance of both environments (wᵢ).
- E₁ is environment 1; E₂ is environment 2.
- In the basic situation (see Table 2): w₁ = w₂ = 0.5
- Strategy TE-1 and TJ-1 consists of two breeding programs – each row is one breeding program.

**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).

**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
Breeding for different environments

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. Selection 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% was considered as potential DS. Other dams were excluded for various reasons not directly related to the breeding goal. The 80% best cows were selected as DD each year within their own environment to produce female replacements using artificial insemination ( \( p_{DD} = 0.80 \)). The heritability ( \( h^2 \) ) of milk yield was 0.3 in both environments and the genetic correlation 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).
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.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Basic</th>
<th>Alternative range</th>
</tr>
</thead>
<tbody>
<tr>
<td>Genetic correlation ($r_g$)</td>
<td>0 – 1</td>
<td></td>
</tr>
<tr>
<td>Heritability ($h^2$)</td>
<td>0.3</td>
<td>0.05, 0.1, 0.3 and 0.6</td>
</tr>
<tr>
<td>Phenotypic variance ($\sigma_p^2$)</td>
<td>1.0</td>
<td></td>
</tr>
<tr>
<td>Number of test-bulls</td>
<td>400</td>
<td></td>
</tr>
<tr>
<td>Number of progeny per bull</td>
<td>100</td>
<td>10, 20, 100, 1000</td>
</tr>
<tr>
<td>Population size cows per environment</td>
<td>1,000,000</td>
<td></td>
</tr>
<tr>
<td>Relative importance$^1$ of environment 1 ($w_1$)</td>
<td>0.5</td>
<td>0.5 – 1.0</td>
</tr>
<tr>
<td>Selected proportion sires to breed bulls ($p_{SS}$)</td>
<td>0.05</td>
<td>0.01, 0.02, 0.05, 0.10, 0.20</td>
</tr>
<tr>
<td>Selected proportion sires to breed cows ($p_{SD}$)</td>
<td>0.10</td>
<td>0.01, 0.02, 0.05, 0.10, 0.20</td>
</tr>
<tr>
<td>Selected proportion dams to breed bulls ($p_{DS}$)</td>
<td>0.005</td>
<td>0.01, 0.02, 0.05, 0.10, 0.20</td>
</tr>
<tr>
<td>Selected proportion dams to breed cows ($p_{DD}$)</td>
<td>0.80</td>
<td></td>
</tr>
</tbody>
</table>

$^1 w_2 = 1 - w_1$.

Evaluation of breeding strategies

**Genetic gain.** Genetic gains in both environments ($\Delta G_1$ and $\Delta G_2$) 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 ($\Delta G$) was calculated using Equation 1. In strategy TE-1, however, genetic gain was different for both breeding programs. Therefore, $\Delta G$ was calculated using genetic gain in environment 1 of breeding program 1 ($\Delta G_1$) and genetic gain in environment 2 of breeding program 2 ($\Delta G_2$).

**Break-even genetic correlation.** The optimum breeding strategy with respect to $\Delta G$ 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 $\Delta G$ of strategy TE-1 was equal to $\Delta G$ 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 $2 \times 2$ 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 strategy TE-1 and TJ-1, SS and SD were selected by truncation across breeding programs, while 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 $i$ ($R_{i,k,r(i)}$) were calculated for animals selected in selection path $r$ within environment $k$ in generation $t$ as:

$$R_{i,k,r(i)} = \frac{i_{k(i)} \times b'_{i,k(i)} g_{i,k(i)}}{\sigma_{i,k(i)}}$$

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

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

where $\mu_{i,k,r(i)}$ 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 genetic 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 \( 1.0 \times 10^{-10} \). 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**

Figure 1A and Figure 1B shows genetic gain in environment 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), while 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 environment 1 and 2. When the genetic correlation decreased, genetic gain in both environments decreased linearly (Figure 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 (Figure 1A and 1B). Both environments always contributed to the selected parents in SS, SD and DS, in contrast to strategy TE-1.

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).

Comparison of strategies

Genetic gain. Strategy OE-1 had the highest genetic gain in environment 1 ($\Delta G_1$), 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 $\Delta G_1$, due to reduced selection intensity. Strategies OJ-2 and TJ-1 both had higher $\Delta G_1$ than TE-1, when the genetic correlation was higher than 0.61 and 0.70, respectively. Strategy OJ-2 always had a higher $\Delta G_1$ than strategy TJ-1. When the genetic correlation was unity, $\Delta G_1$ of all strategies was equal.

Strategy OE-1 had the lowest genetic gain in environment 2 ($\Delta G_2$) 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 ($\Delta G$) 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 $\Delta G$. When the genetic correlation was lower, strategy TE-1 had the highest $\Delta G$. Strategy TJ-1 had higher $\Delta G$ than strategy TE-1 when the genetic correlation was higher than 0.70, whereas strategy OE-1 had higher $\Delta G$ than strategy TE-1 when the genetic correlation was higher than 0.75.

![Figure 2](image-url)

**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 (1 environment-specific breeding programs) and TJ-1 (1 breeding programs with a joint breeding goal) in the basic situation (see Table 2).

**Genetic gain relative to OJ-2.** Table 3 shows $\Delta G_1$, $\Delta G_2$ and $\Delta G$, 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 $\Delta G$ when the genetic correlation was higher than 0.61. Within strategy, $\Delta G_1$, $\Delta G_2$ and $\Delta G$ 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 $\Delta G_1$ and a 6 to 41% lower $\Delta G_2$, resulting in 2 to 12% lower $\Delta G$ in comparison with strategy OJ-2. Strategy TE-1 had 10% lower $\Delta G$ than strategy OJ-2 when the genetic correlation was 0.90, but 5% higher $\Delta G$ when the genetic correlation was 0.5. Strategy TJ-1 had 2 to 6% lower $\Delta G$ than strategy OJ-2.
Breeding for different environments

<table>
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<th>Trait</th>
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<td>1.05</td>
<td>0.94</td>
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1 Genetic gain in the overall objective was calculated as $\Delta G = w_1\Delta G_1 + w_2\Delta G_2$, where $\Delta G_i$ is genetic gain in environment $i$ and $w_i$ is relative importance of environment $i$ ($w_1 = w_2 = 0.5$).

2 Heritability = 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 $DD = 0.80$.

**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.
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).

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. 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 \(\Delta G\) than the other strategies, regardless of the genetic correlation. The break-even genetic correlation...
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correlation of TE-1 with TJ-1 was less sensitive to \( w_i \), 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 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 \( \Delta G \) (results not shown). In comparison to 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 \( w_i \). 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 strategy OE-1, OJ-2 or TJ-1 and was only best with low genetic correlations (\( \leq 0.50 \)). 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 \( \Delta G \) of strategy OJ-2, OE-1, and TJ-1 at a genetic correlation of unity and the horizontal part of the curve of \( \Delta G \) 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.
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).

Heritability and number of progeny per bull. Table 4 shows break-even genetic correlations for different values of the heritability and number of progeny per bull in combination with $w_i$ 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 $w_i$ 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 $w_i$ 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 sensitivity to changes in heritability or number of progeny per bull.
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Table 4. Break-even genetic correlations\(^1\) 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 two values of relative importance of environment \(1 \times (w_1)\)^2.

<table>
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<td>1,000</td>
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<td>0.58</td>
</tr>
</tbody>
</table>

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

\(^2\) Phenotypic 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 \(i\) \((\text{TE/TJ-1}) = w_i \times 400\); number of progeny per bull environment \(i\) \((\text{OJ-2}) = w_i \times \text{progeny/bull}\).

DISCUSSION

Methodology and results

In this study, breeding strategies for dairy cattle were compared in the presence of G × E. The three strategies proposed by James (1961) served as starting point. In contrast to James (1961), four paths of selection were 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 two 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 to 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 represent 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, while 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 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 × 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. As a consequence, 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.

**CONCLUSION**

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 × 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.

ACKNOWLEDGEMENT

The first author would like to thank Sijne van der Beek, Henk Geertsema and Chris Schrooten for fruitful discussions about this study.

REFERENCES

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APPENDIX 1

Pseudo-BLUP selection index

Selection indices were constructed in generation $t$ as $I_{(t)} = v'EBV_{(t)}$ for all bulls and cows being selection candidates, where $EBV_{(t)}$ 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 $EBV_{j(t)} = b'_{j(t)}x_{(t)}$ with $b_{j(t)} = P_{j(t)}^{-1}g_{j(t)}$, where $P_{j(t)}$ is the variance-covariance matrix of information sources in $x_{(t)}$ and $g_{j(t)}$ is the covariance vector between information sources in $x_{(t)}$ and the true breeding
value of environment \( j \). With multivariate breeding value estimation, the selection index could be equivalently calculated as \( I_{(i)} = b'_{I(i)} x_{(i)} \) with \( b_{I(i)} = P_{(i)}^{-1} G_{(i)} v = B'_{(i)} v \), where \( B_{(i)} \) is a matrix of both \( b_{j(i)} \)-vectors. The matrix \( G_{(i)} \) consists of both \( g_{j(i)} \) vectors. The vector \( b_{I(i)} \) was used in calculation of the genetic selection differentials \( R_{(i)} \) and in calculation of the variance of the selection index \( \sigma^2_{I(i)} = b'_{I(i)} P_{(i)} b_{I(i)} \).

The information sources in \( x_{(i)} \) 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 \( x_{(i)} \) 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 \( P_{(i)} \)-matrix and the \( g_{j(i)} \)-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. As a consequence, the formulas to update sire and dam genetic variance-covariance matrices (\( C_{S_{(i)}} \) and \( C_{D_{(i)}} \)) and variance-covariance matrices of sire and dam EBV (\( S_{(i)} \) and \( D_{(i)} \)) were slightly different and given below.

The \( C_{S_{(i)}} \)-matrix and \( C_{D_{(i)}} \)-matrix were updated each generation according to Bijma et al. (2001); for example, for an element \( C_{S_{g,j(i)}} \) of breeding program \( I \) (strategy TE-1) in generation \( t \):

\[
C_{S_{g,j(i)}} = \sum_{1}^{k} \left\{ f_{k(t-1)} \left[ C_{g,k(t-1)} - \frac{\text{Cov}(A_{j}, I_{kl(t-1)}) \text{Cov}(A_{j}, I_{kl(t-1)})}{\sigma^2_{I(kl(t-1))}} k_{g,kl(t-1)} \right] \right\} + \sum_{1}^{k} \left\{ f_{k(t-1)} \left[ \bar{\mu}_{g,kl(t-1)} - \bar{\mu}_{g,kl(t-1)} \right] \left[ \bar{\mu}_{g,kl(t-1)} - \bar{\mu}_{g,kl(t-1)} \right] \right\}
\]
where \( C_{ij,k(t-1)} \) = genetic variance between trait \( i \) and \( j \) in environment \( k \) in generation \( t-1 \),
\[
\text{Cov}(A_i, I_{j,k})_{(t-1)} = b'_{j,k(t-1)}g_{i,k(t-1)}, \quad I_{j,k} = \text{selection criterion of animals selected for breeding program} \ l \ \text{within environment} \ k \ \text{in generation} \ t-1, \quad \text{and} \ k_{x,k(t-1)} = i_{x,k(t-1)}(i_{x,k(t-1)} - x_{x,k(t-1)})
\]
= variance reduction coefficient, where \( i_{x,k(t-1)} \) is the selection intensity of sires selected for breeding program \( l \) within environment \( k \) in generation \( t-1 \) and \( x_{x,k(t-1)} \) is the corresponding standardized truncation point. The \( \mathbf{C_d}_{(i)} \)-matrix was calculated similarly using \( k_{d,k(t-1)} \) instead of \( k_{x,k(t-1)} \).

Elements of \( \mathbf{S}_{(i)} \)-matrix and \( \mathbf{D}_{(i)} \)-matrix were updated each generation, e.g., for an element \( S_{y,l(t)} \) of breeding program \( l \) (strategy TE-1) in generation \( t \):
\[
S_{y,l(t)} = \sum_{l(t)} \left\{ f_{l(t)} \left[ \frac{\text{Cov}(A_i,EBV_{j,k})_{(t-1)} - \text{Cov}(A_i,I_{j,k})_{(t-1)} \text{Cov}(EBV_{j,k},I_{j,k})_{(t-1)}}{\sigma^2_{I,j,k(t-1)}} \right] k_{x,k(t-1)} \right\}
+ \sum_{l(t)} \left\{ f_{l(t)} \left[ \frac{\mu_{i,k(t-1)} - \bar{\mu}^*_i}{\sigma_{I,j,k(t-1)}} \right] \left[ \mu_{i,k(t-1)} - \bar{\mu}^*_i \right] \right\}
\]

where \( EBV_{j,k} \) = EBV for performance in environment \( j \) for an animal selected for breeding program \( l \) within environment \( k \), \( \text{Cov}(A_i,EBV_{j,k})_{(t-1)} = b'_{j,k(t-1)}g_{i,k(t-1)} \), and \( \text{Cov}(EBV_{j,k},I_{j,k})_{(t-1)} = b'_{j,k(t-1)}G_{i,k(t-1)} \).

The given formulas were appropriate for strategy TE-1 and TJ-1. In strategy OE-1 and OJ-2, the given formulas for the \( \mathbf{C_s}_{(i)} \)-matrix and \( \mathbf{S}_{(i)} \)-matrix were reduced to the formulas given in Mulder and Bijma (2005), because there was only one group of bulls. The formulas for the \( \mathbf{C_d}_{(i)} \)-matrix and \( \mathbf{D}_{(i)} \)-matrix were still applicable in its complicated form, because DS were selected in both environments.
Chapter 5

Prediction of breeding values and selection responses with genetic heterogeneity of environmental variance

H. A. Mulder¹, P. Bijma¹, W. G. Hill²

¹ Animal Breeding and Genetics Group, Wageningen University, PO Box 338, 6700 AH Wageningen, The Netherlands,
² Institute of Evolutionary Biology, School of Biological Sciences, University of Edinburgh, Edinburgh, EH9 3JT, United Kingdom.

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ABSTRACT: There is empirical evidence that genotypes differ not only in mean, but also in environmental variance of the traits they affect. Genetic heterogeneity of environmental variance may indicate genetic differences in environmental sensitivity. The aim of this study was to develop a general framework for prediction of breeding values and selection responses in mean and environmental variance with genetic heterogeneity of environmental variance. Both means and environmental variances were treated as heritable traits. Breeding values and selection responses were predicted with little bias using linear, quadratic and cubic regression on individual phenotype, or using linear regression on the mean and within-family variance of a group of relatives. A measure of heritability was proposed for environmental variance to standardize results in the literature and to facilitate comparisons to ‘conventional’ traits. Genetic heterogeneity of environmental variance can be considered as a trait with a low heritability. Although a large amount of information is necessary to accurately estimate breeding values for environmental variance, response in environmental variance can be substantial, even with mass selection. The methods developed allow use of the well-known selection index framework to evaluate breeding strategies and effects of natural selection that simultaneously change the mean and the variance.

Keywords: selection response, breeding value, multiple regression, genetic heterogeneity of environmental variance, prediction

INTRODUCTION

The standard genetic model in quantitative genetics is that phenotype \( P \) is the sum of genotype \( G \) and environment \( E \): \( P = G + E \) (Falconer and Mackay, 1996). The phenotypic variance can be written as \( \sigma_P^2 = \sigma_G^2 + \sigma_E^2 \), assuming no covariance between \( G \) and \( E \). This model allows for genetic differences in mean \( (\bar{G}) \), with a genetic variance \( \sigma_G^2 \). For different genotypes, environmental variances \( (\sigma_E^2) \) are assumed to be constant. Based on analysis of field data and laboratory (selection) experiments, there is, however, some empirical evidence that genotypes differ in \( \sigma_E^2 \).

Several studies have been carried out to quantify genetic differences in environmental variance in field data. SanCristobal-Gaudy et al. (2001), Sorensen and Waagepetersen (2003), and Ros et al. (2004) explicitly modeled genetic differences in environmental variance and found substantial genetic variance in environmental variance for litter size in sheep, litter size in pigs, and body weight in snails, respectively. Van Vleck (1968) and Clay et al. (1979), in analysis of milk yield in dairy cattle, and Rowe et al. (2006), in analysis of body weight in broiler chickens, found large differences between sires in phenotypic variance within progeny.
groups. In these studies, it was not possible to distinguish whether these differences were due to heterogeneity of environmental variance, genetic variance or both.

Several selection experiments have been carried out to investigate whether phenotypic variance can be changed by selection. Phenotypic variance changed in some selection experiments with *Drosophila melanogaster* and *Tribolium castaneum* (Rendel et al., 1966; Kaufman et al., 1977; Cardin and Minvielle, 1986), while it did not in an experiment with mice (Falconer and Robertson, 1956). In these experiments, it was not always clear whether the response in variance was due to a change in environmental variance, genetic variance or both.

Mackay and Lyman (2005) derived 300 isofemale lines of *Drosophila* and computed the coefficient of variation (CV) for environmental variance within each homozygous line, effectively a clone, and within crosses of each line with another inbred line. They found highly significant genetic variance in CV and in environmental variance between lines. Homozygotes had higher environmental variance, in agreement with findings of Robertson and Reeve (1952). This study is probably the cleanest known example showing genetic variance in environmental variance because the design allowed repetition of genotypes.

In livestock and plant breeding, uniformity of end product is an important topic. In meat type animals, for instance, uniformity has economic benefits because excessive variability in carcass weight or conformation is penalized by slaughterhouses. Hohenboken (1985) reviewed the potential of mating systems (crossing, inbreeding) and breeding schemes to change variability. To evaluate breeding strategies, methods to predict responses to selection for uniformity are necessary. SanCristobal-Gaudy et al. (1998) derived prediction equations and SanCristobal-Gaudy et al. (2001) evaluated different selection indices using Monte Carlo simulation when the aim was to select for an optimum phenotype and thereby decrease the variance around the optimum (canalizing selection). Sorensen and Waagepetersen (2003) evaluated response to selection using an index including the mean and the variance of multiple records of an individual and Ros et al. (2004) discussed the use of a restricted index aiming at decreasing the environmental variance, while maintaining the mean. Hill and Zhang (2004) derived simple equations to predict response to directional mass selection with genetic heterogeneity of environmental variance. In general, these prediction equations can be used only in special cases. A general framework to predict responses in mean and variance is lacking.

The objective of the present study was to develop a general framework for prediction of breeding values and responses to selection with genetic heterogeneity of environmental variance. Responses to selection were predicted for different forms of selection based on a single phenotype, as well as selection on a mean or variance of a group of relatives. Furthermore, a measure of heritability for environmental variance was developed, enabling a
Responses in mean and variance

direct comparison between selection to change the environmental variance of a trait and the well-established framework of selection to change its mean.

DERIVATION AND EVALUATION OF EXPRESSIONS

In this section, the model incorporating genetic heterogeneity of environmental variance is defined and the framework for prediction is explained. Prediction of breeding values and selection responses based on a single phenotype and a group of relatives are then considered, in each case using Monte Carlo simulation to investigate the relationships between true breeding values and phenotypic information. Using these observations, multiple regression equations are derived for one generation of selection and their goodness of fit evaluated by simulation. Finally, a measure of heritability for environmental variance is proposed.

Genetic model and framework for prediction

The classical model, in the absence of dominance and epistasis, \( P = A + E \) (Falconer and Mackay, 1996), is extended to include an additive genetic effect for the environmental variance (Hill and Zhang, 2004):

\[
P = \mu + A_m + \chi \sqrt{\sigma_E^2 + A_v}
\]  

(1)

where \( \mu \) and \( \sigma_E^2 \) are, respectively, the mean trait value and the mean environmental variance of the population, \( A_m \) and \( A_v \) are, respectively, the breeding value for the mean and environmental variance and \( \chi \) is a standard normal deviate for the environmental effect. It is assumed that \( A_m \) and \( A_v \) are the sum of the effects at an infinite number of loci each with small additive effects and follow a multivariate normal distribution \( N\left(\begin{pmatrix} 0 \\ 0 \end{pmatrix}, \mathbf{C} \otimes \mathbf{A}\right) \), where

\( \mathbf{A} \) is the additive genetic relationship matrix, \( \mathbf{C} = \begin{bmatrix} \sigma_{m}^2 & \text{cov}_{m}\text{v} \\ \text{cov}_{m}\text{v} & \sigma_{v}^2 \end{bmatrix} \), \( \sigma_{m}^2 \) is the additive genetic variance in \( A_m \), \( \sigma_{v}^2 \) is the additive genetic variance in \( A_v \), \( \text{cov}_{m}\text{v} = \text{cov}(A_m, A_v) = r_A \sigma_m \sigma_v \), and \( r_A \) is the additive genetic correlation between \( A_m \) and \( A_v \). The term \( \chi \) is normally distributed \( N(0,1) \) and is scaled by \( \sqrt{\sigma_E^2 + A_v} \) to obtain the environmental effect. The notation is listed in Table 1.
Table 1. Notation used.

<table>
<thead>
<tr>
<th>Notation</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>(P, \mu, A_m, A_v)</td>
<td>Phenotype, mean, breeding values for mean and environmental variance</td>
</tr>
<tr>
<td>(Z, MS)</td>
<td>Standard normal deviate, Mendelian Sampling term</td>
</tr>
<tr>
<td>(\sigma^2_{\mu m}, \sigma^2_{\mu v}, r_{A_m}, C)</td>
<td>Genetic variance in mean and environmental variance, genetic correlation between (A_m) and (A_v), genetic variance-covariance matrix</td>
</tr>
<tr>
<td>(\sigma^2_E, \sigma^2_p)</td>
<td>Mean environmental and phenotypic variances</td>
</tr>
<tr>
<td>(\bar{P}_x, \bar{P}^2_x, \bar{P}^3_x)</td>
<td>Mean (P), (P^2), and (P^3) of selected animals</td>
</tr>
<tr>
<td>(\bar{P}, (\bar{P})^2, P^2, n)</td>
<td>Mean phenotype of relatives, mean phenotype squared, mean squared phenotype of relatives, number of relatives</td>
</tr>
<tr>
<td>(\text{var}W, \ln(\text{var}W))</td>
<td>Within-family variance, log-transformed within-family variance</td>
</tr>
<tr>
<td>(a_j, a_w)</td>
<td>Additive genetic relationships between animal (j) and the group of relatives and between animals within the group of relatives</td>
</tr>
<tr>
<td>(\mathbf{a}, \mathbf{x})</td>
<td>Vectors of breeding values (A_m) and (A_v) and of phenotypic information</td>
</tr>
<tr>
<td>(\mathbf{P}, \mathbf{G}, \mathbf{g}<em>{A_m}, \mathbf{g}</em>{A_v})</td>
<td>Variance-covariance matrix of (\mathbf{x}), covariance matrix between (\mathbf{x}) and (\mathbf{a}), vectors with (\mathbf{G} = \begin{bmatrix} \mathbf{g}<em>{A_m} &amp; \mathbf{g}</em>{A_v} \end{bmatrix} )</td>
</tr>
<tr>
<td>(\bar{\mathbf{P}}_n, \bar{\mathbf{G}}_n, \mathbf{L})</td>
<td>(\mathbf{P})- and (\mathbf{G})-matrices with (\ln(\text{var}W)), scalar matrix</td>
</tr>
<tr>
<td>(\mathbf{B}, \mathbf{b}<em>{A_m}, \mathbf{b}</em>{A_v})</td>
<td>Matrix with regression coefficients, vectors with (\mathbf{B} = \begin{bmatrix} \mathbf{b}<em>{A_m} &amp; \mathbf{b}</em>{A_v} \end{bmatrix} )</td>
</tr>
<tr>
<td>(i, x, p, z)</td>
<td>Selection intensity, truncation point, selected proportion, ordinate of standard normal distribution</td>
</tr>
<tr>
<td>(\Delta A_m, \Delta A_v, r_{A_mA_v})</td>
<td>Response in (A_m) and (A_v), accuracy of (\hat{A}_v)</td>
</tr>
<tr>
<td>(h^2_m, h^2_v, GCV_E)</td>
<td>Heritability of mean and environmental variance, evolvability of environmental variance</td>
</tr>
<tr>
<td>(\sigma^2_{E,exp}, A_{v,exp})</td>
<td>Environmental variance, breeding value for environmental variance and genetic variance in environmental variance for exponential genetic model</td>
</tr>
</tbody>
</table>

The genetic model in Equation 1 does not allow for random environmental effects on the magnitude of the environmental variance, because without repeated measurements on each individual these can not be separated from the usual random environmental effects. With repeated measurements on each individual, these environmental effects on environmental variance become equivalent to permanent environmental effects (e.g. SanCristobal-Gaudy et al., 1998; Sorensen and Waagepetersen, 2003).

To predict the breeding values \(\hat{A}_m\) and \(\hat{A}_v\) and selection responses \(\Delta A_m\) and \(\Delta A_v\), multiple regression was used. Selection index theory is essentially an application of multiple
Responses in mean and variance

regression (Hazel, 1943). Multiple regression gives the best linear prediction (BLP), which is equal to best linear unbiased prediction (BLUP) when fixed effects are known without error (Henderson, 1984). When variables are multivariate normally distributed, regressions are linear and homoscedastic (Lynch and Walsh, 1998). Although the distribution of $P$ slightly deviates from normality with genetic heterogeneity of environmental variance ($\sigma_{A_e}^2 > 0$), $P$, $A_m$ and $A_v$ follow an approximately multivariate normal distribution for values of $\sigma_{A_e}^2$ observed in the literature (e.g. SanCristobal-Gaudy et al., 2001; Sorensen and Waagepetersen, 2003; Ros et al., 2004; Rowe et al., 2006), justifying the use of multiple regression.

**Multiple regression with selection on a single phenotype**

**Monte Carlo simulation.** Monte Carlo simulation was used to investigate the relationships between $A_m$ and $A_v$ with $P$, with the objective to decide which order of fit would be required for accurate prediction, and then to evaluate the fit of predictions based on multiple regressions. Fifty replicates with one phenotypic observation on each of 500,000 unrelated animals in each replicate were generated according to the genetic model in Equation 1, assuming $\mu = 0$. The breeding values $A_m$ and $A_v$ and the environmental effect $\chi$ were randomly drawn from $N(0,1)$ and scaled by their corresponding standard deviations. When the genetic correlation between $A_m$ and $A_v$ was nonzero, $A_v$ was sampled given the expected value based on $A_m$ with variance $(1 - r_A)^2 \sigma_{A_e}^2$. Expected breeding values were calculated as the mean $A_m$ and $A_v$ within successive intervals of 0.01 units of $P$ ($\sigma_{P}^2 = 1$) and averaged over replicates. Expected selection responses to directional mass selection were calculated as the mean $A_m$ and $A_v$ of all selected animals having $P \geq x$ and averaged over replicates, where $x$ is the truncation point. The selected proportion was assumed to be the same in both sexes.

**Breeding value estimation.** Figures 1A and 1B present, respectively, the expectation of $A_m$ given $P$ and the expectation of $A_v$ given $P^2$ when $r_A = 0$, obtained by simulation. These show that the relationship between $A_m$ and $P$ is almost linear and that the relationship between $A_v$ and $P^2$ is also almost linear (quadratic in $P$). Therefore, $P - \mu$ roughly predicts $A_m$ and regression on $\left[ P - \mu \right]^2 - E\left[ P - \mu \right]^3$ roughly predicts $A_v$. As a consequence of genetic heterogeneity of environmental variance, the distribution of $P$ is slightly leptokurtic and is slightly skewed when $r_A \neq 0$. By fitting curves to the simulation results, it was found that regression on $\left[ P - \mu \right]^3 - E\left[ P - \mu \right]^4$ explained most of the residual non-linearity and skewness when $r_A \neq 0$. Moments of $P$ of higher order did not improve the fit and were therefore not considered in the rest of this study.
Based on this curve fitting, breeding values were predicted using multiple regression on the first through third order of $P$:

$$\hat{a} = B'x$$  \hfill (2)

where $a = \begin{bmatrix} A_m \\ A_v \end{bmatrix}$, $x = \begin{bmatrix} P - \mu \\ \frac{P - \mu}{P^2 - \sigma_P^2} \end{bmatrix}$, $B = P^{-1}G$, $P = \text{cov}(x,x)$, and $G = \text{cov}(x,a)$.

Elements of $P$ and $G$ were derived using the higher-order moments of the normal distribution (e.g. Stuart and Ord, 1994) and standard variance-covariance rules (see Appendix 1). Elements in these matrices were verified with Monte Carlo simulation.

**Figure 1.** Expected $A_m$ (Panel A) and $A_v$ (B) as a function of respectively $P$ and $P^2$ respectively ($\sigma_{Am}^2 = 0.3$; $\sigma_{Av}^2 = 0.05$; $r_A = 0$; $\sigma_E^2 = 0.7$; $\sigma_P^2 = \sigma_{Am}^2 + \sigma_E^2 = 1.0$).
Evaluation of predictions. Predictions of Equation 2 were close to the expectations obtained from Monte Carlo simulation when \( r_A = 0 \), as could be expected from the almost linear relationships shown in Figures 1A and 1B (\( R^2 > 0.98 \)). For \( r_A = 0.5 \), Figure 2A shows that \( A_m \) is approximately linear in \( P \), with a slope close to \( h_m^2 = \frac{\sigma_{A_m}^2}{\sigma_{A_m}^2 + \sigma_E^2} = 0.3 \), for \( P \) within two standard deviations (SD) of its mean, but becomes curvilinear for extreme \( P \). The predicted \( A_m \) using the full model with multiple regressions on \( P \), \( P^2 \) and \( P^3 \) fitted well to the expectations obtained from Monte Carlo simulation (\( R^2 > 0.99 \)) and, in contrast to multiple regressions on only \( P \) and \( P^2 \), also explained the nonlinearity in the extremes.

Figure 2B shows that the relationship between \( A_v \) and \( P \) is highly curvilinear for \( r_A = 0.5 \), with higher \( A_v \) for more extreme \( P \). As for \( \hat{A}_m \), the predicted \( A_v \) using the full model with multiple regressions on \( P \), \( P^2 \) and \( P^3 \) fitted well to the expectation from Monte Carlo simulation (\( R^2 > 0.99 \)). The use of only \( P \) and \( P^2 \) was adequate only within 2 SD of the mean, but was biased for extreme \( P \).

**Figure 2.** Expected (MC) and predicted breeding values \( A_m \) (Panel A) and \( A_v \) (B) based on a single phenotype as a function of phenotype using the full model with multiple regression on \( P \), \( P^2 \) and \( P^3 \) (MR3) or the reduced model with multiple regression on \( P \) and \( P^2 \) (MR2) (\( \sigma_{A_m}^2 = 0.3 \); \( \sigma_{A_v}^2 = 0.05 \); \( r_A = 0.5 \); \( \sigma_E^2 = 0.7 \); \( \sigma_P^2 = \sigma_{A_m}^2 + \sigma_E^2 = 1.0 \)).
Response to mass selection. Response to selection ($\Delta G$) is predicted as $\Delta G = bS$, where $b$ is the regression coefficient of the breeding value on the selection criterion, and $S$ is the selection differential in units of the selection criterion (e.g. phenotype) (Falconer and Mackay, 1996). With homogenous environmental variance and directional mass selection, $b = h^2$ and $S = i\sigma_p$, where $i$ is the selection intensity, and $\Delta G = ih^2\sigma_p$, the breeders’ equation (Falconer and Mackay, 1996; Lynch and Walsh, 1998). With genetic heterogeneity of environmental variance, directional mass selection leads to responses in mean and variance (Hill and Zhang, 2004). To predict this, Equation 2 can be rewritten as $\Delta a = B'\Delta x$ giving:

$$
\begin{bmatrix}
\Delta A_m \\
\Delta A_v
\end{bmatrix} = B' \begin{bmatrix}
\bar{P}_s \\
\bar{P}_s^2 - \sigma_p^2 \\
\bar{P}_s^3 - 3\text{cov}_{\lambda m}
\end{bmatrix}_{\mu=0}
$$

(3)

where $\bar{P}_s$, $\bar{P}_s^2$, and $\bar{P}_s^3$ are the respective means for the selected animals.

Directional selection. With directional selection by truncation, $\bar{P}_s = i\sigma_p$, where $i = z / p$ for normally distributed observations, $z$ is the height of the standardized normal at the truncation point $x$ and $p$ is the selected proportion (Falconer and Mackay, 1996; Lynch and Walsh, 1998). $\bar{P}_s^2$ and $\bar{P}_s^3$ were calculated by integration assuming that $P$ is normally distributed, which is approximately the case for observed values of $\sigma_{\lambda m}^2$ in the literature:

$$
\bar{P}_s^2 = (ix + 1)\sigma_p^2
$$

(4a)

$$
\bar{P}_s^3 = (ix^2 + 2i)\sigma_p^3
$$

(4b)

The predicted response to directional mass selection is thus:

$$
\begin{bmatrix}
\Delta A_m \\
\Delta A_v
\end{bmatrix} = B' \begin{bmatrix}
i\sigma_p \\
ix\sigma_p^2 \\
(ix^2 + 2i)\sigma_p^3 - 3\text{cov}_{\lambda m}
\end{bmatrix}
$$

(5)

The term $\bar{P}_s^2 - \sigma_p^2$ is similar to the term $\frac{1}{2}ix\sigma_p^2$ derived by Hill and Zhang (2004), who calculated the probability of selection by using a Taylor series approximation, where the factor $\frac{1}{2}$ appears here in the $B$-matrix, assuming that $r_A = 0$ and $\sigma_{\lambda m}^2$ is small. Equation 5
can be rewritten using the regression coefficients in $B$ and ignoring the terms involving $P^3$, which were not included by Hill and Zhang (2004):

$$\Delta A_m = \frac{\sigma_{\Delta_m}^2 (2\sigma_p^2 + 3\sigma_{h_p}^2) - 3\text{cov}_{\Delta_m, \Delta_m}^2 i\sigma_p + (\sigma_p^2 - 3\sigma_{h_p}^2)\text{cov}_{\Delta_m, \Delta_m}^2 i\sigma_p^2}{D}$$

$$\Delta A_v = \frac{2\sigma_p^4 \text{cov}_{\Delta_m, \Delta_m}^2 i\sigma_p + \sigma_p^2 \sigma_{h_p}^2 - 3\text{cov}_{\Delta_m, \Delta_m}^2 i\sigma_p^2}{D}$$

where $D = \text{det}(P) = \sigma_p^2 (2\sigma_p^2 + 3\sigma_{h_p}^2) - 9\text{cov}_{\Delta_m, \Delta_m}^2$. When $\sigma_{h_p}^2$ and $r_A$ are close to zero, Equations 6 and 7 approach $\Delta A_m = (\sigma_{\Delta_m}^2 / \sigma_p^2) i\sigma_p$ and $\Delta A_v = (\sigma_{h_p}^2 / 2\sigma_p^2) i\sigma_p^2$, which are Equations 10 and 11 of Hill and Zhang (2004). Differences arise when $r_A$ is substantially different from zero, as the covariance between $P$ and $P^2$ was ignored by Hill and Zhang.

Stabilizing and disruptive selection. Stabilizing and disruptive selection can be considered as selecting the animals with low or high $P^2$, respectively (Falconer and Mackay, 1996). Assuming that selection is by truncation, selection differentials $\overline{P_s^2}$ for $P^2$ can be obtained from Equation 4a and selection differentials for $P$ and $P^3$ are zero for these types of selection when $P$ is normally distributed. With stabilizing selection by truncation, animals only in the middle of the distribution are selected, giving a selection differential:

$$\overline{P_s^2} = \left[1 - (2p^* i^* x^*/(1 - 2p^*))\right] \sigma_p^2$$

(8a)

where $i^*$ and $x^*$ are respectively the selection intensity and truncation point corresponding to $p^* = \frac{1}{2}(1 - p)$, the proportion of animals culled on one side of the distribution. With disruptive selection by truncation, the extreme animals in both tails of the distribution are selected, giving a selection differential:

$$\overline{P_s^2} = (i^* x^* + 1) \sigma_p^2$$

(8b)

where $p^* = \frac{1}{2} p$, the proportion of animals selected on one side of the distribution. The standardized selection differentials $\overline{P_s^2} - \sigma_p^2$ for directional, stabilizing and disruptive selection are in Table 2.
Table 2. Standardized selection differentials of $P_i^2$ for directional, stabilizing and disruptive selection by truncation on a normal distribution corrected for the expectation of $P^2$ (= 1) for different selected proportions ($p$).

<table>
<thead>
<tr>
<th>Type of selection</th>
<th>Selected proportion ($p$)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>0.80</td>
</tr>
<tr>
<td>Directional</td>
<td>-0.29</td>
</tr>
<tr>
<td>Stabilizing</td>
<td>-0.56</td>
</tr>
<tr>
<td>Disruptive</td>
<td>0.24</td>
</tr>
</tbody>
</table>

Evaluation of predictions with directional mass selection. The predictions of Equation 5 (MR3), Equations 6 and 7 (MR2) and those of the Hill-Zhang model (HZ) (Hill and Zhang, 2004) are compared in Table 3 with the observed responses obtained from Monte Carlo simulation (MC), for different values of $r_d$ and selected proportions. Multiple regressions on $P$, $P^2$ and $P^3$ (MR3) predicted the responses well, with prediction errors less than 5% when the selected proportion was at least 5% (prediction error relative to $\Delta A_m$ with $\sigma^2_{A_m} = 0.05$, $r_d = 0$, $p = 0.05$). Prediction errors were on average smaller for MR3 than MR2, although occasionally larger. They were also on average slightly smaller for MR2 than for the Hill-Zhang model, especially with $r_d = 0.5$, because in the latter the covariance between $P$ and $P^2$ was not accounted for in calculation of the regression coefficients. Prediction errors using multiple regressions (MR) were mainly due to poor prediction of selection differentials because of deviations from normality, and thus increased with decreasing selected proportion as the tails of the distribution were most affected (results not shown). When $\sigma^2_{A_m}$ increased to 0.10 or 0.15, which reflect the upper range of estimates in the literature (e.g. Ros et al., 2004; SanCristobal-Gaudy et al., 2001), prediction errors increased up to 10-20% (prediction error relative to $\Delta A_m$ with $\sigma^2_{A_m} = 0.05$, $r_d = 0$, $p = 0.05$), especially with selected proportion of 1% (results not shown). Increasing $\sigma^2_{A_v}$ increases deviations from normality in $P$, but it seems that the multiple regression framework is robust against these relatively small deviations from normality, except when the selected proportion is very small. It can be concluded that MR3 is the preferred method for predicting responses in $A_m$ and $A_v$ with directional mass selection, having prediction errors less than 5% when at least 5% are selected.
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**Table 3.** Response to directional mass selection in $A_m$ ($\Delta A_m$) and $A_v$ ($\Delta A_v$) for different values $r_A$ and selected proportions comparing predictions\(^1\) (as prediction errors (predicted – observed)) with observed responses obtained from Monte Carlo simulation (MC)\(^2\).

<table>
<thead>
<tr>
<th>$r_A$</th>
<th>Method(^1)</th>
<th>$\Delta A_m$ Selected proportion</th>
<th>$\Delta A_v$ Selected proportion</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>20%</td>
<td>5%</td>
</tr>
<tr>
<td>-0.5</td>
<td>MC</td>
<td>0.410</td>
<td>0.547</td>
</tr>
<tr>
<td></td>
<td>MR3</td>
<td>0.004</td>
<td>0.025</td>
</tr>
<tr>
<td></td>
<td>MR2</td>
<td>0.006</td>
<td>0.061</td>
</tr>
<tr>
<td></td>
<td>HZ</td>
<td>-0.026</td>
<td>-0.032</td>
</tr>
<tr>
<td>0</td>
<td>MC</td>
<td>0.422</td>
<td>0.597</td>
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<tr>
<td></td>
<td>MR3</td>
<td>0.002</td>
<td>0.002</td>
</tr>
<tr>
<td></td>
<td>MR2</td>
<td>-0.002</td>
<td>0.021</td>
</tr>
<tr>
<td></td>
<td>HZ</td>
<td>-0.002</td>
<td>0.021</td>
</tr>
<tr>
<td>0.5</td>
<td>MC</td>
<td>0.434</td>
<td>0.638</td>
</tr>
<tr>
<td></td>
<td>MR3</td>
<td>-0.002</td>
<td>-0.021</td>
</tr>
<tr>
<td></td>
<td>MR2</td>
<td>-0.011</td>
<td>-0.010</td>
</tr>
<tr>
<td></td>
<td>HZ</td>
<td>0.022</td>
<td>0.085</td>
</tr>
</tbody>
</table>

\(^1\) MR3 = multiple regressions on $P$, $P^2$ and $P^3$ (see Equation 5); MR2 = multiple regressions on $P$ and $P^2$ (see Equation 6 and 7); HZ = prediction based on Hill and Zhang (2004).

\(^2\) $\sigma_{A_m}^2 = 0.3$; $\sigma_{A_v}^2 = 0.05$; $\sigma_E^2 = 0.7$; $\sigma_p^2 = \sigma_{A_m}^2 + \sigma_E^2 = 1.0$.

**Multiple regression with selection based on a group of relatives**

**Monte Carlo simulation.** In animal breeding sires are often selected on performance of their half-sib progeny. Monte Carlo simulation was used to investigate relationships between the $A_m$ and $A_v$ of the sires and statistics on phenotypes of their progeny, and then to evaluate the fit of predictions based on multiple regressions. Fifty replicates were generated of 500,000 unrelated sires each with 10 or 100 half-sib progeny or of 50,000 unrelated sires each with 1000 or 10,000 half-sib progeny. Data were simulated according to the genetic model in Equation 1. The breeding values of sires ($A_{s,m}$ and $A_{s,v}$) and unrelated random mated dams ($A_{d,m}$ and $A_{d,v}$) were randomly sampled with variance $\sigma_{A_m}^2$ or $\sigma_{A_v}^2$, respectively. For each progeny, the Mendelian sampling terms $MS_m$ and $MS_v$ were randomly sampled with variance $\frac{1}{2}\sigma_{A_m}^2$ and $\frac{1}{2}\sigma_{A_v}^2$, respectively, to give breeding values for each progeny ($A_{p,m}$ and $A_{p,v}$):
\[ A_p = \frac{1}{2} A_m + \frac{1}{2} A_v + MS \]

When the genetic correlation between \( A_m \) and \( A_v \) was nonzero, breeding values \( A_v \) and Mendelian sampling terms \( MS \) were sampled as expected based on \( A_m \) or \( MS \), and with variance \((1 - r_{av})^2 \sigma_{A_v}^2 \) or \( \frac{1}{2}(1 - r_{av})^2 \sigma_{A_m}^2 \), respectively. For each progeny, the environmental effect \( X \) was randomly sampled and scaled with its standard deviation.

Expected breeding values of sires were calculated as the mean \( A_m \) and \( A_v \) within successive intervals of 0.01 SD units of progeny mean \( \overline{P} \) or log-transformed within-family variance (\( \ln(varW) \)) and averaged over replicates. Expected genetic selection differentials of directional selection on \( \overline{P} \) were calculated as the mean \( A_m \) and \( A_v \) of all selected sires with \( (\overline{P}/\sigma_p) \geq x \) and averaged over replicates.

**Breeding value estimation.** When there is an observation on only a single phenotype, there is no independent information available on the mean and variance of the genotype, although \( P \) and \( P^2 \) provide point estimates. When phenotypes of a group of relatives each having the same relationship to an individual are available (e.g. progeny), statistics such as \( \overline{P}, (\overline{P})^2 \) and \( varW \) can be used to predict its \( A_m \) and \( A_v \). Here \( \overline{P} \) is the mean phenotype and \( \overline{P}^2 \) is the mean \( P^2 \) of the relatives, \( varW = [n/n-1]([P^2 - (\overline{P})^2]) \) is the within-family variance and \( n \) is the number of relatives within the group. With large \( n \), \( varW \) becomes the main predictor of \( A_v \), but otherwise \((\overline{P})^2\) contains additional information because animals with a high \( A_v \) have a higher probability of having a very high or low \( \overline{P} \). This is similar to directional mass selection and the term \((\overline{P})^2\) therefore plays an equivalent role to \( P^2 \). Although the Monte Carlo simulation was based on sires with half-sib progeny, the prediction of breeding values generalizes to any group of relatives with the same relationship. The multiple regression equation can be represented as:

\[
\begin{bmatrix}
A_m \\
A_v
\end{bmatrix}
= B' \begin{bmatrix}
\overline{P} - E(\overline{P}) \\
varW - E(varW)
\end{bmatrix}
= (P^{-1}G)' \begin{bmatrix}
\overline{P} \\
varW - E(varW)
\end{bmatrix}
\]

\[
\begin{bmatrix}
\sigma_p^2 + a_w(n-1)\sigma_{A_m}^2 \\
\sigma_p^2 - a_w^2\sigma_{A_m}^2
\end{bmatrix}
\]

\( (9) \)

where \( a_w \) is the additive genetic relationship between relatives within the family,
Responses in mean and variance

\[
P = \begin{bmatrix}
\left(\sigma_p^2 + a_w (n-1)\sigma_{hm}^2\right)/n & \left[3 + 3a_w (n-1)\text{cov}_{\text{hmv}}\right]/n^2 & \left[3 + a_w (n-3)\text{cov}_{\text{hmv}}\right]/n \\
2\left[\left(\sigma_p^2 + a_w (n-1)\sigma_{hm}^2\right)/n\right]^2 & \left[3 + a_w (n-3)\sigma_{hv}^2\right]/n^2 & \\
\left[3 + 3a_w (n-1)\sigma_{hv}^2\right]/n^3 & & \\
\end{bmatrix},
\]

\[
\text{symmetric}
\]

\[
G = \begin{bmatrix}
a_j \sigma_{hm}^2 & a_j \text{cov}_{\text{hmv}} & a_j \sigma_{hv}^2/n \\
a_j \text{cov}_{\text{hmv}}/n & a_j \sigma_{hv}^2/n & \\
a_j \text{cov}_{\text{hmv}} & a_j \sigma_{hv}^2 \\
\end{bmatrix},
\]

and \( a_j \) is the relationship of relatives to individual \( j \). Elements in the \( P \)- and \( G \)-matrices, derived in Appendix 1, were verified with Monte Carlo simulation for the case of sires with half-sib progeny.

Log-transformation of \( \text{var}W \). In multiple regression linearity is assumed, and is typically satisfied if the explanatory variables are normally distributed. Because variances of normally distributed variates are \( \chi^2 \)-distributed, the distribution of \( \text{var}W \) is not normal. As the number of relatives increases, \( \text{var}W \) approaches a normal distribution, but the convergence is slow (Stuart and Ord, 1994). The relationship between \( A_v \) and \( \text{var}W \) is therefore nonlinear if there are a finite number of relatives (see Figure 3B), and also the sampling variance of \( \text{var}W \) increases with its mean. A logarithmic transformation of \( \text{var}W \) seems a logical choice to reduce both the non-normality of \( \text{var}W \) and the positive relationship between the mean and its sampling variance. When using \( \ln(\text{var}W) \) instead of \( \text{var}W \), the elements in the \( P \)- and \( G \)-matrices involving \( \text{var}W \) were transformed using a first-order Taylor series approximation (Lynch and Walsh, 1998). The matrices \( P_{\text{ln}} \) and \( G_{\text{ln}} \) involving \( \ln(\text{var}W) \) were calculated, respectively, as \( P_{\text{ln}} = LPL \) and \( G_{\text{ln}} = LG \), where \( L = \text{diag}(1, 1, 1/\text{var}W) \) with \( 1/\text{var}W \) based on a first-order Taylor series approximation. The quantity \( E(\ln(\text{var}W)) \) was calculated using a second-order Taylor series approximation.
(Lynch and Walsh, 1998): \( E(\ln(\text{var}W)) = \ln(\text{var}W) - \frac{\sigma^2_{\text{var}W}}{2\text{var}W^2} \), replacing \( E(\text{var}W) \) in Equation 9.

\[ \begin{align*}
\text{Figure 3.} & \text{ Expected (MC) and predicted } A_m \text{ as a function of the standardized mean phenotype of half-sib progeny (Panel A) and expected and predicted } A_v \text{ as a function of } \text{var}W \text{ (B) using either } \text{var}W \text{ (MR linear) or } \ln(\text{var}W) \text{ (MR log) in multiple regression (} \sigma^2_{A_m} = 0.3; \ \sigma^2_v = 0.05; \ r_d = 0; \ \sigma^2_E = 0.7; \ \sigma^2_p = \sigma^2_{A_m} + \sigma^2_e = 1.0; \ \text{number of half-sib progeny/sire} = 100).} \\
& \text{Evaluation of predictions. Predictions of Equation 9, which holds for any group of relatives with the same relationship, were evaluated for the case of sires with half-sib progeny. The expected and predicted values of } A_m \text{ are shown as a function of the standardized } \overline{P} \text{ of 100 half-sib progeny in Figure 3A for } r_d = 0. \ A_m \text{ is linear in standardized } \overline{P} \text{ with a slope of } \frac{\frac{1}{2} \sigma^2_{A_m}}{\sqrt{\left(\sigma^2_p + \frac{1}{4} (n-1) \sigma^2_e\right)/n}} = 0.517. \ The \ predicted \ A_m \ fitted \ well \ the \ expectation \ from \ Monte \ Carlo \ simulation \ (R^2 > 0.99) \ and \ the \ predictions \ using \ \text{var}W \ \text{or } \ln(\text{var}W) \ \text{did not differ if } r_d = 0. \\
& \text{Figure 3B shows that the relationship between } A_v \text{ and } \text{var}W \text{ is curvilinear for the case of 100 half-sib progeny when } r_d = 0. \ The \ predicted \ A_v \ using \ untransformed \ \text{var}W \ (\text{MR linear}) \ \text{overestimated} \ A_v \ \text{for extreme values of } \text{var}W, \ \text{whereas predicted} \ A_v \ \text{using log-transformed}
\end{align*} \]
varW (MR log) was curvilinear in varW and fitted well the expectation from Monte Carlo simulation ($R^2 > 0.99$).

Table 4. The expectation of $A_v$ and bias in $\hat{A}_v$ at $\ln(\text{varW}) \pm \chi \sigma_{\ln(\text{varW})}$ using either varW or $\ln(\text{varW})$ in multiple regression for different values of $\sigma^2_{A_v}$ and number of half-sib progeny per sire\(^1\).

<table>
<thead>
<tr>
<th>$\sigma^2_{A_v}$</th>
<th>Number of progeny</th>
<th>$\chi$ ($= \ln(\text{varW}) \pm \chi \sigma_{\ln(\text{varW})}$)</th>
<th>E($A_v$)</th>
<th>Bias in $\hat{A}_v$ ($= A_v - \hat{A}_v$)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>$\text{varW}$</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>0.01</td>
<td>10</td>
<td>-0.016</td>
<td>0.032</td>
<td>-0.001</td>
</tr>
<tr>
<td></td>
<td>100</td>
<td>-0.066</td>
<td>0.076</td>
<td>-0.004</td>
</tr>
<tr>
<td></td>
<td>1000</td>
<td>-0.155</td>
<td>0.155</td>
<td>-0.009</td>
</tr>
<tr>
<td></td>
<td>10,000</td>
<td>-0.187</td>
<td>0.198</td>
<td>-0.001</td>
</tr>
<tr>
<td>0.05</td>
<td>10</td>
<td>-0.084</td>
<td>0.133</td>
<td>-0.011</td>
</tr>
<tr>
<td></td>
<td>100</td>
<td>-0.286</td>
<td>0.283</td>
<td>-0.042</td>
</tr>
<tr>
<td></td>
<td>1000</td>
<td>-0.392</td>
<td>0.436</td>
<td>-0.014</td>
</tr>
<tr>
<td></td>
<td>10,000</td>
<td>-0.407</td>
<td>0.484</td>
<td>-0.002</td>
</tr>
<tr>
<td>0.10</td>
<td>10</td>
<td>-0.173</td>
<td>0.234</td>
<td>-0.039</td>
</tr>
<tr>
<td></td>
<td>100</td>
<td>-0.467</td>
<td>0.475</td>
<td>-0.072</td>
</tr>
<tr>
<td></td>
<td>1000</td>
<td>-0.556</td>
<td>0.658</td>
<td>-0.025</td>
</tr>
<tr>
<td></td>
<td>10,000</td>
<td>-0.569</td>
<td>0.710</td>
<td>-0.017</td>
</tr>
</tbody>
</table>

\(^1\) $\sigma^2_{A_m} = 0.3$; $r_A = 0$; $\sigma^2_{E} = 0.7$; $\sigma^2_{P} = \sigma^2_{A_m} + \sigma^2_{E} = 1.0$.

As the bias in $\hat{A}_v$ was largest with extreme values of varW, the bias in $\hat{A}_v$ at 2 SD from the mean $\ln(\text{varW})$ predicted by multiple regression using either varW or $\ln(\text{varW})$ was computed for different values of $\sigma^2_{A_v}$ and number of progeny per sire (Table 4). Multiple regression on varW was seen to overestimate, but on $\ln(\text{varW})$ to underestimate $\hat{A}_v$. The bias using $\ln(\text{varW})$ was negligible when the number of progeny was 100, but increased when the number of progeny was small (10) or large (10,000). The bias with varW was negligible with 10,000 progeny, as could be expected from the slow convergence of a $\chi^2$-distribution to a normal distribution, and was small with a few progeny. Note that a higher degree of symmetry between the expected $A_v$ at -2 and 2 SD of the mean $\ln(\text{varW})$
corresponded with a smaller bias in $\hat{A}$, with $\ln(\text{var}W)$. The value of log-transformation of $\text{var}W$ thus depends on the number of progeny per sire.

**Response to directional selection on family mean.** With the common procedure in livestock breeding to directionally select animals by truncation on the mean $(\overline{P})$ of relatives, e.g. progeny, information on the within-family variance $(\text{var}W)$ is ignored. As for mass selection, if there is genetic heterogeneity of environmental variance, animals with a higher $A_v$ would have a higher probability of selection when the selected proportion is less than 50%, diminishing as the number of relatives increases. If $A_m$ and $A_v$ are uncorrelated, the response in $A_v$ is proportional to the selection differential $(\overline{P})^2$:

$$\Delta A_v = b[(\overline{P})_s^2 - E(\overline{P})^2] = b \times \text{var} \overline{P}$$

(10)

where

$$b = \frac{\text{cov}(A_{v,j}, (\overline{P})^2)}{\text{var}(\overline{P})^2} = \frac{a_v n^2 \sigma_{A_v}^2}{2n \sigma_p^4 + 4a_v n (n-1) \sigma_p^2 \sigma_{A_m}^2 + 2a_w^2 n(n-1)^2 \sigma_{A_m}^4 + (3 + 3a_w (n-1)) \sigma_{A_m}^2}$$

$$\lim_{n \to \infty} b = \frac{a_v \sigma_{A_v}^2}{2a_w^2 n \sigma_{A_m}^2} = 0$$

(11)

There is therefore no selection pressure on $A_v$ with an infinite number of relatives (Equation 11), as suggested by Hill and Zhang (2004) using a different argument.

Response in $A_m$ and $A_v$ with selection on $\overline{P}$ can be generalized as:

$$\begin{bmatrix} \Delta A_m \\ \Delta A_v \end{bmatrix} = B^r \begin{bmatrix} \overline{P}_s - \mu \\ (\overline{P}_s)^2 - \text{var} \overline{P} \end{bmatrix}_{\mu=0} = B^r \begin{bmatrix} i \sigma_{\overline{P}} \\ i \sigma_{\overline{P}}^2 \end{bmatrix}$$

(12)

To compute (12), $\text{var}W$ was not included in the information vector $x$ because selection is solely on $\overline{P}$. For infinitely many relatives, Equation 12 can be rewritten as

$$\Delta A_m = a_j i \sigma_{\overline{P}} \sqrt{a_w}, \text{ which is the corresponding standard breeders’ equation, and}$$

$$\Delta A_v = a_j i r_a \sigma_{A_v} \sqrt{a_w}, \text{ showing that response in } A_v \text{ then becomes solely a correlated response to selection on } \overline{P}.$$

**Evaluation of predictions.** Table 5 shows predicted responses (Equation 12) in $A_m$ and $A_v$ when selecting on the mean of half-sib progeny ($\overline{P}$) in comparison to observed responses from Monte Carlo simulation. In general, these agreed well, although prediction errors were
slightly higher when \( r_d \neq 0 \), especially with high selection intensity. As expected, the response in \( A_m \) increased with more progeny (higher accuracy of selection) and lower selected proportion (higher selection intensity). The response in \( A_v \) was small, becoming negligible with 100 progeny/sire when \( r_d = 0 \), but was, however, substantial when \( r_d \neq 0 \), basically as a correlated response to selection on the mean. Response in \( A_v \) increased nonlinearly with increasing selection intensity, similar to directional mass selection, but to a lesser extent. In conclusion, responses in \( A_m \) and \( A_v \) to selection on \( \bar{P} \) can be predicted accurately using multiple regression.

**Table 5.** Response to selection on mean of half-sib progeny (\( \bar{P} \)) in \( A_m \) (\( \Delta A_m \)) and \( A_v \) (\( \Delta A_v \)) for different values of \( r_d \), different numbers of progeny/sire and different selected proportions comparing predictions (MR) (as prediction errors (predicted – observed)) with observed responses obtained from Monte Carlo simulation (MC)\(^1\).

<table>
<thead>
<tr>
<th>( r_d )</th>
<th>Number of progeny</th>
<th>Method</th>
<th>( \Delta A_m ) Selected proportion</th>
<th>( \Delta A_v ) Selected proportion</th>
</tr>
</thead>
<tbody>
<tr>
<td>(-0.5)</td>
<td>10</td>
<td>MC</td>
<td>0.517 0.759 0.976</td>
<td>-0.099 -0.134 -0.160</td>
</tr>
<tr>
<td></td>
<td></td>
<td>MR</td>
<td>0.005 0.021 0.044</td>
<td>-0.001 -0.005 -0.012</td>
</tr>
<tr>
<td>100</td>
<td></td>
<td>MC</td>
<td>0.724 1.071 1.386</td>
<td>-0.146 -0.215 -0.275</td>
</tr>
<tr>
<td></td>
<td></td>
<td>MR</td>
<td>0.003 0.006 0.011</td>
<td>-0.001 -0.001 -0.003</td>
</tr>
<tr>
<td>0</td>
<td>10</td>
<td>MC</td>
<td>0.513 0.752 0.968</td>
<td>0.009 0.025 0.045</td>
</tr>
<tr>
<td></td>
<td></td>
<td>MR</td>
<td>0.000 0.004 0.009</td>
<td>0.000 0.000 0.001</td>
</tr>
<tr>
<td>100</td>
<td></td>
<td>MC</td>
<td>0.723 1.068 1.379</td>
<td>0.002 0.005 0.009</td>
</tr>
<tr>
<td></td>
<td></td>
<td>MR</td>
<td>0.000 -0.002 -0.002</td>
<td>0.000 0.000 0.000</td>
</tr>
<tr>
<td>0.5</td>
<td>10</td>
<td>MC</td>
<td>0.512 0.749 0.963</td>
<td>0.111 0.171 0.227</td>
</tr>
<tr>
<td></td>
<td></td>
<td>MR</td>
<td>-0.006 -0.015 -0.026</td>
<td>-0.002 -0.003 -0.003</td>
</tr>
<tr>
<td>100</td>
<td></td>
<td>MC</td>
<td>0.721 1.061 1.368</td>
<td>0.149 0.220 0.286</td>
</tr>
<tr>
<td></td>
<td></td>
<td>MR</td>
<td>-0.002 -0.005 -0.010</td>
<td>0.000 -0.001 -0.002</td>
</tr>
</tbody>
</table>

\(^{1}\) \( \sigma_{A_m}^2 = 0.3; \sigma_{A_v}^2 = 0.05; \sigma_E^2 = 0.7; \sigma_P^2 = \sigma_{A_m}^2 + \sigma_E^2 = 1.0 \).
Defining a measure of heritability for environmental variance at phenotypic level

Heritability \( h^2 = \frac{\sigma_A^2}{\sigma_P^2} \) is a central parameter in quantitative genetics (Falconer and Mackay, 1996; Lynch and Walsh, 1998). For standardization of results of analysis of genetic heterogeneity of environmental heterogeneity in field data and for making comparisons to “conventional” traits easier, it would be helpful to define a measure of heritability \( h^2_e \) for environmental variance at phenotypic level. Heritability equals the regression coefficient of the breeding value \( A \) on the phenotype \( P \). Here we propose a definition of \( h^2_e \), which equals the genetic variance in environmental variance as a proportion of the variance of \( P^2 \). This definition is equal to the regression of \( A_v \) on \( P^2 \) where \( b = \text{cov}(A_v, P^2)/\text{var}(P^2) = \sigma_{A_v}^2/\text{var}(P^2) \) and \( \text{var}(P^2) = 2\sigma_p^4 + 3\sigma_{A_v}^2 \), and \( h^2_e \) is therefore:

\[
h^2_e = \frac{\sigma_{A_v}^2}{2\sigma_p^4 + 3\sigma_{A_v}^2}
\]  

(13)

Alternatively, \( h^2_e \) could be defined at the level of environmental variance, which equals one in Equation 1. Based on single phenotypic records, the environmental variance of a genotype is, however, not estimable. The measure of heritability in Equation 13 is directly related to single squared phenotypic records and as such is the natural analogy of the classical heritability of the mean \( h^2_m \), which can be used in prediction of response to mass selection when \( r_A = 0 \).

Under the assumption of \( \sigma_{A_m}^2 = 0 \) and making use of Equation 13, Equation 9 can be greatly simplified when selecting on information of a group of relatives, for example half-sib progeny. When \( \sigma_{A_m}^2 = 0 \), var\( W \) reduces to \( (n/n-1)\bar{P}^2 \) because \( E(\bar{P}) = 0 \), so the multiple regression for \( \hat{A}_v \) can be simplified by regressing solely on \( \bar{P}^2 \). The accuracy of \( \hat{A}_v \) can then be derived as:

\[
r_{A_{\text{hy},A_{\text{hy}}}} = \sqrt{\frac{\mathbf{g}_p \mathbf{g}_p \mathbf{A}_p}{\sigma_{A_p}}} = \frac{1}{\sigma_{A_p}} \sqrt{\frac{\frac{1}{n} n \sigma_{A_p}^2}{2\sigma_p^4 + 3\sigma_{A_v}^2 + \frac{1}{4(n-1)}\sigma_{A_v}^2}} \times \frac{1}{\sigma_{A_v}} = \sqrt{\frac{\frac{1}{4} n h^2_e}{1 + \frac{1}{4}(n-1) h^2_e}}
\]  

(14)

where \( \mathbf{b}_{A_v} \) and \( \mathbf{g}_{A_v} \) are columns of \( \mathbf{B} \) and \( \mathbf{G} \) corresponding to \( A_v \). The resulting expression is exactly the same as that for accuracy of \( A_m \) (Cameron, 1997), except that \( h^2 \) is replaced by \( h^2_e \). To investigate the effect of assuming \( \sigma_{A_m}^2 = 0 \), the accuracy of \( \hat{A}_v \) predicted with
Equation 14 was compared to that predicted using Equation 9 and Monte Carlo simulation when \( r_A = 0 \) (Table 6). In general, accuracies were slightly underestimated by Equation 14, increasingly so with greater \( \sigma^2_{\delta_m} \) (\( \sigma^2_p = 1 \)), whereas the ones of Equation 9 were close to those from simulation. It seems that \( h_v^2 \) can be used as a first approximation in standard prediction equations when \( r_A = 0 \), but predictions should be interpreted with caution.

Table 6. Realized (MC) and predicted accuracy of \( \hat{A}_v \) for different numbers of half-sib progeny per sire and \( \sigma^2_{\delta_m} \) using either the exact prediction (MR exact) or the approximate prediction (MR approx)\(^{1,2}\).

<table>
<thead>
<tr>
<th>( \sigma^2_{\delta_m} )</th>
<th>MC</th>
<th>MR exact</th>
<th>MR approx</th>
<th>MC</th>
<th>MR exact</th>
<th>MR approx</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.0</td>
<td>0.235</td>
<td>0.235</td>
<td>0.235</td>
<td>0.607</td>
<td>0.607</td>
<td>0.607</td>
</tr>
<tr>
<td>0.1</td>
<td>0.236</td>
<td>0.236</td>
<td>0.235</td>
<td>0.615</td>
<td>0.615</td>
<td>0.607</td>
</tr>
<tr>
<td>0.3</td>
<td>0.243</td>
<td>0.244</td>
<td>0.235</td>
<td>0.633</td>
<td>0.633</td>
<td>0.607</td>
</tr>
<tr>
<td>0.6</td>
<td>0.251</td>
<td>0.260</td>
<td>0.235</td>
<td>0.648</td>
<td>0.663</td>
<td>0.607</td>
</tr>
</tbody>
</table>

\(^{1}\) The exact prediction with multiple regression: \( r_{A_v, A_v} = \sqrt{b_{A_v} g_{A_v}} / \sigma_{A_v} \), where \( b_{A_v} \) and \( g_{A_v} \) are columns of \( B \) and \( G \); the approximate prediction (Equation 14):

\[
r_{A_v, A_v} = \sqrt{\frac{1}{n} h_v^2 / (1 + \frac{1}{n}(n-1) h_v^2)} ,
\]

where \( h_v^2 = \sigma^2_{A_v} / (2 \sigma^4_p + 3 \sigma^2_{A_v}) \) and with assumption \( \sigma^2_{\delta_m} = 0 \).

\(^{2}\) \( \sigma^2_{A_v} = 0.05 \); \( r_A = 0 \); \( \sigma^2_E = 1 - \sigma^2_{\delta_m} \), \( \sigma^2_p = \sigma^2_{\delta_m} + \sigma^2_E = 1.0 \).

**EXAMPLES OF CHANGING ENVIRONMENTAL VARIANCE BY SELECTION**

In the previous section, the focus was mainly on evaluating the goodness of fit of multiple regression predictions with Monte Carlo simulation, but the results also show the effects of selection on environmental variance. For example, the response in \( A_v \) with directional mass selection increased nonlinearly with increasing selection intensity (Table 3), and environmental variance increased unless \( r_A < 0 \). The response in \( A_v \) was, however, negligible with directional selection on a half-sib progeny mean when \( r_A = 0 \) (Table 5), but was substantial when \( r_A \neq 0 \), due to a correlated response.
We now use the formulae (Equation 2, 3 and 9) to assess the effects of selection strategies aimed at changing the environmental variance, taking values of $\sigma^2_{A_v}$ between 0.01 and 0.10. These correspond to a low $h^2_v$ but are large relative to $\sigma^2_E = 0.7$, indicating a genetic coefficient of variation between 14% and 45%, higher than for standard quantitative traits (Houle, 1992). As expected, the accuracy of $\hat{A}_v$ increased with $\sigma^2_{A_v}$ (Table 7). The accuracy was low when using information only on own phenotype or a small number of progeny, but increased with number of relatives, especially with half-sib progeny, and when $r_A \neq 0$. With 1000 half-sib progeny, the accuracy was higher than 0.90, unless $\sigma^2_{A_v} = 0.01$.

Table 7. Predicted accuracy of $\hat{A}_v$ based on a single phenotype or different numbers of full-sibs or half-sib progeny for different values of $\sigma^2_{A_v}$ and $r_A$.

<table>
<thead>
<tr>
<th>Information</th>
<th>Number of progeny</th>
<th>Predicted accuracy $\hat{A}_v$</th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>$r_A = 0$</td>
<td>$r_A = 0.5$</td>
<td>$r_A = 0$</td>
<td>$r_A = 0.5$</td>
<td>$r_A = 0$</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$\sigma^2_{A_v}$</td>
<td>0.01</td>
<td>0.05</td>
<td>0.10</td>
<td>0.01</td>
<td>0.05</td>
</tr>
<tr>
<td>Phenotype</td>
<td>-</td>
<td>0.070</td>
<td>0.152</td>
<td>0.209</td>
<td>0.279</td>
<td>0.299</td>
<td>0.319</td>
</tr>
<tr>
<td>Full-sibs</td>
<td>10</td>
<td>0.123</td>
<td>0.252</td>
<td>0.327</td>
<td>0.299</td>
<td>0.348</td>
<td>0.388</td>
</tr>
<tr>
<td></td>
<td>50</td>
<td>0.267</td>
<td>0.468</td>
<td>0.544</td>
<td>0.394</td>
<td>0.505</td>
<td>0.560</td>
</tr>
<tr>
<td></td>
<td>100</td>
<td>0.355</td>
<td>0.553</td>
<td>0.610</td>
<td>0.442</td>
<td>0.570</td>
<td>0.617</td>
</tr>
<tr>
<td>Half-sib progeny</td>
<td>10</td>
<td>0.115</td>
<td>0.244</td>
<td>0.325</td>
<td>0.346</td>
<td>0.386</td>
<td>0.424</td>
</tr>
<tr>
<td></td>
<td>50</td>
<td>0.257</td>
<td>0.499</td>
<td>0.618</td>
<td>0.490</td>
<td>0.597</td>
<td>0.671</td>
</tr>
<tr>
<td></td>
<td>100</td>
<td>0.353</td>
<td>0.633</td>
<td>0.745</td>
<td>0.545</td>
<td>0.693</td>
<td>0.772</td>
</tr>
<tr>
<td></td>
<td>1000</td>
<td>0.768</td>
<td>0.933</td>
<td>0.962</td>
<td>0.798</td>
<td>0.936</td>
<td>0.963</td>
</tr>
</tbody>
</table>

$^1$ $\sigma^2_{A_m} = 0.3; \sigma^2_E = 0.7; \sigma^2_P = \sigma^2_{A_m} + \sigma^2_E = 1.0$
Table 8. Predicted response in $A_v$ ($\Delta A_v$) for directional (up/down), stabilizing and disruptive selection based on phenotype and downward directional selection on $A_v$ based on 100 half-sib progeny for different values of $\sigma^2_{A_v}$ and selected proportions$^1$.

<table>
<thead>
<tr>
<th>Selection criterion</th>
<th>Selection type</th>
<th>Selected proportion</th>
<th>$\Delta A_v$</th>
<th>$\sigma^2_{A_v}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Phenotype</td>
<td>Directional</td>
<td>0.20</td>
<td>0.006</td>
<td>0.027</td>
</tr>
<tr>
<td></td>
<td></td>
<td>0.10</td>
<td>0.011</td>
<td>0.052</td>
</tr>
<tr>
<td></td>
<td></td>
<td>0.05</td>
<td>0.017</td>
<td>0.079</td>
</tr>
<tr>
<td></td>
<td></td>
<td>0.01</td>
<td>0.031</td>
<td>0.144</td>
</tr>
<tr>
<td></td>
<td>Stabilizing</td>
<td>0.20</td>
<td>-0.005</td>
<td>-0.023</td>
</tr>
<tr>
<td></td>
<td></td>
<td>0.10</td>
<td>-0.005</td>
<td>-0.023</td>
</tr>
<tr>
<td></td>
<td></td>
<td>0.05</td>
<td>-0.005</td>
<td>-0.023</td>
</tr>
<tr>
<td></td>
<td></td>
<td>0.01</td>
<td>-0.005</td>
<td>-0.023</td>
</tr>
<tr>
<td></td>
<td>Disruptive</td>
<td>0.20</td>
<td>0.011</td>
<td>0.052</td>
</tr>
<tr>
<td></td>
<td></td>
<td>0.10</td>
<td>0.017</td>
<td>0.079</td>
</tr>
<tr>
<td></td>
<td></td>
<td>0.05</td>
<td>0.023</td>
<td>0.107</td>
</tr>
<tr>
<td></td>
<td></td>
<td>0.01</td>
<td>0.037</td>
<td>0.173</td>
</tr>
<tr>
<td>$\hat{A}_v$ progeny</td>
<td>Directional</td>
<td>0.20</td>
<td>-0.049</td>
<td>-0.198</td>
</tr>
<tr>
<td></td>
<td></td>
<td>0.10</td>
<td>-0.062</td>
<td>-0.249</td>
</tr>
<tr>
<td></td>
<td></td>
<td>0.05</td>
<td>-0.073</td>
<td>-0.292</td>
</tr>
<tr>
<td></td>
<td></td>
<td>0.01</td>
<td>-0.094</td>
<td>-0.377</td>
</tr>
</tbody>
</table>

$^1$ $\sigma^2_{A_v} = 0.3; \ r_A = 0; \ \sigma^2_e = 0.7; \ \sigma^2_P = \sigma^2_{A_m} + \sigma^2_e = 1.0$, equal selection differentials in both sexes.

Table 8 shows the predicted response in $A_v$ for directional, stabilizing and disruptive selection based on phenotype (Equation 3, selection differentials from Table 2, neglecting the terms involving $P^3$) and for directional downward selection on $A_v$ based on 100 half-sib progeny assuming $r_A = 0$ (calculated as $\Delta A_v = ir_{A_v,A_v} \sigma_{A_v}$, where $r_{A_v,A_v} = \sqrt{\frac{b(A_v)}{g_{A_v}} / \sigma_{A_v}}$).

Predictions were close to observed responses in Monte Carlo simulation. For all selection strategies, responses in $A_v$ increased with $\sigma^2_{A_v}$ due to a higher accuracy and a higher genetic variance in itself.
With directional and disruptive selection on phenotype, the predicted response in $A_v$ was positive and environmental variance increased substantially, and nonlinearly with selection intensity. Disruptive selection gave a slightly larger response because the selection intensity in each tail of the distribution of $P$ was higher. With stabilizing selection on phenotype, the response in $A_v$ was negative but small, even when the selection was intense because selection differentials remain small and were nearly constant (Table 2). With directional downward selection on $\hat{A}_v$ based on 100 half-sib progeny, response in $A_v$ was negative and environmental variance decreased substantially, which in an agricultural context would imply increased uniformity of end product. Responses increased linearly with selection intensity and became large, especially with $\sigma^2_{A_v} \geq 0.05$. When the best 5% of the sires are selected on $\hat{A}_v$ and dams are selected at random with $\sigma^2_{A_v} = 0.05$, the environmental variance would be 0.554 in the next generation, which is only 79.1% of that in the current generation! In conclusion, a large number of progeny is necessary to predict $\hat{A}_v$ with high accuracy, but responses in $A_v$ can be large relative to the environmental variance in the current generation.

**DISCUSSION**

A multiple regression framework has been developed to predict breeding values and selection responses in mean and variance for mass selection and selection between families in the presence of genetic heterogeneity of environmental variance. The model of Hill and Zhang (2004) has been refined for directional mass selection and extended to stabilizing and disruptive selection based on phenotype and to between family selection. The phenotypic variance increases nonlinearly with selection intensity under directional mass selection when $r_d = 0$. It increases even more with disruptive selection, but decreases only slightly with stabilizing selection, which is in agreement with results of Gavrilets and Hastings (1994) and Wagner et al. (1997). With selection on family mean, phenotypic variance is expected to change little unless $r_d \neq 0$, but with selection on within-family variance, response in phenotypic variance may be large providing $\sigma^2_{A_v} > 0$, even though a large number of relatives is necessary to estimate $\hat{A}_v$ accurately.

**Methodology**

**Comparison of genetic models.** Different genetic models to account for genetic heterogeneity of environmental variance appear in the literature, basically either additive effects both at the level of the mean and the environmental variance (Hill and Zhang, 2004;
Zhang and Hill, 2005; this study) or additive effects on the mean and an exponential model for the environmental variance (SanCristobal-Gaudy et al., 1998, 2001; Sorensen and Waagepetersen, 2003; Ros et al., 2004). In the exponential model:

$$P = \mu + A_m + \chi \exp\left(\frac{\ln(\sigma_{E,exp}^2) + A_v,exp}{2}\right)$$  \hspace{1cm} (15)

where $\sigma_{E,exp}^2$ is the environmental variance when $A_v,exp = 0$, and $A_v,exp$ is the individual’s breeding value for environmental variance in the exponential model, such that environmental variances are multiplicative on the observed scale and additive on a log-scale. (Note that $\ln(\sigma_{E,exp}^2) = \eta$ in the notation of SanCristobal-Gaudy et al. (1998).) The distribution of true variances (not variance estimates) is unknown in practice and can not help in guiding whether the additive model or the exponential model better reflects the real world. Clearly, each model has specific (dis)advantages. The exponential model has tractable properties so it is easier to use in data analysis, for example the environmental variance can never become negative, whereas in the additive model the term $\sqrt{\sigma_{E}^2 + A_v}$ is defined only when $\sigma_{E}^2 + A_v > 0$. The additive model, however, fits nicely in quantitative genetic theory leading to better properties for deterministic predictions of selection response. A disadvantage of the exponential model is that the average environmental variance in the population is $\sigma_{E}^2 = \sigma_{E,exp}^2 \exp(\frac{1}{2} \sigma_{A_v,exp}^2)$, so there is no full separation of the mean environmental variance and the genetic variance in environmental variance, and $\sigma_{A_v,exp}^2$ has to be known in order to interpret $\sigma_{E,exp}^2$.

Fortunately, the models are sufficiently similar that their genetic parameters can be interconverted. The breeding values for environmental variance can be converted by equating the expectations of the second central moments of the environmental effects (see Appendix 2):

$$A_v = \sigma_{E,exp}^2 \exp(A_v,exp) - \sigma_{E}^2$$  \hspace{1cm} (16)

(A first-order Taylor series approximation of Equation 16 is $A_v = A_v,exp \times \sigma_{E,exp}^2 + (\sigma_{E,exp}^2 - \sigma_{E}^2)$, illustrating the factor $\sigma_{E,exp}^2$ between breeding values and a correction for the difference between $\sigma_{E,exp}^2$ and $\sigma_{E}^2$). The genetic variances can be converted by equating the fourth central moments of the environmental effects:

$$\sigma_{A_v}^4 = \sigma_{E,exp}^4 \exp(2\sigma_{A_v,exp}^2) - \sigma_{E}^4$$  \hspace{1cm} (17)
A first-order Taylor series approximation of Equation 17 is 
\[ \sigma_{A_0}^2 = \sigma_{E,\text{exp}}^4 \times \sigma_{A_0,\exp}^2 + (\sigma_{E,\text{exp}}^4 - \sigma_{E}^4), \]
showing a factor \( \sigma_{E,\exp}^4 \) between genetic variances and a correction for the difference between \( \sigma_{E,\exp}^4 \) and \( \sigma_{E}^4 \). Thus, results obtained using the exponential model in data analysis could be converted using Equations 16 and 17 to the additive model and the deterministic equations derived in this study used to predict selection responses. Gavrilets and Hastings (1994) and Wagner et al. (1997) adopted slightly different multiplicative models to deal with genetic heterogeneity of environmental variance, but these are in essence very similar to the exponential model.

**Multiple regression framework.** In this study, a multiple regression framework was used to predict breeding values and selection responses. Prediction equations were derived for incorporating phenotypic information of only one type, individual or family statistics, but the method can easily be extended to situations where phenotypic information is available from different kinds of relatives. For the common situation of optimal weighting own performance and family information, most of the necessary elements in the prediction equation have either been derived here or can be derived straightforwardly using the same methods. Furthermore, the regression structure enables prediction of responses in mean and variance with different selection strategies using the classical selection index theory and extension to give optimal changes in mean and variance via a selection index (Hazel, 1943). The framework presented can be used only for prediction of selection response after one generation of selection, due to build-up of gametic phase disequilibrium, genetic variance would decrease with directional selection, lowering selection responses (Bulmer, 1971). Furthermore, gametic phase disequilibrium induces an unfavorable covariance between the additive genetic effects for mean and environmental variance, counteracting desired changes in mean and variance (Hill and Zhang, 2004). Inclusion of the Bulmer-effect was beyond the scope of this paper, but could be implemented (Hill and Zhang 2004, 2005).

In the multiple regression framework, fixed effects are assumed to be known without error, but in practice they are estimated from the data, thereby reducing accuracy and selection response. Therefore, results in this study should be interpreted using an effective number of observations, which is lower than the actual number of observations. To predict breeding values in the presence of fixed effects on mean (e.g. herd effect) and variance (e.g. heterogeneity of variance between herds, environments with different stress levels), a model with genetically structured environmental variance can be used (SanCristobal-Gaudy et al., 1998; Sorensen and Waagepetersen, 2003). Modeling of environmental heterogeneity of variance (e.g. between herds) has been reviewed by Foulley and Quaas (1995) and Hill (2004). To predict selection responses with genetic heterogeneity of environmental variance in environments differing in mean environmental variance (e.g. herds, stress levels), the present framework can be used by adjusting \( \sigma_{E}^2 \).
Responses in mean and variance

A disadvantage of the multiple regression framework is that it relies on the assumption that the explanatory variables \(x\) are linearly related to the dependent variables \(y\), which is ensured when \(x\) and \(y\) are bivariate normally distributed. As a consequence, results may not be robust against deviations from normality, particularly when higher order terms such as \(P^3\) are included in predictions. The multiple regression framework was, however, robust against small deviations from normality induced by genetic heterogeneity of environmental variance. SanCristobal-Gaudy et al. (1998) and Sorensen and Waagepetersen (2003) also assumed multivariate normality in predictions of selection responses, but their approaches were more flexible in allowing for other distributions. Their approaches were not very different from those in this study, but some expressions were much more complex due to the use of the exponential model.

Multiple regression methods would be useful to study the evolution of phenotypic variance in natural populations, to further develop analyses of Zhang and Hill (2005). Selection for reduced environmental variance could result in environmental canalization, a phenomenon of long-standing interest (e.g. Waddington, 1942; Waddington, 1960; reviews: Scharloo, 1991; Debat and David, 2001; Flatt, 2005). Based on our predictions, stabilizing selection can not cause environmental canalization of traits within a few generations, but may do so eventually. With long-term canalizing selection, the question arises whether the limit of environmental variance is zero, whereas most quantitative traits in nature under stabilizing selection still exhibit environmental variance (e.g. Wagner et al., 1997). We know little about how levels of environmental variation are determined and maintained in nature in the face of stabilizing selection. Different mechanisms have been proposed (e.g. Wagner et al., 1997), such as introducing a cost for homogeneity or canalization (Zhang and Hill, 2005). To further investigate long-term effects of natural selection on environmental variance, the current framework can be extended to include the effects of gametic phase disequilibrium, inbreeding and mutation, analogous to effects of selection on the mean of traits.

Evidence for genetic heterogeneity of environmental variance

Although the tools for evaluating breeding strategies to change the mean and the size of environmental variance are now available, the whole exercise would just be a theoretical game if \(\sigma^2_{Av} = 0\). As reviewed in the introduction, there is empirical evidence that genotypes differ in environmental variance, but it is not abundant. To compare results of different studies analyzing field data we use Equation 17, because some are based on the exponential genetic model (SanCristobal-Gaudy et al., 1998, 2001; Sorensen and Waagepetersen, 2003; Ros et al., 2004) and some on the additive genetic model (Rowe et al., 2006). The measure of heritability \(h^2\) developed in this study (Equation 13) and the genetic coefficient of variation for environmental variance \(GCV_E = \sigma_A / \mu = \sigma_{Av} / \sigma^2_E\), denoted ‘evolvability’ (Houle, 1992),
are used to compare results from different studies (Table 9). Heritabilities of environmental variance were low, in the range 0.02 to 0.05 as used in this study, and $GCV_E$ were large, in the range of 0.30 to 0.58 (excluding 0). Note that $GCV_E^2$ is close to $\sigma_{A_v,exp}^2$. The low values of $h_v^2$ show that a large amount of information is necessary to estimate $\hat{A}_v$ accurately, but the high values of $GCV_E$ show that there is substantial opportunity for genetic change.

Table 9. Comparison of literature estimates of genetic variance in environmental variance.

<table>
<thead>
<tr>
<th>Source</th>
<th>Trait</th>
<th>$\sigma_{A_v,exp}^2$</th>
<th>$\sigma_{A_v}^2$</th>
<th>$h_v^2$</th>
<th>$GCV_E$</th>
</tr>
</thead>
<tbody>
<tr>
<td>SanCristobal-Gaudy et al. (1998)</td>
<td>Fat/protein goat milk</td>
<td>0.000</td>
<td>0.000</td>
<td>0.000</td>
<td>0.000</td>
</tr>
<tr>
<td></td>
<td>pH pig</td>
<td>0.150</td>
<td>1.2E-04</td>
<td>0.039</td>
<td>0.402</td>
</tr>
<tr>
<td>SanCristobal-Gaudy et al. (2001)</td>
<td>Litter size sheep</td>
<td>0.230</td>
<td>0.057</td>
<td>0.048</td>
<td>0.509</td>
</tr>
<tr>
<td>Sorensen and Waagepetersen (2003)$^1$</td>
<td>Litter size pigs</td>
<td>0.090</td>
<td>4.291</td>
<td>0.026</td>
<td>0.307</td>
</tr>
<tr>
<td>Ros et al. (2004)$^1$</td>
<td>Body weight (g) snails</td>
<td>0.290</td>
<td>0.368</td>
<td>0.017</td>
<td>0.580</td>
</tr>
<tr>
<td>Rowe et al. (2006)</td>
<td>Body weight (kg) broiler</td>
<td>0.086</td>
<td>8460</td>
<td>0.029</td>
<td>0.299</td>
</tr>
<tr>
<td></td>
<td>Body weight (kg) broiler</td>
<td>0.096</td>
<td>5310</td>
<td>0.031</td>
<td>0.318</td>
</tr>
</tbody>
</table>

$^1$ Models included permanent environmental variance, environmental variance was taken from their model $1$ estimates.

$^2$ Equation 17: $\sigma_{A_v}^2 = \sigma_{E,exp}^4 \exp(2\sigma_{A_v,exp}^2) - \sigma_{E}^4$.

$^3$ $h_v^2 = \sigma_{A_v}^2 / (2\sigma_p^2 + 3\sigma_{A_v}^2)$ = heritability of environmental variance.

$^4$ $GCV_E = \sigma_{A_v} / \sigma_E^2$, a measure of evolvability (Houle, 1992).

Other evidence of the existence of genetic heterogeneity of environmental variance can come from selection experiments. With genetic heterogeneity of environmental variance, environmental variance would decrease with stabilizing selection and increase with disruptive selection. In most studies (e.g. Rendel et al., 1966; Cardin and Minvielle, 1986), however, only changes in phenotypic variance are reported, which are not separated into changes in genetic and environmental variance. Interpretation of any selection experiment is complicated by possible changes in genetic variance due to gene frequency change, which cannot be predicted from simple base population parameters. Under infinitesimal model assumptions, effects of gene frequency change can be ignored and that due to gametic phase disequilibrium
Responses in mean and variance

can be predicted. Due to negative gametic phase disequilibrium, genetic variance is expected to decrease with stabilizing selection and increase with disruptive selection (Bulmer, 1971). In agreement with this expectation, Kaufman et al. (1977) found substantial decreases in genetic and environmental variance with stabilizing selection in Tribolium castaneum and Scharloo et al. (1972) observed substantial increases in genetic and environmental variance with disruptive selection in Drosophila melanogaster, indicating a substantial genetic variance in environmental variance. Sorensen and Hill (1983), however, found large increases only in genetic variance with disruptive selection in Drosophila melanogaster.

Even though some studies analyzing field data or selection experiments show existence of genetic heterogeneity of environmental variance, it could still be due to statistical artifacts, e.g. due to confounding genetic and environmental effects on variance or violation of the infinitesimal model assumption. If genetic heterogeneity of environmental variance is a truly biological phenomenon, it could be due to scaling, genetic variance in environmental sensitivity, or a combination of both. Traits seem to have a rather constant CV, even when the mean changes dramatically due to selection (Hill and Bünger, 2004). A constant CV would require a correlation of unity between mean and standard deviation, which has not been found in analysis of field data (Sorensen and Waagepetersen, 2003; Ros et al., 2004; Rowe et al., 2006). Genetic heterogeneity of environmental variance can arise from genetic differences in environmental sensitivity (Falconer and Mackay, 1996; Lynch and Walsh, 1998). When genotypes perform under variable environmental conditions, which are unknown to the researcher, genetic differences in response to environmental conditions may be observed as genetic heterogeneity of environmental variance.

Genetic heterogeneity of environmental variance is a complicated phenomenon and there is not yet abundant evidence of its existence. The results in this study may help in understanding the consequences of genetic heterogeneity of environmental variance on phenotypes and the methods can help in designing selection experiments and in evaluating breeding strategies or the effects of natural selection that change both the mean and the variance. Genetic heterogeneity of environmental variance may indeed be exploited to breed more “robust” or “stable” genotypes.

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REFERENCES

   CAB International, Wallingford, United Kingdom.
Cardin, S. and F. Minvielle. 1986. Selection on phenotypic variation of pupa weight in
Debat, V. and P. David. 2001. Mapping phenotypes: canalization, plasticity and
   Pearson Education Limited, Essex, United Kingdom.
Falconer, D. S. and A. Robertson. 1956. Selection for environmental variability of body size
Foulley, F. L. and R. L. Quaas. 1995. Heterogeneous variances in Gaussian linear mixed
Henderson, C. R. 1984. Applications of linear models in animal breeding. University of
   Guelph, Guelph, Canada.
Hill, W. G. and L. Bünger. 2004. Inferences on the genetics of quantitative traits from long-
   86:160.
Hohenboken, W. D. 1985. The manipulation of variation in quantitative traits: a review of
   130:195-204.

APPENDIX 1

Derivation of elements in the P - and G -matrices

Selection on a single phenotype: The elements in the P - and G -matrices were derived as follows, using the Roman E to denote expectation, the italic E to denote the environmental deviation $E = Z\sqrt{\sigma^2_E + A_v}$ and noting that $E(Z^2) = 1$:

$E(P) = 0,$

$E(P^2) = \sigma^2_p$

$E(P^3) = E(A^2_m + 3A^2_m E + 3A_m E^2 + E^3) = 0 + 0 + 3E(A_m (\sigma^2_E + A_v)) = 0 + 3cov_{A_{env}}$

$E(P^4) = E(A^4_m + 4A^3_m E + 6A^2_m E^2 + 4A_m E^3 + E^4) = 3\sigma^4_p + 3\sigma^2_A$

$E(P^5) = E(A^5_m + 5A^4_m E + 10A^3_m E^2 + 10A^2_m E^3 + 5A_m E^4 + E^5) = 30\sigma^5_p cov_{A_{env}}$

$E(P^6) = E(A^6_m + 6A^5_m E + 15A^4_m E^2 + 20A^3_m E^3 + 15A^2_m E^4 + 6A_m E^5 + E^6) = 15\sigma^6_p + 45\sigma^5_p \sigma^2_{A_{env}} + 90\sigma^4_p \sigma^2_{A_{env}} + 45\sigma^3_p \sigma^3_{A_{env}}$

$\text{var}(P) = E(P^2) - (E(P))^2$

$\text{var}(P^2) = E(P^4) - (E(P^2))^2$

$\text{cov}(P, P^2) = E(P^3) - E(P)E(P^2)$

$\text{cov}(P, P^3) = E(P^4) - E(P)E(P^3)$

$\text{cov}(P^2, P^3) = E(P^5) - E(P^2)E(P^3)$

$\text{var}(P^3) = E(P^6) - (E(P^3))^2$

$\text{cov}(P, A_m) = \sigma^2_{A_{env}}$

$\text{cov}(P^2, A_m) = \text{cov}(A^2_m + 2A_m E + E^2, A_m) = 0 + 0 + \text{cov}(E^2, A_m) = \text{cov}_{A_{env}}$

$\text{cov}(P^3, A_m) = \text{cov}(A^3_m + 3A^2_m E + 3A_m E^2 + E^3, A_m)$

$= \text{cov}(A^3_m, A_m) + \text{cov}(3A_m E^2, A_m) = 3\sigma^4_{A_{env}} + 3\sigma^2_{A_{env}} \sigma^2_E = 3\sigma^2_{A_{env}} \sigma^2_{A_{env}}$

Similarly $\text{cov}(P, A_v) = \text{cov}_{A_{env}}, \text{cov}(P^2, A_v) = \sigma^2_{A_{env}}$, and $\text{cov}(P^3, A_v) = 3\sigma^2_{A_{env}} \text{cov}_{A_{env}}$. 

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Selection based on a group of relatives:

$$\text{var}(\overline{P}) = \frac{(\sigma_P^2 + a_w(n-1)\sigma_{Am}^2)}{n}$$

$$\text{cov}(\overline{P}_r, \overline{P}_{l}) = \left[ n \text{cov}(P_r, P_{l}^2) + n(n-1)\left\{ \text{cov}(P_k, P_{l}^2) + 2 \text{cov}(P_k, P_l) \right\} \right]/n^3$$

$$= \left[ 3 + 3a_w(n-1)\text{cov}_{Am} \right]/n^2$$

$$\text{var}(\overline{P}_r^2) = \left[ n \text{var}(P_r^2) + n(n-1)\left\{ \text{cov}(P_k^2, P_{l}^2) + 4 \text{cov}(P_k^2, P_l) + 2 \text{cov}(P_k P_l, P_l) \right\} \right]/n^4$$

$$= 2\left[ (\sigma_P^2 + a_w(n-1)\sigma_{Am}^2)/n \right]^2 + \left[ 3 + 3a_w(n-1)\sigma_{Am}^2 \right]/n^3$$

$$\text{var}(\overline{P}) = \left[ n \text{var}(P_r^2) + n(n-1)\text{cov}(P_k^2, P_{l}^2) \right]/n^2 = \left[ 2\sigma_P^4 + 3\sigma_{Am}^2 \right]/n$$

$$\text{cov}(\overline{P}, \overline{P}_r^2) = \left[ n \text{cov}(P_r, P_{l}^2) + n(n-1)\text{cov}(P_k, P_{l}^2) \right]/n^2 = \left[ 3 + a_w(n-1)\text{cov}_{Am} \right]/n$$

$$\text{cov}(\overline{P}, \text{var}W) = \left[ n(n-1)\times \text{cov}(\overline{P}, \overline{P}_r^2) - \text{cov}(\overline{P}, (\overline{P}_r^2)) \right] = \left[ 3 + a_w(n-3)\text{cov}_{Am} \right]/n$$

$$\text{cov}(\overline{P}_r^2, \overline{P}_r^2) = \left[ \text{var}(P_r^2) + (n-1)\text{cov}(P_k^2, P_{l}^2) + 2 \text{cov}(P_k^2, P_l) \right]/n^2$$

$$= \left[ 2\sigma_P^4 + 3\sigma_{Am}^2 \right]/n^2$$

$$\text{cov}(\overline{P}_r^2, \text{var}W) = \left[ n(n-1)\times \text{cov}(\overline{P}_r^2, \overline{P}_r^2) - \text{var}(\overline{P}_r^2) \right]/n^2$$

$$= \left[ 2\sigma_P^2 + 4\sigma_{Am}^2 \right]/(n-1)$$

where $k, l, m$ and $n$ are different relatives within the family.

$$\text{cov}(\overline{P}, A_{m,j}) = a_j\sigma_{Am}^2$$

$$\text{cov}(\overline{P}_r^2, A_{m,j}) = \left[ n \text{cov}(P_k^2, A_{m,j}) + n(n-1)\text{cov}(P_k P_l, A_{m,j}) \right]/n^2 = a_j\text{cov}_{Am}/n$$
\[
\text{cov}(\text{var}W, A_{m,j}) = \text{cov}\left(\frac{n}{n-1} \left( \overline{P}^2 - \left(\overline{P}\right)^2 \right), A_{m,j}\right) = a_j \text{cov}_{\text{env}}
\]

and similarly:
\[
\text{cov}(\overline{P}, A_{v,j}) = a_j \text{cov}_{\text{env}}
\]
\[
\text{cov}(\overline{P}^2, A_{v,j}) = a_j \sigma_v^2 \big/ n
\]
\[
\text{cov}(\text{var}W, A_{v,j}) = a_j \sigma_v^2.
\]

**APPENDIX 2**

**Similarities between exponential and additive genetic model**

The breeding values for environmental variance were converted from the exponential model (Equation 15) to the additive model (Equation 1) by equating the second central moments of the environmental effects of both models resulting in Equation 16:

\[
E(E^2) = E(E_{\text{exp}}^2)
\]
\[
\sigma_v^2 + A_v = \exp(\ln \sigma_{E,\text{exp}}^2 + A_{v,\text{exp}})
\]
\[
A_v = \exp(\ln \sigma_{E,\text{exp}}^2 + A_{v,\text{exp}}) - \sigma_E^2
\]

The genetic variance in environmental variance were converted from the exponential model to the additive model by equating the fourth central moments of the environmental effects of both models resulting in Equation 17 (e.g. Stuart and Ord, 1994):

\[
E(E^4) = E(E_{\text{exp}}^4)
\]
\[
3E\left(\sqrt[4]{\sigma_E^2 + A_v}\right)^4 = 3E\left(\exp\left(\frac{1}{2} \ln \sigma_{E,\text{exp}}^2 + \frac{1}{2} A_{v,\text{exp}}\right)\right)^4
\]
\[
\sigma_E^4 + \sigma_{A_v}^2 = \sigma_{E,\text{exp}}^4 \exp(2\sigma_{A_v,\text{exp}}^2)
\]
\[
\sigma_{A_v}^2 = \sigma_{E,\text{exp}}^4 \exp(2\sigma_{A_v,\text{exp}}^2) - \sigma_E^4
\]
Chapter 6

Selection for uniformity in livestock by exploiting genetic heterogeneity of environmental variance

H. A. Mulder\textsuperscript{1}, P. Bijma\textsuperscript{1}, W. G. Hill\textsuperscript{2}

\textsuperscript{1} Animal Breeding and Genetics Group, Wageningen University, PO Box 338, 6700 AH Wageningen, The Netherlands
\textsuperscript{2} Institute of Evolutionary Biology, School of Biological Sciences, University of Edinburgh, Edinburgh, EH9 3JT, United Kingdom.

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**ABSTRACT:** In some situations, it is worthwhile to change not only the mean, but also the variability of traits by selection. Genetic variation in environmental variance may be utilized to improve uniformity in livestock populations by selection. The objective of this study was to investigate the effects of genetic parameters, breeding goal and breeding scheme on selection responses in mean and variance when applying index selection. Genetic parameters were obtained from the literature. Economic values for mean and variance were derived for some standard non-linear profit equations, e.g. for traits with an intermediate optimum. The economic value of variance was in most situations negative, indicating that selection for reduced variance increases profit. Responses in environmental variance were large, in some cases more than 10% of the current environmental variance. Progeny testing schemes were more efficient than sib testing schemes in decreasing environmental variance. With optimum traits, selection pressure shifts gradually from the mean to the variance when approaching the optimum and most economic gain is initially due to change in mean. Near the optimum, reduction of variance further improves economic merit. Genetic improvement of uniformity is particularly of interest for traits where the current population mean is near an intermediate optimum.

**Keywords:** genetic heterogeneity of environmental variance, index selection, uniformity, economic value, optimum trait

**INTRODUCTION**

Uniformity of livestock is of economic interest in many cases. For example, the preference for some meat quality traits, such as pH, is to be in a narrow range (Hovenier et al., 1993). Farmers get premiums when they deliver animals in the preferred range and penalties for animals outside it (Kanis et al., 2006). Uniformity of animals and animal products is also of interest for traits with an intermediate optimum value, such as litter size in sheep (SanCristobal-Gaudy et al., 2001) or egg weight in laying hens (Dekkers et al., 1995). Different strategies can be used to reduce variability, e.g. management, mating systems and genetic selection (Hohenboken, 1985), but selection can be effective only when there are genetic differences among animals in phenotypic variability.

There is some empirical evidence for the presence of genetic variance in environmental variance, so-called genetic heterogeneity of environmental variance. SanCristobal-Gaudy et al. (2001), in analysis of litter size in sheep, and Sorensen and Waagepetersen (2003), in analysis of litter size in pigs, found substantial genetic variance in environmental variance. Van Vleck (1968) and Clay et al. (1979), in analysis of milk yield in dairy cattle, and Rowe et al. (2006), in analysis of body weight in broiler chickens, found large differences between
sires in phenotypic variance within progeny groups. In those studies, heritabilities of environmental variance were low (0.02-0.05), but the genetic standard deviations were high relative to the population average environmental variance (25-60%) (reviewed by Mulder et al., 2007).

When the aim is to change the mean and the variance of a trait simultaneously, e.g. by applying index selection, not only the genetic parameters but also the economic values for mean and variance of the trait need to be known. For most traits, economic values have been derived for their mean, but not for their variance. Because the variance of a trait is a quadratic function of trait value, it will have a non-zero economic value if the profit equation is non-linear. Non-linear profit equations are most obvious for traits with an intermediate optimum, such as egg weight in laying hens (Dekkers et al., 1995), carcass weight and carcass quality traits in pigs and broilers (Hovenier et al., 1993; Hammerstedt, 1999; Garnier et al., 2003), marbling in beef (Barwick and Henzell, 1999), and litter size in sheep (SanCristobal-Gaudy et al., 2001).

The effects of selection strategies on responses in mean and variance have been investigated for mass selection (Hill and Zhang, 2004; Mulder et al., 2007), canalizing selection using a quadratic index with phenotypic information of progeny (SanCristobal-Gaudy et al., 1998, 2001), index selection using arbitrary weights to increase the mean and to decrease the variance with repeated measurements on the same animal (Sorensen and Waagepetersen, 2003), and for selection either on progeny mean or on within-family variance (Mulder et al., 2007). In none of these studies were possibilities investigated for simultaneously changing the mean and the variance of traits in livestock breeding programs by using a selection index with optimal weights. In combination with a derivation of economic values for mean and variance, the framework developed by Mulder et al. (2007) allows extension to a selection index to optimize responses in mean and variance and comparison of different breeding strategies for simultaneously changing them.

The objective of this study is to investigate the effects of genetic parameters, breeding goals and breeding schemes, e.g. progeny and sib testing, when changing the mean and the variance of a trait by exploiting genetic heterogeneity of environmental variance. Economic values for the mean and the variance are derived for situations with non-linear profit and these economic values are applied in index selection to study how the mean and the variance respond to selection.
MATERIAL AND METHODS

Genetic model
In this study, it is assumed that selection is for one trait in the presence of genetic heterogeneity of environmental variance. Both the mean and the environmental variance are partly under genetic control according to the genetic model (Hill and Zhang, 2004; Mulder et al., 2007):

\[
P = \mu + A_m + \chi \sqrt{\sigma_E^2 + A_v}
\]

where \( P \) is phenotype, \( \mu \) and \( \sigma_E^2 \) are, respectively, the mean trait value and the mean environmental variance of the population, \( A_m \) and \( A_v \) are, respectively, the breeding value for the mean and environmental variance and \( \chi \) is a standard normal deviate for the environmental effect. It is assumed that \( A_m \) and \( A_v \) follow a multivariate normal distribution \( \mathcal{N} \left( \begin{pmatrix} 0 \\ 0 \end{pmatrix}, C \otimes A \right) \), where \( A \) is the additive genetic relationship matrix, 

\[
C = \begin{bmatrix} \sigma_{A_m}^2 & \text{cov}_{A_m A_v} \\ \text{cov}_{A_v A_m} & \sigma_{A_v}^2 \end{bmatrix},
\]

\( \sigma_{A_m}^2 \) and \( \sigma_{A_v}^2 \) are the additive genetic variances in \( A_v \) and \( A_m \), respectively, \( \text{cov}_{A_m A_v} = \text{cov}(A_m, A_v) = r_A \sigma_{A_m} \sigma_{A_v} \), and \( r_A \) is the additive genetic correlation between \( A_m \) and \( A_v \). The term \( \chi \) is scaled by \( \sqrt{\sigma_E^2 + A_v} \) to obtain the environmental effect. The mean phenotypic variance of the population (\( \sigma_P^2 \)) is the sum of \( \sigma_{A_m}^2 \) and \( \sigma_E^2 \). The distribution of \( P \) is approximately normal, but is slightly leptokurtic and, when \( r_A \neq 0 \), also slightly skewed (Mulder et al., 2007).

Breeding schemes
Breeding schemes are based on either sib testing or progeny testing. Sib testing is considered as the basis, because it is most commonly applied in pig and poultry improvement, in which uniformity of animals is likely to be of most interest (Hammerstedt, 1999; Garnier et al., 2003). Progeny testing is considered as an alternative with the advantage of a higher accuracy of selection, which is (partly) offset by a longer generation interval.

Selection is for one trait and the breeding goal comprises both its mean and variance:

\[
H = v_{A_m} A_m + v_{A_v} A_v = \mathbf{v} \mathbf{a}
\]
where $H$ is the aggregate genotype, $v_{A_m}$ and $v_{A_r}$ are respectively the economic values for $A_m$ and $A_r$, $v' = [v_{A_m} v_{A_r}]$ and $a' = [A_m A_r]$. The trait is measured in both sexes before selection (e.g. body weight). The available phenotypic information is: own phenotype $P$, own phenotype squared $P^2$, mean phenotype of half-sibs $\overline{P}$, mean phenotype of half-sibs squared $(\overline{P})^2$ and the within-family variance of half-sibs $varW$. It is assumed that half-sib groups consist of 100 half-sibs with one progeny/dam to keep the selection index relatively simple, although in pigs and poultry dams have multiple progeny. Sires are either sib tested or progeny tested; dams are always sib tested. Generations are discrete. Each generation 20% of the dams and 5% of the sires are selected by truncation on an index $I$:

$$I = b'x$$  \hspace{1cm} (3)

where $b = P^{-1}Gv$, $x$ is the vector with phenotypic information, expressed as deviations from the expectations, $P = \text{cov}(x,x)$ and $G = \text{cov}(x,a)$. Details of the $P$- and $G$-matrices are in Appendix 1.

Economic values for common cases with non-linear profit

In this section, economic values for the mean and the variance are derived for some standardized situations with non-linear profit. A non-zero economic value for variance implies that the profit equation is non-linear, because the variance of a trait is a quadratic function of its value. Linear profit equations are, therefore, not of interest in this study. The clearest example of non-linear profit is for traits with an intermediate optimum (e.g. Hovenier et al., 1993; Dekkers et al., 1995).

**Quadratic profit.** Traits may have a quadratic profit equation with the maximum profit at an intermediate optimum value. An example is days open in dairy cattle (Groen et al., 1994). A quadratic profit equation at the individual animal level is:

$$M = a_1(P - O)^2 + a_2$$  \hspace{1cm} (4)

where $M$ is the profit of an animal, $a_1$ and $a_2$ are the coefficients of the profit equation with $a_1$ describing the curvature ($a_1 < 0$) and $a_2$ the profit at the optimum value, $O$ of the trait. The average profit ($\overline{M}$) of the population is:

$$\overline{M} = \int_{-\infty}^{\infty} Mf(P)dP = a_1 \mu^2 - 2a_1 \mu O + a_1 O^2 + a_2 + a_1 \sigma^2_P$$  \hspace{1cm} (5)
where \( f(P) \) is the probability density function of a normal distribution. The economic values are given by the first derivatives of Equation 5:

\[
\begin{align*}
v_{s_m} &= \frac{\text{d} \bar{M}}{\text{d} \mu} = 2a_i(\mu - \bar{O}) \quad (6a) \\
v_{s_r} &= \frac{\text{d} \bar{M}}{\text{d} \sigma_r^2} = a_i 
\end{align*}
\]

The ratio of \( v_{s_m} \) to \( v_{s_r} \) depends solely on the location of the population mean relative to the optimum trait value (see Appendix 2).

**Differential profit based on thresholds.** In some practical cases, profit is not a continuous function of phenotype, but a discontinuous function with differential revenues according to thresholds. A clear example is traits with two thresholds with an optimum range in which the profit of animals or animal products is higher than outside the optimum range. Examples are pH in meat of pigs (Hovenier et al., 1993) or egg weight in poultry (Rose, 1996). Assume that animals with a phenotype between the lower threshold (\( T_l \)) and higher threshold (\( T_u \)) have a profit \( M = 1 \) and animals with a phenotype outside these thresholds have a profit \( M = 0 \) (see Figure 1 for a schematic representation). The average profit of the population is:

\[
\bar{M} = M_{P<T_l} \int_{-\infty}^{T_l} f(P)\text{d}P + M_{T_l<P<T_u} \int_{T_l}^{T_u} f(P)\text{d}P + M_{P>T_u} \int_{T_u}^{\infty} f(P)\text{d}P = \int_{T_l}^{T_u} f(P)\text{d}P 
\]  

(7)

The economic values are:

\[
\begin{align*}
v_{s_m} &= \frac{\text{d} \bar{M}}{\text{d} \mu} = \frac{\text{d} \bar{M}}{\text{d} \mu} \frac{\text{d} \mu}{\text{d} \mu} = \frac{1}{\sigma_p} (z_l - z_u) \quad (8a) \\
v_{s_r} &= \frac{\text{d} \bar{M}}{\text{d} \sigma_p^2} = \frac{\text{d} \bar{M}}{\text{d} \sigma_p^2} \frac{\text{d} \sigma_p^2}{\text{d} \sigma_p^2} = \frac{1}{2} (z_l t_l - z_u t_u) \quad (8b)
\end{align*}
\]

where \( z_l \) and \( z_u \) are, respectively, the ordinate of the standard normal distribution at the standardized lower and upper thresholds \( t_l = \frac{T_l - \mu}{\sigma_p} \) and \( t_u = \frac{T_u - \mu}{\sigma_p} \). The ratio of \( v_{s_m} \) to \( v_{s_r} \) is determined mainly by the location of the population mean relative to both thresholds, but is also affected by \( \sigma_p^2 \). In Appendix 2, it is shown that on a standardized scale the relative
emphasis of $A_v$ in the breeding goal ($\frac{v_{A_v} \sigma_{A_v}}{v_{A_v} \sigma_{A_v} + v_{A_m} \sigma_{A_m}}$) is independent of $\sigma^2_p$, and that this is also the case when economic values for optimum traits are based on quadratic profit. Equation 8a is in agreement with previous research on economic values for optimum traits (Hovenier et al., 1993; Von Rohr et al., 1999), whereas 8b is new.

Derivation of economic values can be extended easily to situations with a different number of thresholds, as is shown for economic values for the mean of traits (Bekman and Van Arendonk, 1993; Dekkers, 1994; Von Rohr et al., 1999). A special case is one threshold, in which the terms relating to the second threshold in Equation 8a and 8b can be omitted. An example is avoidance of poor animal performance, which may reduce consumer acceptance of the production system, such that an objective may be to reduce the proportion of animals below a certain threshold (Kolmodin and Bijma, 2004).

---

**Figure 1.** Schematic representation when profit is based on two thresholds ($P = -1$, $P = 1$) with optimum profit between both thresholds when the trait is normally distributed ($N(0,1)$; population mean = optimum = 0).

**Prediction of genetic gain**

Genetic gain after one generation of selection was calculated deterministically using classical selection index theory (Hazel, 1943) using elements in the $P$- and $G$-matrices as derived by Mulder et al. (2007). To check the goodness of fit of selection index equations, predicted selection responses were compared with realized selection responses obtained from Monte Carlo simulation (see Appendix 3). Prediction errors (Table A1) were small to moderate, but small enough to use selection index equations in this exploratory study.
Genetic gain was calculated per unit of time to account for the longer generation interval of sires with progeny testing, where one unit of time was equal to the generation interval for sib testing (Mulder and Bijma, 2005). Genetic gain per unit of time for trait $j$ ($A_m$, $A_e$, $H$) was:

$$
\Delta G_j = \frac{R_{S,j} + R_{D,j}}{L_S + L_D}
$$

(11)

where $R_{S,j}$ and $R_{D,j}$ are the genetic selection differentials for sires and dams and $L_S$ and $L_D$ are the relative generation intervals of sires and dams. Genetic selection differentials for $A_m$ and $A_e$ were calculated as:

$$
R_j = \frac{ib^j g_j}{\sigma_j}
$$

(12)

where $i$ is the selection intensity, $g_j$ is the column of $G$ corresponding to $A_m$ or $A_e$, and $\sigma_j = \sqrt{b^j Pb}$ is the standard deviation of the index. Genetic selection differentials of the aggregate genotype were calculated as:

$$
R_H = v_{A_m} R_{A_m} + v_{A_e} R_{A_e}
$$

(13)

Selection intensities were calculated assuming an infinite population of selection candidates without correction for correlated index values among relatives (Hill, 1976; Meuwissen, 1991). Furthermore, gametic phase disequilibrium due to selection (Bulmer, 1971) was ignored. Although Hill and Zhang (2004) developed prediction equations to account for gametic phase disequilibrium with mass selection, prediction equations have not yet been developed for index selection in the presence of genetic heterogeneity of environmental variance.

### Parameter values and common cases with non-linear profit

Parameter values are listed in Table 1. The heritability of the mean ($h_m^2 = \sigma_{A_m}^2 / \sigma_p^2$) was assumed to be 0.3; the phenotypic variance was assumed to be 1.0. The genetic variance in environmental variance $\sigma_{A_e}^2$ was varied between 0.01 and 0.10, corresponding to the range of heritabilities of environmental variance $h_e^2 = \sigma_{A_e}^2 / (2\sigma_p^4 + 3\sigma_{A_e}^2)$ observed in the literature (reviewed by Mulder et al., 2007). The additive genetic correlation ($r_{A_e}$) between $A_m$ and $A_e$,
was varied between -0.5 and 0.5, corresponding to the range in the literature (Sorensen and Waagepetersen, 2003; Ros et al., 2004; Rowe et al., 2006). Economic values $v_{\lambda_m}$ and $v_{\lambda_v}$ were varied and arbitrary values were initially used. The relative generation interval of progeny testing was varied between to 1.4 and 2 (Mulder and Bijma, 2005), because for most species the minimum is 1.6 (e.g., Merks, 1988; Meuwissen, 1989).

**Non-linear profit.** Sib testing schemes were simulated with three types of non-linear profit: quadratic profit ($a_1 = -1$, $a_2 = 2$ and $O = 0$), and differential profit based on one threshold ($P = -1$) or two thresholds ($P = -1$, $P = 1$, $O = 0$). The initial population mean was -2 ($=-2\sigma_p$). Five generations of selection were simulated with updating of economic values and index weights to changes in mean and phenotypic variance, but without updating the P-matrix and thus ignoring changes in phenotypic variance due to $\Delta A_v$. To avoid oscillations around the optimum when the mean of the trait was close to the optimum with quadratic profit or differential profit based on two thresholds ($<\Delta A_m$ in previous generation), the economic value $v_{\lambda_m}$ was derived iteratively to obtain the desired gain in $A_m$ to reach and stay in the optimum, which is similar to a desired gains approach (e.g. Brascamp, 1984).

**Table 1.** Parameter values used in the basic situation and in alternative situations.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Basic</th>
<th>Alternative</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\sigma^2_{\lambda_m}$</td>
<td>0.3</td>
<td>0.1, 0.6</td>
</tr>
<tr>
<td>$\sigma^2_{\lambda_v}$</td>
<td>1.0</td>
<td>-</td>
</tr>
<tr>
<td>$\sigma^2_{\sigma}$</td>
<td>0.05</td>
<td>0.01, 0.10</td>
</tr>
<tr>
<td>$r_i$</td>
<td>0</td>
<td>-0.5, 0.5</td>
</tr>
<tr>
<td>$v_{\lambda_m}$</td>
<td>1</td>
<td>variable</td>
</tr>
<tr>
<td>$v_{\lambda_v}$</td>
<td>-1</td>
<td>variable</td>
</tr>
<tr>
<td>Number of half-sib progeny</td>
<td>100</td>
<td>-</td>
</tr>
<tr>
<td>Selected proportion sires</td>
<td>0.05</td>
<td>-</td>
</tr>
<tr>
<td>Selected proportion dams</td>
<td>0.20</td>
<td>-</td>
</tr>
</tbody>
</table>
RESULTS

Effects of parameters and breeding scheme

Genetic variances $\sigma^2_{A_m}$ and $\sigma^2_{A_v}$. Table 2 shows genetic gain in $A_m$, $A_v$ and the effect on the environmental variance in the next generation ($\sigma^2_{E,1}$) for different values of $\sigma^2_{A_m}$ and $\sigma^2_{A_v}$. When $\sigma^2_{A_m}$ increases, $\Delta A_m$ increases substantially and $\Delta A_v$ decreases. When $\sigma^2_{A_v}$ increases the opposite occurs but to a lesser extent. Both trends accord with the behavior of a selection index, which puts most emphasis on the trait with the highest heritability and/or with the largest contribution to the genetic variance in the breeding goal. The decrease in environmental variance is 4%-16% of the current environmental variance when $\sigma^2_{A_v} \geq 0.05$ ($h_v^2 \geq 0.023$), but is smaller when $\sigma^2_{A_v} = 0.01$ ($h_v^2 = 0.005$). Simultaneous improvement of the mean and the variance of a trait with index selection thus requires a heritability of environmental variance of at least 0.02 and reduction of environmental variance is particularly of interest for traits with a low heritability of the mean.

Table 2. Genetic gain per time unit in sib testing schemes for different values of $\sigma^2_{A_m}$ and $\sigma^2_{A_v}$.

<table>
<thead>
<tr>
<th>Genetic parameters</th>
<th>Genetic gain</th>
<th>Environmental variance$^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\sigma^2_{A_m}$</td>
<td>$\sigma^2_{A_v}$</td>
<td>$\Delta A_m$</td>
</tr>
<tr>
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<tr>
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<td>0.10</td>
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1 Parameters values: $\sigma^2_p = 1$, $r_A = 0$, $v_{A_m} = 1$, $v_{A_v} = -1$, number of progeny per sire = 100, selected proportion sires = 0.05, selected proportion dams = 0.20.

2 Environmental variance in generation 0 ($\sigma^2_{E,0}$) and in generation 1 ($\sigma^2_{E,1}$) after selection.
**Genetic correlation** \( r_A \) and breeding goal. Table 3 shows the effect of \( r_A \) and breeding goal on selection responses. With a relatively low emphasis on \( A_v \) \( (v'=[1 \ -1]) \); e.g. when \( \mu \) is \( 0.5\sigma_p \) lower than the optimum value with quadratic profit, \( \Delta A_v \) is mostly a correlated response to selection on the mean, as indicated by the similar \( \Delta A_v \) with \( v'=[1 \ 0] \). When increasing the emphasis on \( A_v \), \( \Delta A_v \) is in the direction of the economic value and \( \Delta A_m \) is now more affected by \( r_A \). With a breeding goal \( v'=[1 \ -5] \) (e.g. when \( \mu \) is \( 0.1\sigma_p \) lower than the optimum value with quadratic profit), \( \sigma_E^2 \) decreases by 14-22% after one generation of selection at the expense of a lower genetic gain in the mean \( (\Delta A_m) \). Thus relatively large changes in environmental variance in the desired direction are possible if substantial emphasis is put on \( A_v \) in the breeding goal.

<table>
<thead>
<tr>
<th>Breeding goal</th>
<th>Description</th>
<th>( v_{A_m} )</th>
<th>( v_{A_v} )</th>
<th>( r_A )</th>
<th>( \Delta A_m )</th>
<th>( \Delta A_v )</th>
<th>( \sigma_{E,1}^2 )</th>
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<tr>
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<td>-0.50</td>
<td>0.612</td>
<td>-0.126</td>
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<td></td>
<td></td>
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<td></td>
<td></td>
<td>0.50</td>
<td>0.612</td>
<td>0.126</td>
<td>0.826</td>
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<td>-0.50</td>
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<td>0.536</td>
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<td>0.50</td>
<td>-0.469</td>
<td>-0.164</td>
<td>0.536</td>
<td></td>
</tr>
</tbody>
</table>

1 Parameters values: \( \sigma_p^2 = 1 \), \( \sigma_{A_m}^2 = 0.3 \), \( \sigma_{E,0}^2 = 0.7 \), \( \sigma_{A_v}^2 = 0.05 \), number of progeny per sire = 100, selected proportion sires = 0.05, selected proportion dams = 0.20.

2 Environmental variance in generation 1 \( (\sigma_{E,1}^2) \) after selection.
**Progeny testing versus sib testing.** Table 4 shows genetic gain per time unit for progeny testing schemes in comparison to sib testing schemes. Progeny testing schemes are always superior for decreasing the environmental variance \((\Delta A_v)\), but are inferior for \(\Delta A_m\) unless the relative generation interval of progeny tested sires is short \((= 1.4)\). With \(v_{A_v} = -1\) (e.g. when \(\mu = 0.5\sigma_p\) lower than the optimum value with quadratic profit), progeny testing schemes give higher \(\Delta H\) than sib testing schemes only when the relative generation interval of progeny tested sires is short. With \(v_{A_v} = -5\) (e.g. when \(\mu = 0.1\sigma_p\) below the optimum), however, progeny testing schemes yield as good as or better \(\Delta H\) unless the relative generation interval of sires is 2.0. Progeny testing schemes are, therefore, superior for decreasing environmental variance, but in most cases provide a lower genetic gain in the aggregate genotype than sib testing schemes.

**Table 4.** Genetic gain per time unit in \(A_m\) and \(A_v\) and in the breeding goal for progeny testing schemes in comparison to sib testing schemes for different breeding goals as a function of the relative generation interval of progeny tested sires \((L_S)\).

<table>
<thead>
<tr>
<th>Breeding scheme</th>
<th>Breeding goal</th>
<th>Genetic gain</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>(v_{A_m})</td>
<td>(v_{A_v})</td>
</tr>
<tr>
<td>Sib testing</td>
<td>1</td>
<td>-1</td>
</tr>
<tr>
<td>Progeny testing</td>
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<td>-1</td>
</tr>
<tr>
<td></td>
<td>1.6</td>
<td>-1</td>
</tr>
<tr>
<td></td>
<td>1.8</td>
<td>-1</td>
</tr>
<tr>
<td></td>
<td>2.0</td>
<td>-1</td>
</tr>
<tr>
<td>Sib testing</td>
<td>1</td>
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<td>Progeny testing</td>
<td>1.4</td>
<td>-5</td>
</tr>
<tr>
<td></td>
<td>1.6</td>
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</tr>
<tr>
<td></td>
<td>1.8</td>
<td>-5</td>
</tr>
<tr>
<td></td>
<td>2.0</td>
<td>-5</td>
</tr>
</tbody>
</table>

1 Parameters values: \(\sigma_p^2 = 1, \sigma_{A_m}^2 = 0.3, \sigma_{A_v}^2 = 0.05, r_A = 0\), number of progeny per sire \(e = 100\), selected proportion sires \(e = 0.05\), selected proportion dams \(e = 0.20\).

2 Genetic gain in the aggregate genotype as a percentage relative to a sib testing scheme \((\Delta H / \Delta H_{sib}) \times 100\%\).
Common cases with non-linear profit

Quadratic profit. Figure 2A, B, and C show respectively the mean, phenotypic variance and the weighted profit of the population as a function of generation number for different values of $r_d$ with index selection in sib testing schemes for a quadratic profit equation. The population mean reaches the optimum in four generations and remains there in the fifth generation (Figure 2A), which is a consequence of a desired gains approach. In the first three generations $v_{A_m}$ is much larger than $v_{A_v}$ in absolute terms. Genetic gain in mean depends little on $r_d$ in the first three generations and the phenotypic variance changes mostly as a correlated response to selection on the mean (Figure 2B). In generations 4 and 5, the phenotypic variance decreases for all values of $r_d$. Profit increases curvilinearly, mostly due to increasing the mean to the optimum value (Figure 2C). The increase in profit due to decreasing phenotypic variance after generation 4 is small, relative to that due to changing the population mean to the optimum value. The improvement in profit is, however, still about $|0.25a_1|/a_2$ in comparison to ignoring $A_v$ in the breeding goal ($v_{A_v} = 0$). Therefore, for optimum traits with quadratic profit, it is most important to bring the mean to the optimum value and reduce the variance of the population when at the optimum.

Differential profit based on one threshold. Figure 3A shows the economic values of $A_m$ and $A_v$ as a function of the population mean when profit is based on one threshold. At the threshold ($P = -1$), $v_{A_m}$ is maximum and $v_{A_v}$ is zero, and animals below and above the threshold are equally frequent, such that the profit would increase substantially when the mean increases, but not when the variance changes. While $v_{A_m}$ is always positive, $v_{A_v}$ is positive (negative) when the population mean is lower (higher) than the threshold, because increasing (decreasing) the variance would increase the frequency of animals above the threshold.

Figures 4A and 4B show the population mean and phenotypic variance as a function of generation number. With index selection in sib testing schemes when profit is based on one threshold, the population mean increases almost constantly each generation, whereas the phenotypic variance increases slightly in the first two generations and decreases slightly afterwards. Thus with one threshold, most emphasis is on changing the mean and changing the variance is of minor importance.
Figure 2. Mean (A), phenotypic variance (B) and profit (C) as a function of generation number with a quadratic profit equation \( M = -(P - 0)^2 + 2 \) for different values of the genetic correlation \( (\sigma_p^2 = 1, \sigma_{\mu}^2 = 0.3, \sigma_{\nu}^2 = 0.05) \), number of progeny per sire = 100, selected proportion sires = 0.05, selected proportion dams = 0.20).
Differential profit based on two thresholds. When profit is based on two thresholds, the economic value of $A_m (v_{m_m})$ is at a maximum or minimum close to both thresholds, is zero in the optimum $P = 0$ and is positive (negative) when the population mean is lower (higher) than the optimum (Figure 3B). When the population mean is outside both thresholds, $v_{A_v}$ is slightly positive because increasing the variance will increase the frequency of animals within the thresholds. When the population mean is within the thresholds, $v_{A_v}$ is negative because decreasing variance will increase the frequency of animals within the optimum range. The pattern of $v_{A_m}$ is similar to that observed by Hovenier et al. (1993).

With continuous index selection the mean increases up to the optimum (Figure 4A) and the phenotypic variance increases for the first two generations and decreases afterwards with a substantial rate after generation 3 when the mean is (almost) in the optimum (Figure 4B). Due to the decreased phenotypic variance, 82% of the animals in generation 5 are within the optimum range, whereas only 68% of the animals would have been so without selection for reduced phenotypic variance. The mean and phenotypic variance change in a similar way as for quadratic profit. Furthermore, their changes are very similar for other threshold values as well (results not shown). As an approximation, one can say that the selection index forces first the mean to reach the optimum and after that the selection index targets the phenotypic variance to decrease. Changes in mean and variance of optimum traits are not very sensitive to the shape of the profit equation.
Figure 4. The mean (A) and phenotypic variance (B) as a function of generation number with selection on non-linear profit (quadratic \( a_1 = -1, \ a_2 = 2 \) and \( O = 0 \)), one threshold \( (P = -1) \) or two thresholds \( (P = -1, \ P = 1, \ O = 0) \) \( (\sigma_E^2 = 1, \ \sigma_{m}^2 = 0.3, \ \sigma_{p}^2 = 0.05, \ r_s = 0, \ \text{number of progeny per sire} = 100, \ \text{selected proportion sires} = 0.05, \ \text{selected proportion dams} = 0.20) \).
selection in the presence of genetic heterogeneity of environmental variance (Mulder et al., 2007). In general, accounting for the ‘Bulmer effect’ would decrease selection responses as a consequence of a lower genetic variance at the equilibrium, but the effect on ranking of breeding schemes is small (Wray and Hill, 1989). More importantly, perhaps, the Bulmer effect leads to changes in the genetic variance in mean and as such obscures the responses in phenotypic variance obtained from changing the environmental variance. The contribution of the Bulmer effect to the phenotypic variance is at most about 6-8% of the phenotypic variance with an initial $h_m^2 = 0.3$ (based on formulae in Dekkers (1992), comparing the equilibrium genetic variance with the genetic variance in the base generation). However, if the breeding goal has been to select on the mean for more than two or three generations, the genetic variance in mean becomes rather stable and responses in phenotypic variance would be almost entirely due to responses in environmental variance.

In this study, selection responses were predicted using a selection index framework in which, in principle, fixed effects are assumed to be known without error. In practice, fixed and random effects are estimated simultaneously using a mixed model BLUP analysis. There may be fixed effects both for the mean (e.g. herd effect) and the variance (e.g. heterogeneity of variance between herds). Heterogeneity of variance between herds is commonly found for milk production of dairy cattle (e.g. Brotherstone and Hill, 1986), for example, and is accounted for in standard breeding value estimation (e.g. Meuwissen et al., 1996). A model with genetically structured environmental variance can be used to estimate simultaneously breeding values and fixed effects for mean and environmental variance (SanCristobal-Gaudy et al., 1998; Sorensen and Waagepetersen, 2003). Disentangling heterogeneity of environmental variance due to genotype from that due to herd environment is, however, challenging and may require even larger half-sib groups than suggested by Mulder et al. (2007). Results in this study should therefore be interpreted as using an effective number of half-sibs that is lower than the actual number.

There is evidence that heterozygotes tend to have a smaller environmental variance than homozygotes (Robertson and Reeve, 1952; Mackay and Lyman, 2005), such that selection for reduced variance would favor heterozygotes. Furthermore, inbreeding reduces the Mendelian sampling variance among progeny, such that selection for reduced variance would favor more inbred animals. Both aspects reduce genetic variance in mean amongst selected individuals, which would be an unfavorable consequence while genetic improvement of the mean is still important. The effect of inbreeding level of a parent on Mendelian sampling variance in its progeny can be eliminated, however, by using the additive genetic relationship matrix. Furthermore, the effect of selective advantage of heterozygotes on genotype frequencies is negligible for the infinitesimal model. Although selection experiments in Drosophila and Tribolium have indeed shown that selection for reduced phenotypic variance decreases both the environmental and the genetic variances (Kaufman et al., 1977; Cardin and Minvielle,
1986), it is not known whether the latter is due to build up of gametic phase disequilibrium or break-down of infinitesimal model assumptions.

**Exploiting genetic heterogeneity of environmental variance in breeding programs**

When there is genetic variation in environmental variance and the economic value of variance (per unit²) is at least of the same magnitude as the economic value of the mean (per unit), it can be worthwhile to exploit this genetic heterogeneity in breeding programs. We consider in turn steps needed for implementation in practice: 1) estimation of breeding values for environmental variance, 2) construction of a selection criterion, and 3) optimization of the breeding program.

For the first step, breeding values for mean and environmental variance can be estimated by extending the mixed model framework (SanCristobal-Gaudy et al., 1998; Sorensen and Waagepetersen, 2003) and implementing this in software for routine genetic evaluation. Due to the low heritability of environmental variance, EBV for environmental variance would heavily rely on family information. Large family group sizes (e.g. 100 half-sibs progeny) are necessary to estimate $EBV_v$ with sufficient accuracy (Mulder et al., 2007).

Secondly, when EBV are based on a multivariate approach (SanCristobal-Gaudy et al., 1998; Sorensen and Waagepetersen, 2003), a linear selection index, $I = \gamma_m EBV_m + \gamma_v EBV_v$, can be used as the selection criterion. A linear index with economic values derived as first derivatives is, however, not optimal with non-linear profit equations (Goddard, 1983). If there is genetic variance only for the mean and if economic values are updated each generation, such an index is almost as effective as one with weights optimized to maximize profit over a given time horizon and better than quadratic selection indices (Goddard, 1983; Groen et al., 1994). Formally, the proposed index is not linear, because the $EBV_v$ is based upon quadratic terms of phenotype ($\overline{P^2}$ and $varW$). Consequently, the conclusion of Goddard (1983) that the optimum linear index is always better than a non-linear index does not hold if there is genetic variation in environmental variance. A quadratic index as proposed by Wilton et al. (1968) and implemented by SanCristobal-Gaudy et al. (1998) to breed for an optimum trait with genetic variation in environmental variance puts too much emphasis on $\overline{P^2}$, however, which contains no information about genetic variation in mean and very little about genetic variation in environmental variance. Hence, it is worse than a continuously updated linearized selection index as used in this study (results not shown). Therefore, a linear index with updating economic values each generation is recommended for practical implementation.

Finally, the breeding program may need to be optimized when including environmental variance in the breeding goal and in the index. For example, our results show that progeny testing schemes are more efficient in reducing environmental variance than sib testing
schemes. Therefore, when reducing variance is a major goal, progeny testing schemes may be better than sib testing schemes even at the cost of a longer generation interval.

CONCLUSIONS

This study shows that it is possible to change simultaneously the mean and the variance of traits in livestock breeding programs if there is genetic heterogeneity of environmental variance. The ability to change the variance in the desired direction depends on the genetic correlation between the additive genetic effects for mean and environmental variance and on the economic values in the breeding goal. Inclusion of environmental variance in the breeding goal is of importance only when the profit equation is non-linear, for example a trait with an intermediate optimum. With optimum traits, selection pressure shifts gradually from the mean to the variance when approaching the optimum and most economic gain is initially due to change in mean. As the optimum is approached, such that uniformity is the main goal, reduction of variance could further improve economic merit. Progeny testing schemes are predicted to give more rapid change in the environmental variance than sib testing schemes, but at the cost of a lower genetic gain in mean, mainly due to prolonging generation intervals.

ACKNOWLEDGEMENT

HM thanks Johan van Arendonk, Bart Ducro and Roel Veerkamp for helpful comments on earlier versions of this article and Egbert Knol and Addie Vereijken for valuable discussions about the practical relevance of this research. WGH thanks the Biotechnology and Biological Sciences Research Council for research support.

REFERENCES

Selection for uniformity in livestock


APPENDIX 1

The P - and G - matrix of the selection index

The P - and G - used in setting up the selection index are given here without giving the derivation of the elements (see Mulder et al., 2007):

\[
P = \begin{bmatrix}
\text{var}(P_k) & \text{cov}(P_k, P_k^2) & \text{cov}(P_k, \overline{P}) & \text{cov}(P_k, (\overline{P})^2) & \text{cov}(P_k, \text{var}W) \\
\text{cov}(P_k, P_k^2) & \text{var}(P_k^2) & \text{cov}(P_k^2, \overline{P}) & \text{cov}(P_k^2, (\overline{P})^2) & \text{cov}(P_k^2, \text{var}W) \\
\text{cov}(P_k, \overline{P}) & \text{cov}(P_k^2, \overline{P}) & \text{var}(\overline{P}) & \text{cov}(\overline{P}, (\overline{P})^2) & \text{cov}(\overline{P}, \text{var}W) \\
\text{cov}(P_k, (\overline{P})^2) & \text{cov}(P_k^2, (\overline{P})^2) & \text{cov}(\overline{P}, (\overline{P})^2) & \text{var}((\overline{P})^2) & \text{cov}((\overline{P})^2, \text{var}W) \\
\text{symmetric} & \text{cov}((\overline{P})^2, \text{var}W) & \text{var}(\overline{P}) & \text{var}(\overline{P}) & \text{var}(\text{var}W)
\end{bmatrix}
\]

\[
\text{var}(P_k) = \sigma_p^2
\]

\[
\text{cov}(P_k, P_k^2) = 3\text{cov}_{\lambda_{mv}}
\]

\[
\text{var}(P_k^2) = 2\sigma_p^4 + 3\sigma_{\lambda_{mv}}^2
\]

\[
\text{cov}(P_k, \overline{P}) = a_k \sigma_{\lambda_{mv}}^2
\]

\[
\text{cov}(P_k^2, \overline{P}) = a_k \text{cov}_{\lambda_{mv}}
\]

\[
\text{var}(\overline{P}) = \left(\sigma_p^2 + a_w(n-1)\sigma_{\lambda_{mv}}^2 \right)/n
\]

\[
\text{cov}(P_k, (\overline{P})^2) = a_k \text{cov}_{\lambda_{mv}} / n
\]

\[
\text{cov}(P_k^2, (\overline{P})^2) = 2a_k^2 \sigma_{\lambda_{mv}}^4 + a_k \sigma_{\lambda_{mv}}^2 / n
\]

\[
\text{cov}(\overline{P}, (\overline{P})^2) = \left[3 + 3a_w(n-1)\text{cov}_{\lambda_{mv}} \right]/n^2
\]

\[
\text{var}((\overline{P})^2) = 2\left(\sigma_p^2 + a_w(n-1)\sigma_{\lambda_{mv}}^2 \right)/n + \left[3 + 3a_w(n-1)\sigma_{\lambda_{mv}}^2 \right]/n^3
\]

\[
\text{cov}(P_k, \text{var}W) = a_k \text{cov}_{\lambda_{mv}}
\]

\[
\text{cov}(P_k^2, \text{var}W) = a_k \sigma_{\lambda_{mv}}^2
\]

\[
\text{cov}(\overline{P}, \text{var}W) = \left[3 + a_w(n-3)\text{cov}_{\lambda_{mv}} \right]/n
\]
\[ \text{cov}(\bar{P}^2, \text{var}W) = \left[ 3 + a_w(n-3)\sigma_{\tau_w}^2 \right] / n^2 \]

\[ \text{var(var}W) = \left[ 2\left(\sigma_p^2 - a_w\sigma_{\tau_w}^2 \right) \right]/(n-1) + \left[ \frac{(3(n-1) + a_w(n^2 - 2n + 3)\sigma_{\tau_w}^2}{n(n-1)} \right] \]

and \[ G = \begin{bmatrix} \sigma_{\tau_w}^2 & \text{cov}_{\tau_w}\tau_w \\ \text{cov}_{\tau_w}\tau_w & \sigma_{\tau_w}^2 \\ a_k\sigma_{\tau_w}^2 & a_k\text{cov}_{\tau_w}\tau_w \\ a_k\text{cov}_{\tau_w}\tau_w & a_k\sigma_{\tau_w}^2/n \end{bmatrix}, \]

where \( a_k \) is the additive genetic relationship between animal \( k \) and the group of half-sibs \(( a_k = 0.25 \) for sib testing; \( a_k = 0.5 \) for progeny testing), \( a_w \) is the additive genetic relationship among relatives within the group \(( a_w = 0.25 \) for half-sibs).

**APPENDIX 2**

**The relative emphasis on variance for optimum traits with quadratic profit and differential profit with two thresholds**

**Quadratic profit:** The relative emphasis of \( A \) in the breeding goal

\[ (\text{Rel}_A) = \left| \frac{v_{A_w}\sigma_{A_w}}{v_{A_w}\sigma_{A_w} + v_{\tau_w}\sigma_{\tau_w}} \right| \] with quadratic profit is \( \text{Rel}_A = \frac{GCV^2 \left(1 - h_m^2 \right)}{GCV^2 \left(1 - h_m^2 \right) + 2xh_m^2} \), where

\[ x = \frac{\mu - \Omega}{\sigma_p} \] and \( GCV^2 = \sigma_{A_w}^2 / \sigma_p^2 \). The relative emphasis \( \text{Rel}_A \) is therefore independent of \( \sigma_p^2 \) and completely determined by the distance of \( \mu - \Omega \) expressed in \( \sigma_p \).

**Differential profit with two thresholds:** With differential profit based on two thresholds, the relative emphasis \( \text{Rel}_A \) can be expressed as \( \text{Rel}_A = \frac{GCV^2 \left(1 - h_m^2 \right)}{GCV^2 \left(1 - h_m^2 \right) + 2y\tau_m^2} \), where

\[ y = \frac{z_i - z_u}{z_i \tau_i - z_u \tau_u} \] The relative emphasis \( \text{Rel}_A \) is therefore independent of \( \sigma_p^2 \) and completely determined by the standardized distances of \( \mu \) with \( T_i \) and \( T_u \). A first order Taylor series
approximation of $y$ when $\mu = 0$ is equal to $x$, showing the similarity between $Rel_{\mu}$ with quadratic profit and differential profit with two thresholds when the population mean is close to the optimum.

**APPENDIX 3**

**Comparison of predicted responses from selection index theory with realized responses from Monte Carlo simulation**

Monte Carlo simulation was used to evaluate the goodness of fit of predictions of Equations 12 and 13 for sib testing and progeny testing schemes after one generation of index selection with different breeding goals. Fifty replicates with 500,000 sires with 100 half-sib progeny per sire were generated. The breeding values and environmental effects were sampled as explained in Mulder et al. (2007). Sires and dams were selected by truncation on an index (Equation 3). Sires were either sib tested or progeny tested; dams were always sib tested. Genetic selection differentials were calculated as the mean $A_m$ and $A_v$ of all selected sires and dams and averaged over replicates. Genetic gain per time unit was calculated with Equation 11, assuming a relative generation interval of progeny tested sires of 1.6. Prediction errors were small for $\Delta A_m$ when $v_{A_s} = 0$ or $v_{A_v} = -1$, but larger when $v_{A_v} = -5$ (see Table A1). For $\Delta A_v$ the opposite was observed: prediction errors were small when $v_{A_v} = -5$. Prediction errors were larger for sib testing schemes than for progeny testing schemes. Although predictions were not perfect, it can be concluded that deterministic predictions based on selection index equations can be used to evaluate the possibility of changing simultaneously the mean and the variance of a trait for different sets of parameters in breeding programs.
Table A1. Predicted genetic gain per time unit (prediction errors\(^1\)) for \(A_m\), \(A_v\) and the breeding goal (\(\Delta A_m\), \(\Delta A_v\) and \(\Delta H\)) with sib testing and progeny testing schemes for different breeding goals (\(v_{A_m} = 1; v_{A_v}\) is varied\(^2\)).

<table>
<thead>
<tr>
<th>Breeding scheme</th>
<th>(v_{A_v})</th>
<th>(\Delta A_m)</th>
<th>(\Delta A_v)</th>
<th>(\Delta H)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sib testing</td>
<td>0</td>
<td>0.612 (0.003)</td>
<td>0.000 (-0.029)</td>
<td>0.612 (0.003)</td>
</tr>
<tr>
<td></td>
<td>-1</td>
<td>0.598 (-0.002)</td>
<td>-0.029 (-0.023)</td>
<td>0.627 (0.021)</td>
</tr>
<tr>
<td></td>
<td>-5</td>
<td>0.414 (0.072)</td>
<td>-0.099 (0.009)</td>
<td>0.907 (0.028)</td>
</tr>
<tr>
<td>Progeny testing</td>
<td>0</td>
<td>0.603 (0.000)</td>
<td>0.000 (-0.008)</td>
<td>0.603 (0.000)</td>
</tr>
<tr>
<td></td>
<td>-1</td>
<td>0.582 (-0.001)</td>
<td>-0.039 (-0.005)</td>
<td>0.622 (0.004)</td>
</tr>
<tr>
<td></td>
<td>-5</td>
<td>0.370 (0.031)</td>
<td>-0.123 (0.009)</td>
<td>0.983 (-0.014)</td>
</tr>
</tbody>
</table>

\(^1\) Prediction errors between brackets: predicted – observed in Monte Carlo simulation.

\(^2\) Parameters values: \(\sigma_p^2 = 1\), \(\sigma_{A_m}^2 = 0.3\), \(\sigma_{A_v}^2 = 0.05\), \(r_A = 0\), number of progeny per sire = 100, selected proportion sires = 0.05, selected proportion dams = 0.20, relative generation interval of progeny tested sires \(L_S = 1.6\).
Chapter 7

General discussion

H. A. Mulder

Animal Breeding and Genetics Group, Wageningen University, PO Box 338, 6700 AH Wageningen, The Netherlands.
The general discussion consists of two parts. Section 7.1 deals with modeling and experimental designs to estimate genetic variation in environmental sensitivity. Section 7.2 deals with optimization of breeding programs with genetic variation in environmental sensitivity and breeding goal differences between environments.

7.1 Modeling and Experimental Designs to Estimate Genetic Variation in Environmental Sensitivity

7.1.1 Introduction

Applied and theoretical geneticists are already for a long time interested in genetic differences in environmental sensitivity or genotype by environment interaction (G × E). In animal breeding, Hammond (1947) advocated to test animals in environments where the trait of interest is best expressed. Falconer (1952) proposed the genetic correlation between performances measured in different environments as a measure of G × E. James (1961) and Dickerson (1962) investigated the consequences of G × E for breeding programs. In plant breeding, Yates and Cochran (1938), Finlay and Wilkinson (1963), Eberhart and Russell (1966) and Shukla (1972) developed different stability measures to rank genotypes based on performance in different genotype × location × year combinations. In evolutionary biology, many selection experiments have been carried out, mostly using Drosophila or Tribolium to investigate the effect of selection under different environmental conditions (Waddington, 1960; Kindred, 1965; Yamada and Bell, 1969). Other selection experiments were carried out to investigate whether phenotypic variance can be decreased by selection (Waddington, 1960; Rendel et al., 1966).

Although we have nowadays much better tools to analyze data and a better statistical understanding of G × E and genetic heterogeneity of environmental variance than 40-50 years ago, we still have limited biological understanding of the complex relationships between genotype and phenotype. Furthermore, it appears that different disciplines use different terminology and models to deal with similar phenomena.

The aim of section 7.1 is, therefore, in the first place to summarize terminology and to review models to account for G × E and genetic heterogeneity of environmental variance in animal breeding, plant breeding and theoretical genetics. Secondly, some simple experimental designs to estimate either G × E or genetic heterogeneity of environmental variance will be evaluated. Thirdly, genetic control of environmental sensitivity will be briefly reviewed. Finally, a few interesting subjects for future research regarding environmental sensitivity will be given from an animal breeding point of view.
7.1.2 DEFINITIONS

G × E is the phenomenon that genotypes differ in their response to environmental differences (Falco
ner and Mackay, 1996; Lynch and Walsh, 1998). Two forms of G × E can be distinguished: reranking of genotypes across environments and different scaling of phenotypic performance in different environments without reranking, causing heterogeneity of variance between environments (Fac
coner and Mackay, 1996). The presence of G × E means the existence of genetic variation in response to environmental parameters, in other words genetic variation in phenotypic plasticity or environmental sensitivity. Phenotypic stability is the opposite of phenotypic plasticity and means, therefore, the genotype’s tendency to exhibit constant phenotypic expression in different environments (Lynch and Walsh, 1998).

![Diagram of genotype by environment interaction]

**Figure 1.** Schematic representation of genotype by environment interaction in macro- and micro-
environments.
General discussion

Environments that differ by some known factor, such as diet or soil for example, are called macro-environments. As a consequence, genotypic differences in environmental sensitivity may be detected as a significant statistical interaction between genotype and macro-environment when a sample of genotypes is tested in a number of macro-environments (Jinks and Pooni, 1988; Falconer and Mackay, 1996; Lynch and Walsh, 1998). A single macro-environment, however, may have micro-environmental differences within it. Consequently, genotypic differences in environmental sensitivity may be detected as a significant heterogeneity of within-family variance within the same macro-environment (Jinks and Pooni, 1988; Falconer and Mackay, 1996; Lynch and Walsh, 1998). Genetic differences in environmental sensitivity within a macro-environment are therefore observed as genetic heterogeneity of environmental variance. Figure 1 gives a schematic representation of $G \times E$ and genetic heterogeneity of environmental variance. Environmental canalization can be defined as phenotypic insensitivity to micro-environmental influences (in contrast, genetic canalization is phenotypic insensitivity to mutations) (Waddington, 1942; 1960; Debat and David, 2001; Flatt, 2005). Definitions are summarized in Table 1.

**Table 1.** Definitions of phenomena related to genotype by environment interaction in macro- and micro-environments.

<table>
<thead>
<tr>
<th>Phenomenon</th>
<th>Definition</th>
</tr>
</thead>
<tbody>
<tr>
<td>Genotype by environment interaction</td>
<td>Different genotypes react differently to environmental differences (Falconer and Mackay, 1996)</td>
</tr>
<tr>
<td>Phenotypic plasticity = environmental sensitivity</td>
<td>The ability of a genotype to alter its phenotypic expression in response to environmental influences (Bradshaw, 1965)</td>
</tr>
<tr>
<td>Phenotypic stability</td>
<td>Genotype’s tendency to exhibit constant phenotypic expression in different environments (Lin et al., 1986; Lynch and Walsh, 1998)</td>
</tr>
<tr>
<td>Reaction norm</td>
<td>Phenotypic expression of a genotype as a function of the environment (Wolterek, 1909; Schmalhausen, 1949)</td>
</tr>
<tr>
<td>Environmental canalization</td>
<td>Reduced sensitivity of a genotype to changes in micro-environment (Waddington, 1942; 1960; Debat and David, 2001; Flatt, 2005)</td>
</tr>
</tbody>
</table>
7.1.3 MODELING GENETIC VARIATION IN ENVIRONMENTAL SENSITIVITY

In this section, models for genotype by macro-environment interaction \((G \times E)\) and for genetic heterogeneity of micro-environmental variance are discussed and compared. With respect to \(G \times E\), the use of models in animal and plant breeding is discussed. Furthermore, a combined model is given that simultaneously accounts for genotype by macro-environment interaction and genetic heterogeneity of micro-environmental variance.

7.1.3.1 Genotype by macro-environment interaction

Models. There are basically three methods to model \(G \times E\) between macro-environments: (1) interaction model, (2) multiple-trait model or (3) reaction norm model (e.g., reviews by Van Eeuwijk, 1995; Lynch and Walsh, 1998; De Jong and Bijma, 2002). All are augmentations of the classic additive model assuming that genotypes perform equally in different environments, i.e. no \(G \times E\) (Falconer and Mackay, 1996; Lynch and Walsh, 1998):

\[
P_{ijk} = \mu + A_i + E_j + e_{ijk}
\]

(1)

where \(P_{ijk}\) is the phenotype of individual \(k\) of genotype \(i\) in environment \(j\), \(A_i\) is the random breeding value of genotype \(i\), \(E_j\) is the fixed environmental main effect and \(e_{ijk}\) is the random residual effect of individual \(k\). In animal breeding, the environmental main effect is usually considered as fixed, whereas the breeding value and the residual effect are considered as random. Consequently, \(\text{E}(P_{ijk}) = \mu + E_j\) and \(\text{var}(P_{ijk} | E_j) = \sigma_A^2 + \sigma_e^2\), where \(\sigma_A^2\) is the additive genetic variance and \(\sigma_e^2\) is the residual environmental variance.

In the interaction model, Equation 1 is extended with the random interaction term \(AE_{ij}\) (Falconer and Mackay, 1996; Lynch and Walsh, 1998):

\[
P_{ijk} = \mu + A_i + E_j + AE_{ij} + e_{ijk}
\]

(2)

with \(\text{E}(P_{ijk}) = \mu + E_j\) and \(\text{var}(P_{ijk} | E_j) = \sigma_A^2 + \sigma_{AE}^2 + \sigma_e^2\), where \(\sigma_{AE}^2\) is the variance of the \(AE_{ij}\)-terms.

In a multiple-trait model, performances in different macro-environments are considered as different traits that are genetically correlated (Falconer, 1952). A non-unity genetic correlation indicates genetic reranking of animals between environments and therefore the existence of \(G \times E\). The model would be similar to (1), except for the variance-covariance structures:
General discussion

\[ P_{ijk} = \mu + A_i + E_j + e_{ijk} \]

(3)

with \( \text{E}(P_{ijk}) = \mu + E_j \) and \( \text{var}(P_{ijk} \mid E_j) = \sigma_{A,i}^2 + \sigma_{e,j}^2 \), where \( A_i \) is the breeding value of genotype \( i \) for performance in environment \( j \), \( \sigma_{A,i}^2 \) is the additive genetic variance in environment \( j \) and \( \sigma_{e,j}^2 \) is the residual environmental variance in environment \( j \). The breeding values in different environments are assumed to follow a multivariate normal distribution with an additive genetic variance-covariance matrix. In case of two environments, the variance-covariance matrix is

\[
G = \begin{bmatrix}
\sigma_{A,1}^2 & r_{A,12} \sigma_{A,1} \sigma_{A,2}
\end{bmatrix},
\]

where \( \sigma_{A,1}^2 \) (\( \sigma_{A,2}^2 \)) is the genetic variance in environment 1 (2) and \( r_{A,12} \) is the additive genetic correlation between environment 1 and 2. In this way, heterogeneity of genetic variance and reranking between environments can be separately accounted for.

In a reaction norm model, a phenotype is modeled as a function of an environmental parameter (Woltzke, 1909; Schmalhausen, 1949). A linear reaction norm model is (Van Eeuwijk et al., 2005; Strandberg, 2006):

\[ P_{ijk} = \mu + E_j + \beta X_j + A_{i,j} + A_{x,j} X_j + e_{ijk} \]

(4)

with \( \text{E}(P_{ijk}) = \mu + E_j + \beta X_j \) and \( \text{var}(P_{ijk} \mid E_j) = \sigma_{A,i}^2 + 2X_j \text{cov}(A_i, A_j) + X_j^2 \sigma_{A,i}^2 + \sigma_{e,j}^2 \), where \( \beta \) is the average slope of the reaction norm on environmental parameter \( X_j \), \( A_{i,j} \) is the breeding value for the level of the reaction norm of genotype \( i \), \( A_{x,j} \) is the breeding value for the slope of the reaction norm of genotype \( i \), \( \sigma_{A,i}^2 \) is the additive genetic variance in \( A_{i,j} \), \( \sigma_{A,i}^2 \) is the additive genetic variance in \( A_{x,j} \), and \( \text{cov}(A_i, A_j) = r_{A,i} \sigma_{A,i} \sigma_{A,j} \), where \( r_{A,i} \) is the genetic correlation between the breeding values \( A_{i,j} \) and \( A_{x,j} \). The environmental main effect \( E_j \) accounts now for all environmental effects, except the effect of \( X_j \), which is accounted for with the fixed reaction norm. The breeding value for the slope is expressed as a deviation from the mean reaction norm. The reaction norm model requires a continuous descriptor of environment, for example, temperature in environment \( j \). The breeding values for the level and the slope are assumed to follow a bivariate normal distribution with a genetic variance-covariance matrix

\[
G_{RN} = \begin{bmatrix}
\sigma_{A,i}^2 & r_{A,i} \sigma_{A,i} \sigma_{A,j}
\end{bmatrix},
\]

In practice, higher-order reaction norms may need to be used and consequently the genetic variance-covariance matrices among reaction norm parameters are larger.
Comparison of models. Six criteria will be used to compare the above mentioned models: (1) estimation of $G \times E$, (2) flexibility of variance-covariance structure, (3) predictability of phenotype, (4) biological interpretation, (5) genetic interpretation, for example, for consequences in breeding programs, and (6) possibility for selection on environmental sensitivity itself. Table 2 gives an overview of advantages and disadvantages of models. The best model is given a ‘+’, the worst model is given a ‘-’ and the model in between a ‘0’. The scores are subjectively given based on qualitative arguments, which are given below.

Table 2. Comparison of models for $G \times E$ between macro-environments. The best model is given a ‘+’, the worst model a ‘-’ and the model in between a ‘0’.

<table>
<thead>
<tr>
<th>Criterion</th>
<th>Interaction model</th>
<th>Multi-trait model</th>
<th>Reaction norm model</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nature of environmental scale</td>
<td>Class</td>
<td>Class</td>
<td>Continuous</td>
</tr>
<tr>
<td>Estimation of $G \times E$</td>
<td>0/-</td>
<td>+</td>
<td>0</td>
</tr>
<tr>
<td>Flexibility variance – covariance structure</td>
<td>-</td>
<td>+</td>
<td>0</td>
</tr>
<tr>
<td>Predictability of phenotype</td>
<td>-</td>
<td>0</td>
<td>+</td>
</tr>
<tr>
<td>Biological interpretation of $G \times E$</td>
<td>-</td>
<td>0/+</td>
<td>+</td>
</tr>
<tr>
<td>Genetic interpretation of $G \times E$</td>
<td>-</td>
<td>+</td>
<td>0</td>
</tr>
<tr>
<td>Selection on macro-environmental sensitivity</td>
<td>-</td>
<td>0/+</td>
<td>+</td>
</tr>
</tbody>
</table>

The interaction model scores low for all criteria. A large problem with the model is the difficult interpretation of the interaction terms, especially with unbalanced data and heterogeneity of variance among environments (Dickerson, 1962; Fernando et al., 1984). Only under the assumption of homogeneity of variances across environments, an average genetic correlation between environments can be calculated as $r_A = \frac{\sigma_A^2}{\sigma_A^2 + \sigma_{AE}^2}$. The multi-trait model and the reaction norm model have both advantages and disadvantages. The multi-trait model excels in flexibility of variance-covariance structures and the utility for investigation of consequences of $G \times E$ for breeding programs (see Chapter 2, 3 and 4). A disadvantage of the multi-trait model is that it can not be used with a large number of environments because of estimation and convergence problems (Strandberg, 2006). The reaction norm model can help in biological understanding of $G \times E$ when genotypes differ in response to a specific environmental parameter, such as temperature, and can be used to predict phenotypic performance in other environments not under study, which can be characterized by the same environmental parameter. The problem, however, is that it is often difficult to find the environmental parameter explaining $G \times E$. When the mean phenotype of all genotypes is used as an environmental parameter due to lack of appropriate environmental parameters, the
genetic variance in slope ($\sigma^2_A$) is underestimated with random regression using REML (Calus et al., 2004). The problem is that the mean phenotype of all genotypes is not known without error. Gibbs sampling techniques are proposed to overcome this problem and seem to better deal with uncertainty about the mean phenotype, resulting in no underestimation of $\sigma^2_A$ (Su et al., 2006). Another potential problem with using the mean phenotype is that environments may rerank, when the true reaction norm is non-linear, for example, with an intermediate optimum. As a consequence, suboptimal and supraoptimal environments may be grouped together in terms of mean phenotype, although these environments are very different (Baker, 1988; Strandberg, 2006). Reaction norm models are useful when the slope of the reaction norm (e.g., heat tolerance) is part of the breeding goal. Reaction norm models are less flexible with respect to variance-covariance structure, for example, with a linear reaction norm the variance function is quadratic, but flexibility increases with increasing the order of the reaction norm. For genetic interpretation of $G \times E$, for example, for breeding programs, a genetic correlation between two environments can be calculated as (Kirkpatrick et al., 1990; De Jong and Bijma, 2002)

$$ r_{A,12} = \frac{x_j G_{RN} x_2}{\sqrt{x_j ' G_{RN} x_1 \times x_2 ' G_{RN} x_2}}, $$

where $x_j ' = [1 \ \ X_j]$ for a linear reaction norm. Overall, it can be concluded that multi-trait models are preferred with a limited number of environments, mainly because of the problems of the reaction norm model with finding appropriate environmental parameters and the good properties of multi-trait models for genetic interpretation of $G \times E$.

**Use of models in animal breeding.** In animal breeding, $G \times E$ is estimated using relatives that are performing in different environments, because individual animals produce in only one environment. Most genetic links originate from sires with progeny in different environments, but other genetic links can be used as well to estimate $G \times E$ by using the additive genetic relationship matrix in mixed models. Animal breeders are interested in comparison of direct and correlated responses, and therefore in the genetic correlation between environments.

The interaction model is hardly used anymore to estimate $G \times E$, because of its limitations with unbalanced data and heterogeneity of variance, but sire-by-herd interaction models are still in use in some countries in breeding value estimation to account for heterogeneity of variance and preferential treatment (e.g., Wiggans and Goddard, 1997). The multi-trait model is heavily used, because of the interest in knowing the genetic correlation between environments. A large application of this model is the international breeding value estimation of dairy bulls by Interbull using Multiple Across-Country Evaluation (MACE) (Schaeffer, 1994; Interbull, 2007). Each country is considered as a different environment and genetic correlations are estimated between all combinations of countries. The reaction norm model is in use since the introduction of random regression in animal breeding (Schaeffer and Dekkers, 1994). The difficulty has been to find appropriate environmental parameters describing $G \times E$.
within and across countries (Calus and Veerkamp, 2003; Fikse et al., 2003; Zwald et al., 2003b; Kolmodin et al., 2004; Windig et al., 2005). External environmental parameter would be favored, such as temperature, instead of derived environmental parameters, such as mean phenotype. Promising results were obtained by Ravagnolo and Misztal (2000, 2002), showing genetic variation in heat tolerance, which could be exploited in breeding programs. So far, the reaction norm model is used only for scientific research and has not yet been implemented in animal breeding practice.

**Use of models in plant breeding.** In plant breeding, different varieties are tested in a number of environments, so-called multi-environment trials (Van Eeuwijk, 1995). Usually a limited number of varieties is tested in a relatively large number of environments. The environmental conditions are, however, likely to be more variable than in animal husbandry, for example due to more direct effects of variation in different weather conditions and soil quality on performance. As a result, G × E is likely to be larger than in animal breeding. Plant breeding programs can be split into two phases: (1) population improvement and (2) variety testing. Most literature about G × E deals with variety testing, mainly about development of tools to rank varieties on mean yield and stability of yield across environments (e.g., Lin et al., 1986; Piepho and Van Eeuwijk, 2002). Furthermore, the use of clones makes it easy to test the same genotype in different environments and to make many replicates of the same genotype. The genotypic effect is, therefore, usually considered as fixed, in contrast to animal breeding.

Interaction models were heavily used in the past, whereas multi-trait model have been hardly used. Reaction norm models have been and are still used. It started with the joint regression model by Finlay and Wilkinson (1963) with regression on the phenotypic mean. The method has been extended to additive main effects and multiplicative interaction models (AMMI) (Gauch, 1988). In AMMI-models the interaction is described in terms of differential sensitivity to the most discriminating environmental variables that can be constructed. These environmental variables are hypothetical and estimated from the data. The random AMMI-model can be formulated as (Van Eeuwijk, 1995):

\[ P_{ijk} = \mu + A_i + E_j + \sum_{m=1}^{M} a_{mi} e_{pj} + e_{ijk} \]  

(5)

where \( a_{mi} \) is the random additive genetic sensitivity score of genotype \( i \) and \( e_{pj} \) is the environmental score for the hypothetical environmental parameter \( m \) for environment \( j \). Essentially, the matrix with interaction terms is decomposed by singular value decomposition (= a more general form of principal component analysis) (Van Eeuwijk, 1995). Van Eeuwijk (1995) and Van Eeuwijk et al. (1995) advocated the use of the AMMI-model as a starting point to explore G × E. Subsequently, factorial regression (= reaction norm model with
external environmental parameter, e.g. temperature) can be used to explain the G × E in terms of external environmental variables. The joint application of both models can lead to an interpretation of G × E in terms of differential sensitivity to external environmental variables. A big advantage of the AMMI-model is that environmental parameters do not need to be known beforehand. AMMI-models are of great interest in animal breeding, because of the difficulties to find appropriate environmental parameters to explain G × E between herds, but they might give computational difficulties due to a large number of herd environments, for example, in dairy cattle. Improper definition of macro-environments might be one of the reasons for the discrepancy between the feelings of farmers that G × E is substantial, whereas geneticists are not detecting substantial G × E. AMMI-models may help in defining proper macro-environments.

7.1.3.2 Genetic heterogeneity of micro-environmental variance
Geneiic heterogeneity of micro-environmental variance can be modeled in three ways: (1) an additive model, (2) an exponential model and (3) a reaction norm model. Within one macro-environment, the additive model is (Hill and Zhang, 2004; Chapter 5&6):

\[ P_i = \mu + A_{m,i} + \chi_i \sqrt{\sigma_e^2 + A_{v,i}} \]  

(6)

where \( \mu \) and \( \sigma_e^2 \) are, respectively, the mean trait value and the mean micro-environmental variance within a macro-environment of the population, \( A_{m,i} \) and \( A_{v,i} \) are, respectively, the breeding value for the mean and micro-environmental variance of genotype \( i \) and \( \chi_i \) is a standard normal deviate for the micro-environmental effect.

The exponential model is (SanCristobal-Gaudy et al., 1998):

\[ P_i = \mu + A_{m,i} + \chi_i \exp\left(\frac{\ln(\sigma_{e,exp}^2) + A_{v,exp,i}}{2}\right) \]  

(7)

where \( \sigma_{e,exp}^2 \) is the micro-environmental variance when \( A_{v,exp} = 0 \), and \( A_{v,exp,i} \) is the breeding value for the micro-environmental variance of genotype \( i \) in the exponential model. In the exponential model, micro-environmental variances are multiplicative on the observed scale and additive on a log-scale.

The linear reaction norm model is (modified from Gavrilets and Hastings, 1994):

\[ P_{ij} = \mu + A_{m,i} + (\beta + A_{e,i})x_i + e_{i,RN} \]  

(8)
where \( x_i \) is a standard normal deviate, describing the unobserved micro-environment. Assuming \( r_{\text{mis}} = 0 \), the average micro-environmental variance is 
\[
\sigma^2_e = \beta^2 \sigma^2_x + \sigma^2_{A_g} \sigma^2_x + \sigma^2_{e,RN},
\]
which shows that the average micro-environmental variance is dependent on the reaction norm parameters. An alternative model is the additive-multiplicative model by Gimelfarb (1994), which is similar to a reaction norm model as in Equation 8.

The models in the Equations 6 and 7 are already compared in the discussion of Chapter 5. The models are slightly different, but parameters can be converted from one model to another (see Appendix 2 of Chapter 5 for comparison of models in Equation 6 and 7). The same analogy can be used to link the model in Equation 8 with the model in Equation 6. The genetic variance in micro-environmental variance in an additive model can be converted to parameters in a linear reaction norm model by equating the fourth central moments of the micro-environmental effects of the models in the Equations 6 and 8.

\[
E(E^4_{\text{Add}}) = E(E^4_{\text{RN}})
\]
\[
3E\left[\left(\sqrt{\sigma^2_x + A_g}\right)^4\right] = 3E\left[\left(\beta + A_g\right) x + e_{RN}\right]^4
\]  

The reaction norm model is overparameterized, because of having \( \beta \), \( \sigma^2_x \), \( \sigma^2_{A_g} \) and \( \sigma^2_{e,RN} \), whereas only \( \sigma^2_e \) (the average micro-environmental variance) and \( \sigma^2_{A_g} \) (via pedigree) are estimable. Two options can be chosen: (1) \( \beta = 0 \) and \( \sigma^2_x = 1 \) or (2) \( \sigma^2_{e,RN} = 0 \) and \( \sigma^2_x = 1 \). With the second option, the fourth moment blows up due to the elements involving \( \beta \). Although, a zero slope of a reaction norm is not likely, the first option \( \beta = 0 \) was chosen. One can say that \( \beta \neq 0 \) is captured in \( \sigma^2_{e,RN} \). Assuming that \( \beta = 0 \), \( \sigma^2_x = 1 \), Equation 9 can be rewritten as:

\[
\sigma^2_{A_g} = 2\sigma_{A_g}^4 \quad \text{(10a)}
\]
\[
\sigma^2_{e,RN} = \frac{1}{2\sigma^2_{A_g}} \quad \text{(10b)}
\]

Equation 10a shows that \( \sigma^2_{A_g} \) is directly related to \( \sigma^2_{A_g} \) and Equation 10b shows vice versa.
7.1.3.3 Combining genotype by macro-environment interaction and genetic heterogeneity of micro-environmental variance

$G \times E$ between macro-environments and $G \times E$ within macro-environments may have the same biological background, for example, differential response to temperature. Assume that we can define macro-environments by the mean temperature (e.g., North- versus South-Europe), then within a macro-environment differences in temperature can still be present. Based on the example given above we can define a combined model, assuming data of different macro-environments characterized by the environmental parameter $X_j$ and with variation in $X_j$ within macro-environment characterized as $x_k$. We can extend Equation 4 as follows:

$$P_{ijk} = \mu + \beta(X_j + x_k) + A_{i,j} + A_{x,j}(X_j + x_k) + e_{ijk} \quad (11)$$

Because $x_k$ is unknown, it is incorporated in the micro-environmental effect, so that Equation 11 becomes:

$$P_{ijk} = \mu + \beta X_j + A_{i,j} + A_{x,j} X_j + [(\beta + A_{x,j}) x_k + e_{ijk}] \quad (12)$$

Equation 12 is now a combination of Equation 4 and 8. In Equation 12, the differential genetic response to $x_k$ is enclosed in the micro-environmental effect (= residual). Consequently, the micro-environmental variance will be heterogeneous between genotypes. Assuming that environmental sensitivity ($A_j$) is the same between macro-environments and within macro-environments, the correlation should be unity as is already indicated by the same breeding value $A_j$ (see Figure 2 for an illustration). The combined model is also mentioned in Lynch and Walsh (1998) and Equation 12 is similar to the model by Wu and O’Malley (1998).

Equation 12 demonstrates a possible link between $G \times E$ and genetic heterogeneity of environmental variance. Assuming that $G \times E$, based on a linear reaction norm with $r_{A_{mx}} = r_{A_{sy}} = 0$, is responsible for genetic heterogeneity of environmental variance, Equation 10b can be used to convert estimates of $\sigma^2_{A_{x}}$ into estimates of average genetic correlations between micro-environments, assuming $A_m = A_j$:

$$r_A = \frac{\sigma^2_{A_m}}{\sigma^2_{A_m} + \frac{1}{n} \sigma^2_{A_x}} \quad (13)$$
Figure 2. Phenotypes of four genotypes as a function of environment; environments E1 and E2 can be considered as macro-environments.

Figure 3 shows that the relationship between $\bar{r}_d$ and $\sigma^2_{\hat{h}}$ is curvilinear. For example, the average genetic correlation is approximately 0.65, when $\sigma^2_{\hat{h}} = 0.05$ ($= h^2 = 0.023$), which approximately corresponds to estimates in Rowe et al. (2006). These values show that substantial G × E interactions can result in genetic heterogeneity of environmental variance. With small G × E interactions (e.g., $\bar{r}_d = 0.90$), genetic heterogeneity of environmental variance will be rather small.

Although Equation 12 demonstrates that G × E can cause genetic heterogeneity of micro-environmental variance, most studies indicate that macro- and micro-environmental sensitivities are weakly genetically correlated (Perkins and Jinks, 1973; Wu, 1997; Wu, 1998; Yampolsky and Scheiner, 1994; Scheiner et al., 1991; Weber and Scheiner, 1992, review by Schlichting and Pigliucci, 1998). The relationship between both phenomena is unknown in animal breeding, whereas macro-environmental sensitivity is often proposed as an indicator for micro-environmental sensitivity (Kolmodin et al., 2003; Kolmodin, 2003; Van der Waay, 2004; Knap, 2005; difference between both phenomena is not explicitly made in these references). This would be ineffective when both phenomena are weakly correlated.
Figure 3. The average genetic correlation between micro-environments based on a reaction norm model (Equation 8) as a function of $\sigma_{h_v}^2$ (Varv) based on the additive model (Equation 6) using Equation 13 for conversion ($\sigma_e^2 = 0.7$, $\sigma_{A_{mu}}^2 = 0.3$, $r_{h_{mu}} = r_{h_l} = 0$, $\sigma_p^2 = 1$).

7.1.4 EXPERIMENTAL DESIGNS TO ESTIMATE ENVIRONMENTAL SENSITIVITY

In this section, some guidelines are given for designs to estimate either $G \times E$ or genetic heterogeneity of micro-environmental variance from field data. The main purpose is to compare designs for estimating genetic heterogeneity of micro-environmental variance within one macro-environment with those for $G \times E$ between two macro-environments. Additionally, guidelines are given for selection experiments to change micro-environmental variance.

7.1.4.1 Analysis of field data

Guidelines for analysis of field data are derived by calculating the power of different experimental designs. The power of an experimental design is the probability to reject the null hypothesis ($H_0$) when it is false. For $G \times E$, $H_0$ is $r_d = 1$ and the alternative hypothesis ($H_1$) is $r_d < 1$. For genetic heterogeneity of micro-environmental variance, $H_0$ is $\sigma_{h_v}^2 = 0$ and $H_1$ is $\sigma_{h_v}^2 > 0$. The power for one-sided tests is calculated as (Lynch and Walsh, 1998):
Power $= 1 - \beta = P(U > \frac{\mu_0 - \mu_1}{\sigma_1} + t\frac{\sigma_0}{\sigma_1})$ (14)

where $\beta$ is the probability of not rejecting the null hypothesis when it is false (Type II error), $U$ is a standard normal variable, $\mu_0$ and $\sigma_0$ are the parameter and its standard error under the null hypothesis, $\mu_1$ and $\sigma_1$ are the parameter and its standard error under the alternative hypothesis and $t$ is the standardized threshold value under the null hypothesis with $\alpha$ ($\alpha = 0.05$) is the probability of rejecting the null hypothesis when it is true (Type I error).

For $G \times E$, designs are based on sires with half-sib progeny in two environments. The error variance of estimates of the genetic correlation between two environments ($= \sigma^2(\hat{\rho}_d)$), as a measure of $G \times E$, is calculated as (Robertson, 1959):

$$\sigma^2(\hat{\rho}_d) = \frac{nt(1-r_d^2) + (1-t)}{(N-1)n^2t^2} + \frac{r_d^2(1-t)^2}{N(n-1)n^2t^2}$$ (15)

where $N$ is the number of sire families, $n$ is the number of family members in one environment, $t = ah^2$ is the intraclass correlation and $a$ is the additive genetic relationship among the family members. Equation 15 assumes equal heritability in both environments, an equal number of family members in each environment, and no environmental correlation among sibs.

For genetic heterogeneity of micro-environmental variance, designs are based on sires with half-sib progeny in one environment and variation in within-family variance is used to estimate genetic variance in micro-environmental variance, accounting for sampling. The error variance of an estimate of $\sigma^2_{\hat{\rho}_d}$ ($= \sigma^2(\hat{\sigma}^2_{\hat{\rho}_d})$), as a measure of genetic heterogeneity of micro-environmental variance, is calculated as (Hill, 2004):

$$\sigma^2(\hat{\sigma}^2_{\hat{\rho}_d}) = \frac{(2/a^2)\left[\frac{2\text{var}W_0^2}{n+1} + a\sigma^2_{\hat{\rho}_d}\right]^2 + 48\frac{\text{var}W_0^2}{(n-1)(n+1)^2}}{N-1}$$ (16)

where $\text{var}W_0 = (1-t)\sigma^2_p$. It should be noted that the Equations 15 and 16 assume that other fixed effects are known without error and, therefore, overpredict the precision of estimates in practice.
**Figure 4.** The power of detecting $G \times E$ between two macro-environments (ra: $r_a = 0.8$) or genetic heterogeneity of micro-environmental variance within one macro-environment (varav: $\sigma^2_{h_v} = 0.05$) as a function of the total number of half-sib progeny per sire (See Equations 14, 15 and 16). ($h_m^2 = 0.3$, $\sigma^2_p = 1$, 50 sire families, progeny equally distributed over both environments with $G \times E$).

Figure 4 shows the power of detecting $G \times E$ between two macro-environments and the power of detecting genetic heterogeneity of micro-environmental variance within one macro-environment as a function of the total number of half-sib progeny per sire with 50 sire families. Although the curves are similar in form, the average $G \times E$ would have been more severe in the case of genetic heterogeneity of micro-environmental variance ($\bar{r}_a = 0.65$, see Equation 13). For both phenomena, the power increases with increasing the number of half-sib progeny. To obtain the same level of power, more progeny are necessary to estimate genetic heterogeneity of micro-environmental variance than to estimate $G \times E$. Table 3 confirms this observation for varying degrees of $G \times E$ and genetic heterogeneity of micro-environmental variance. The minimum number of half-sib progeny to obtain 90% power to reject the null hypothesis becomes rather large when $G \times E$ and genetic heterogeneity of micro-environmental variance are small. It is recommended to use designs with at least 100 half-sib progeny per sire, especially for genetic heterogeneity of environmental variance.
Table 3. Required half-sib progeny group size with corresponding standard error of estimate in that
design (\(\text{Power} > 0.90\) and \(\alpha = 0.05\)) to estimate \(G \times E\) between two environments or genetic
heterogeneity of micro-environmental variance within one macro-environment with 50 sire half-sib
progeny families (\(h_m^2 = 0.3, \sigma_p^2 = 1\)).

<table>
<thead>
<tr>
<th>Type</th>
<th>Parameter (true value)</th>
<th>Progeny group size</th>
<th>Standard error</th>
</tr>
</thead>
<tbody>
<tr>
<td>(G \times E) between 2 macro-environments</td>
<td>(r_A)</td>
<td>0.90</td>
<td>0.047</td>
</tr>
<tr>
<td>(half-sib group equally split)(^1)</td>
<td></td>
<td>0.80, 0.60</td>
<td>0.091, 0.171</td>
</tr>
<tr>
<td>Genetic heterogeneity of micro-environment variance (^2)</td>
<td>(\sigma_{A_v}^2) ((\approx \bar{r}_A))^3</td>
<td>0.02, 0.05, 0.10</td>
<td>0.009, 0.023, 0.045</td>
</tr>
</tbody>
</table>

\(^1\) Standard error of \(r_A\) \((se(\bar{r}_A))\) calculated using Robertson (1959), power calculated based on Lynch and Walsh (1998).

\(^2\) Standard error of \(\sigma_{A_v}^2\) \((se(\hat{\sigma}_{A_v}^2))\) calculated using Hill (2004), power calculated based on Lynch and Walsh (1998).

\(^3\) Equation 13 is used to convert \(\sigma_{A_v}^2\) into \(\bar{r}_A\), which is the average genetic correlation between micro-environments.

7.1.4.2 Selection experiments

The aim of this section is to compare designs of selection experiments that can be used to show response to selection in phenotypic variance in the presence of genetic heterogeneity of micro-environmental variance, based on some simple power calculations. The power is calculated to show response in phenotypic variance due to selection \((H_0: R(\sigma_p^2) = 0; H_1: R(\sigma_p^2) > 0)\). Variance in response to selection is calculated using classical formulas for selection on the mean. When selecting in one direction based on phenotype, the variance in response is calculated as (Hill, 1971):

\[
\sigma^2(R) = (\sigma_p^2 / N_e) \left\{ h^2 \left[ 1 - h^2 (1 - p) \right] + p(2 - \frac{1}{2} h^2) - \frac{1}{2} ph^4 \right\}
\]  

(17)
where \( h^2 = h^2_n = \sigma^2_{h_n} / (2\sigma^2_p + 3\sigma^2_{a_n}) \), \( \sigma^2_p = \sigma^2_{h_n} = \text{var}(P^2) = 2\sigma^2_p + 3\sigma^2_{a_n} \), \( p \) = selected proportion, and \( N_e = \frac{4N_m N_f}{N_m + N_f} \) (Falconer and Mackay, 1996), where \( N_e \) is the effective population size, \( N_m \) and \( N_f \) is the number of selected males and females. When selecting divergently on family information with the same information used in both sexes, the variance in response is calculated as (Hill, 1971):

\[
\sigma^2(R) = \left(2\sigma^2_p / N_e\right)\left[h^2\left[1 - r_{\text{mm}}^2 (1-p)\right] + (1-\frac{1}{2} h^2 r_{\text{mm}}^2) p\right]
\]  

(18)

where \( r_{\text{mm}} \) is the accuracy of selection. Responses are calculated using the formulae in Chapter 5, assuming no genetic variance in mean (\( \sigma^2_{a_n} = 0 \)). Changes in genetic variance due to gametic phase disequilibrium are ignored (Bulmer, 1971), and the effective population size is overestimated, especially with selection on family information. It should be noted that Equations 14, 17 and 18 assume that variances are normally distributed, whereas estimates of variances are \( \chi^2 \)-distributed, which makes a F-test for heterogeneity of variances more appropriate. Therefore, the power is alternatively calculated using a F-test in the last generation (See Appendix).

The following types of selection are compared: stabilizing selection on phenotype to decrease phenotypic variance, disruptive selection on phenotype to increase phenotypic variance, divergent selection on within-family variance based on 20 half-sibs kept within the selection line, divergent selection on within-family variance based on 20 half-sibs kept within the selection line plus 80 extra half-sibs kept outside the selection line (e.g., test station) or divergent selection based on 100 half-sib progeny kept outside the selection line. Selection based on phenotype and sib information is performed for 1-5 generations, whereas selection based on progeny information is only for one generation, because of difficulties to organize progeny testing schemes in selection experiments for multiple generations. For the complete selection experiment, 1000 animal places are available each generation, which are used either for one direction or for two directions in the case of divergent selection. In all cases, the number of females is 4 times the number of males. Each generation both sexes are selected on the same information with a selected proportion of 0.25, which is close to the optimum selected proportion (Hill, 1971) and easy to realize in pigs or poultry. Each sire is mated with 4 dams and each dam produces 4 female and 4 male progeny, from which only 1 is used, resulting in 20 half-sibs per sire within the selection line.
Table 4. Power to detect response to selection in phenotypic variance for different types of selection and different values of $\sigma^2_{s_{a}}$.

<table>
<thead>
<tr>
<th>Type of selection$^2$</th>
<th>Direction</th>
<th>Generation</th>
<th>$\sigma^2_{p}$</th>
<th>$\sigma^2_{s_{a}}$</th>
<th>$\sigma^2_{m}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Stabilizing phenotype</td>
<td>One down</td>
<td>1</td>
<td>0.07</td>
<td>0.11</td>
<td>0.19</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2</td>
<td>0.10</td>
<td>0.19</td>
<td>0.39</td>
</tr>
<tr>
<td></td>
<td></td>
<td>5</td>
<td>0.20</td>
<td>0.55</td>
<td>0.91</td>
</tr>
<tr>
<td>Disruptive phenotype</td>
<td>One up</td>
<td>1</td>
<td>0.09</td>
<td>0.18</td>
<td>0.38</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2</td>
<td>0.15</td>
<td>0.41</td>
<td>0.80</td>
</tr>
<tr>
<td></td>
<td></td>
<td>5</td>
<td>0.43</td>
<td>0.95</td>
<td>&gt;0.99</td>
</tr>
<tr>
<td>Sib testing 20 half-sibs</td>
<td>Divergent</td>
<td>1</td>
<td>0.10</td>
<td>0.22</td>
<td>0.46</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2</td>
<td>0.18</td>
<td>0.50</td>
<td>0.87</td>
</tr>
<tr>
<td></td>
<td></td>
<td>5</td>
<td>0.53</td>
<td>0.98</td>
<td>&gt;0.99</td>
</tr>
<tr>
<td>Sib testing 20 + 80 half-sibs</td>
<td>Divergent</td>
<td>1</td>
<td>0.20</td>
<td>0.50</td>
<td>0.82</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2</td>
<td>0.46</td>
<td>0.93</td>
<td>&gt;0.99</td>
</tr>
<tr>
<td></td>
<td></td>
<td>5</td>
<td>0.98</td>
<td>&gt;0.99</td>
<td>&gt;0.99</td>
</tr>
<tr>
<td>Progeny testing 100 half-sibs</td>
<td>Divergent</td>
<td>1</td>
<td>0.41</td>
<td>0.91</td>
<td>&gt;0.99</td>
</tr>
</tbody>
</table>

1 $\sigma^2_{p} = 1$, $\sigma^2_{m} = 0$, selected proportion = 0.25, number of females = 400, number of males = 100, for stabilizing and disruptive selection numbers of males and females are doubled, because of only one direction of selection.
2 Response was calculated using formulae in Chapter 5; variance of response was calculated with Equation 17 for stabilizing and disruptive selection based on phenotype and with Equation 18 for divergent selection based on family information. Equation 14 was used to calculate the power.

Table 4 summarizes the power of the different possibilities for different values of $\sigma^2_{s_{a}}$. The table in the Appendix shows that the power based on the assumption that variances are normally distributed is similar to the power of a F-test for heterogeneity of variance in the last generation. The advantage of Equation 17 and 18 is that they take into account variance in response due to drift, whereas the F-test does not. Therefore, here only the results based on Equation 14, 17 and 18 are reported.

Stabilizing selection is not powerful, because of the low response per generation. Disruptive selection has a higher power than stabilizing selection, but is worse than divergent selection based on within-family variance of half-sibs or half-sib progeny. Furthermore, disruptive selection would not provide information about possible asymmetric selection responses or a lower selection limit when selecting downward. With divergent selection on
within-family variance of half-sibs, inclusion of 80 commercial half-sibs would substantially increase the power. After only one generation of selection, progeny testing has the highest power, exceeding 90% when $\sigma^2_{d_0} \geq 0.05$. Note however, that in reality only sires can be selected on information of large progeny group leading to overprediction of the power of progeny testing, because in most species it is not possible to select dams on progeny information. Furthermore, genetic variance in mean ($\sigma^2_{d_0}$) may decrease due to gametic phase disequilibrium (increase with disruptive selection), drift or changes in gene frequencies. Decreases in $\sigma^2_{d_0}$ would complicate interpretation of changes in phenotypic variance. Therefore, especially the results after 5 generations of selection should be interpreted with caution. Overall, progeny testing would be advised for a short-term experiment. When the aim is to get insight in the evolution of phenotypic variance over generations, divergent selection based on sib testing with 80 extra half-sibs would be recommended, if progeny testing is not feasible.

### 7.1.5 GENETIC CONTROL OF ENVIRONMENTAL SENSITIVITY

The previous sections mainly deal with modeling and estimation of $G \times E$ and genetic heterogeneity of micro-environmental variance. In this part, the focus is at elucidating the genetic control of macro-environmental and micro-environmental sensitivity, causing statistical significant $G \times E$ or genetic heterogeneity of micro-environmental variance.

Three models have been proposed explaining the genetic basis of environmental sensitivity (Scheiner, 1993): 1) overdominance, 2) pleiotropy and 3) epistasis. The overdominance model states that environmental sensitivity is a function of homozygosity. When genotypes are more homozygous, the phenotype tends to change more across environments (Lerner, 1954). In the pleiotropy model, environmental sensitivity is a function of differential expression of the same gene in different environments, also called allelic sensitivity (Schlichting and Pigliucci, 1995). In the epistasis model, environmental sensitivity is due to genes that determine the magnitude of response to environmental effects, which interact with genes that determine the average expression of the character (Scheiner, 1993). For macro-environmental sensitivity, there is little support for the overdominance model, while substantial evidence exists for the pleiotropy and epistasis model, based on plant and laboratory species (reviewed by Bradshaw, 1965; Scheiner, 1993). Recently, evidence for pleiotropy has been found in broilers (Van Kaam et al., 2006; Ye et al., 2006). Scheiner (1993) and Via et al. (1995) state that pleiotropy and epistasis are probably both involved to varying extents, with slightly more evidence in favor of the epistasis model (Scheiner et al., 1991; Weber and Scheiner, 1992). For micro-environmental sensitivity, there is conflicting
support for the overdominance model. Homozygous strains tend to have higher micro-environmental variance than heterozygous strains (Robertson and Reeve, 1952; Mackay and Lyman, 2005; review by Lynch and Walsh, 1998), however Clarke (1993) and Vølestad et al. (1999), reviewing many different experiments, found little convincing evidence for the relationship between heterozygosity and developmental stability or fluctuating asymmetry, which are both related to micro-environmental sensitivity. The pleiotropy model and epistasis model are supported by the fact that single genes (e.g., heat-shock genes) buffer genetic and environmental variance under certain conditions, but not under other conditions (Rutherford and Lindquist, 1998; Rutherford, 2000; Queitsch et al., 2002).

Molecular genomic information of farm animal species is rapidly increasing (e.g., Hillier et al., 2004) and developments in marker-assisted selection are rapidly developing (e.g., Boichard et al., 2006). The major challenge for molecular genetics is to unravel the complexities of phenotypic variability (Rutherford, 2000). Molecular genetics can help in understanding the black box of problems where quantitative genetics is dealing with. Given that the costs of whole genome SNP scans are decreasing, it would be of interest to study the relationships between heterozygosity and environmental sensitivity and to map plasticity genes by using QTL × environment interaction models in animal breeding populations (e.g., Van Eeuwijk et al., 2005; Malosetti et al., 2006). Statistical models to detect QTL for genetic heterogeneity of micro-environmental variance are also underway (Wittenburg et al., 2006). Given that epistasis is likely to be involved in macro- and micro-environmental sensitivity, epistatic QTL mapping procedures would be recommended and may have larger power to detect QTL than classical QTL mapping studies (Carlborg, 2006; Carlborg et al., 2006). Ultimately, epistatic QTL models and QTL × environment interaction models can be combined taking into account that genes interact with each other and with environmental effects. The question, however, is whether there will be sufficient power to estimate all these complex interactions.
7.1.6 FUTURE RESEARCH

In section 7.1, several interesting topics for future research regarding environmental sensitivity were discussed from an animal breeding point of view. The four most interesting ones are summarized here:

1. Using AMMI-models to estimate $G \times E$ in animal breeding in situations where adequate environmental parameters are not available.
3. Divergent selection experiments based on sib testing or progeny testing to get more insight in evolution of variances when directly selecting on it.
4. Elucidating the genetic control of macro- and micro-environmental sensitivity by mapping plasticity genes using models combining QTL $\times$ environment interaction or QTL accounting for genetic heterogeneity of micro-environmental variance with epistatic QTL.
7.2 OPTIMIZATION OF BREEDING PROGRAMS WITH GENETIC VARIATION IN ENVIRONMENTAL SENSITIVITY AND BREEDING GOAL DIFFERENCES

7.2.1 INTRODUCTION

Breeding organizations face the question how to generate good genetic material for different environments with different breeding goals, whereas they need to work with a limited number of lines in order to run economically and genetically efficient breeding programs. In dairy cattle, organizations have a single breeding program within a breed, but may have a few breeding programs for a few breeds. In pigs and poultry, it is common that breeding organizations have multiple pure lines, so that they can create a variety of crossbred combinations for different markets.

In Chapter 4, it was investigated in dairy cattle whether a single breeding program or two breeding programs was optimal to breed for two environments with $G \times E$. The focus in that study was limited to single-trait selection in two environments and limited to maximizing genetic gain. However, competition between breeding organizations and the recent implementation of genomic selection might affect the optimum breeding strategy.

The aim of 7.2 is to give guidelines and methods for optimization of breeding programs in the presence of both $G \times E$ and breeding goal differences. In 7.2.2, methods are developed to deal with multi-trait selection and multiple environments. In 7.2.3, the effects of competition and genomic selection on optimization of breeding programs are discussed. In 7.2.4, it is discussed how genetic variation in environmental sensitivity can be utilized to breed animals that are more robust to environmental changes.

7.2.2 DEALING WITH MULTIPLE TRAITS AND MULTIPLE ENVIRONMENTS

7.2.2.1 Multiple traits in two environments

In the Chapters 2, 3 and 4, single trait selection was considered in the presence of $G \times E ( = r_d < 1)$. Environments may not only differ due to $G \times E$, but also due to breeding goals, genetic variances and genetic correlations between traits. The challenge is now to find a parameter that accommodates all these differences. In Chapter 3 and 4, the genetic correlation between breeding goals ($r_H$) was already proposed in the discussion to extrapolate results of single-trait selection to multi-trait selection. The aim of this section is to test and show that $r_H$ can be used whether or not it is optimal to split a single breeding program with selection for the average breeding goal in two environments into two separate breeding programs, each
with selection for an environment-specific breeding goal. Furthermore, it is shown how $r_H$ is affected by $G \times E$ and breeding goal differences.

The $r_H$ between two environments $k$ and $l$ can be calculated as:

$$r_{H,kl} = \frac{\mathbf{v}_k^T \mathbf{G} \mathbf{v}_l}{\sqrt{\mathbf{v}_k^T \mathbf{G} \mathbf{v}_k \mathbf{v}_l^T \mathbf{G} \mathbf{v}_l}}$$  \hspace{1cm} (19)

where $\mathbf{v}_k$ and $\mathbf{v}_l$ are the vectors with economic values in environment $k$ and $l$ and $\mathbf{G}$ is the full genetic variance-covariance matrix between all traits ($n$ traits) in both environments with dimensions $2n \times 2n$ in the case of two environments. The vector $\mathbf{v}_k$ ($\mathbf{v}_l$) is augmented with zeros for traits in environment $l$ ($k$). When $r_A$ are equal for all traits and genetic correlations between traits within environment are equal for both environments, Equation 19 can be rewritten as:

$$r_H = r_A \times r_{BG}$$  \hspace{1cm} (20)

where $r_{BG}$ is $r_H$ with $r_A = 1$. Equation 20 indicates that in principal $G \times E$ and breeding goal differences equally affect $r_H$. In the case of 2 environments and 2 traits in the breeding goal, Figure 5 shows $r_H$ as a function of the economic value of trait 1 in environment 1 ($v_{11}$) for representative values of $r_A$. The effects of a negative $v_{11}$ on $r_H$ are large, but opposite breeding goals are uncommon in animal breeding. In more realistic cases, when the directions of the breeding goals are equal (right sight of figure), the effects of $v_{11}$ are smaller and $r_H$ is predominantly determined by $r_A$. Realistic degrees of heterogeneity of genetic variances or heterogeneity of genetic correlations have a small effect on $r_H$ (results not shown). In most practical situations, therefore, $G \times E$ determines $r_H$ to a large extent.

In analogue of Chapter 4 considering selection for two traits in two environments, break-even $r_H$ are calculated to determine when it is optimal to split a single breeding program with selection for the average breeding goal in two environments into two separate breeding programs, each with selection for an environment-specific breeding goal. A simple selection index approach is used considering only selection of bulls. In the single breeding program, bulls are tested with half of the total number of progeny in each environment, whereas in the two separate breeding programs bulls are progeny tested in only one environment (comparable to strategy OJ and TE in Chapter 4, respectively). When the $r_H$ is higher (lower) than the break-even $r_H$, one (two) breeding program(s) has (have) the highest genetic gain.
Figure 5. The genetic correlation between breeding goals (rH) as a function of the economic value for trait 1 in environment 1 (v11) for different levels of G \times E (ra) (v12=1; \sigma^2_p = 1, h^2 = 0.3, genetic correlation between traits 1 and 2 is 0; breeding goal environment 2 = 1 : 1).

Table 5 shows the break-even \( r_H \) for situations in which \( r_H \) is either deviating from unity due to breeding goal differences only, only G \times E or a mixture of G \times E and breeding goal differences. The break-even \( r_H \) is rather stable in these situations. Single-trait breeding goals and multi-trait breeding goals have the same break-even \( r_H \). The situations with only breeding goal differences have a slightly lower break-even \( r_H \), which is attributed to that breeding goal differences do not affect the accuracies of the EBV of the traits in the breeding goal, whereas G \times E does affect the accuracy of EBV in different environments (Goddard, 1992). The values of break-even \( r_H \) are slightly lower than in Chapter 4, which is due to the use of a simple selection index, instead of a pseudo-BLUP selection index.

These results show that \( r_H \) can be used to deal with multi-trait selection in different environments. In absence of G \times E, \( r_I \) may have an advantage when heritabilities differ greatly between traits, because it better reflects the selection pressure on different traits than \( r_H \). In the presence of G \times E, however, \( r_I \) is not suitable, because it is mainly determined by the distribution of phenotypic information over both environments. Furthermore, \( r_H \) is the natural analogue of \( r_A \), in contrast to \( r_I \). Therefore, \( r_H \) is most appropriate to use with multi-trait selection in different environments. Single-trait results, such as in Chapter 4, can be used as guidelines for multi-trait selection replacing \( r_A \) with \( r_H \).
General discussion

<table>
<thead>
<tr>
<th>Varied parameters</th>
<th>Breeding goal difference</th>
<th>Breeding goal(^1)</th>
<th>Break-even  (r_{hi})</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>G × E</strong></td>
<td></td>
<td><strong>E1</strong></td>
<td><strong>E2</strong></td>
</tr>
<tr>
<td>No</td>
<td>Yes</td>
<td>1.00(^4)</td>
<td>1 : 2.07</td>
</tr>
<tr>
<td></td>
<td></td>
<td>1.00</td>
<td>1 : 7.33</td>
</tr>
<tr>
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<td>No</td>
<td>0.49</td>
<td>1 : 0</td>
</tr>
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<td></td>
<td></td>
<td>0.49</td>
<td>1 : 3</td>
</tr>
<tr>
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<td>1 : 1</td>
</tr>
<tr>
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<td>0.68</td>
<td>1 : 0</td>
</tr>
<tr>
<td></td>
<td></td>
<td>0.55</td>
<td>1 : 3</td>
</tr>
</tbody>
</table>

\(^1\) Break-even genetic correlation is the genetic correlation where a single breeding program has equal genetic gain as two separate breeding programs. Above (below) the break-even genetic correlation, a single (two) breeding program(s) is (are) optimal. Genetic gain was calculated with a simple selection index based on one selection path with bulls that are progeny tested.

\(^2\) Input parameters: \(\sigma_p^2 = 1\), \(h^2 = 0.3\), genetic correlation between traits 1 and 2 = 0, number of progeny per bull = 100 (with a single breeding program 50 progeny in each environment), number of selected sires in each breeding program = 20).

\(^3\) Relative economic values on trait 1 and trait 2 in environment E1 and E2; relative economic values on trait 1 in E1 is standardized at 1.

\(^4\) Bold numbers are varied and can be seen as a result and regular numbers are not varied and can be seen as input.

### 7.2.2.2 Multiple traits and multiple environments

In principle, the number of environments can be large, for example equal to the number of farms, whereas breeding organizations can operate only a few breeding programs. Clustering of environments is, therefore, necessary. Clustering farms on farm characteristics, such as mean milk production and herd size, have been proposed to estimate \(G \times E\) within and between countries by using a multiple-trait herd cluster model (e.g., Weigel and Rekaya, 2000; Zwald et al., 2003a,b; Windig et al., 2005). This is, however, not very useful for determining the number of breeding programs necessary to breed optimally for multiple environments, because the cluster analysis is not directly based on \(G \times E\) and breeding goal differences. From a genetic gain point of view, the number of breeding programs should be based on \(r_{hi}\)-values, as shown in 7.2.2.1, combining \(G \times E\) and breeding goal differences.

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Cluster analysis applied upon the $R_{\mu}$-matrix (matrix based on $r_{\mu}$) seems to be an appropriate method to determine the number of breeding programs when breeding for a large number of environments. The aim of this section is to determine the optimal number of breeding programs when breeding for multiple environments and to show how cluster analysis can be used to determine the required number of breeding programs.

**The optimal number of breeding programs.** From a genetic gain point of view, the optimal number of breeding programs refers to finding the right balance between selection intensity and accuracy when breeding for multiple environments. With multiple environments, two situations can be distinguished: (1) fixed total test resources and (2) fixed test resources per environment. With fixed total test resources (e.g., number of bulls progeny tested), increasing the number of breeding programs results in a decreasing amount of test resources per breeding program. An example is when increasing the number of dairy cattle breeding programs within one country, resulting in a decreasing number of cows available per breeding program for progeny testing bulls. On the contrary, with fixed test resources per environment, total test resources increase with the number of environments. An example is in dairy cattle with increasing total cow population when considering more countries. For both situations, break-even genetic $r_{\mu}$ are calculated as a function of the number of environments comparing a single breeding program with selection for average performance in multiple environments with multiple environment-specific breeding programs, each with selection for an environment-specific breeding goal. When $r_{\mu}$ is higher (lower) than the break-even $r_{\mu}$, one (multiple) breeding program(s) is (are) optimal.

Figure 6 shows that with fixed total test resources, the break-even genetic correlation decreased substantially with increasing the number of environments. This result clearly indicates that a single breeding program is in most situations superior and multiple breeding programs are not justified from a genetic point of view. With fixed test resources per breeding program, however, the break-even genetic correlation is rather stable. This indicates that the results from considering only two environments can be extrapolated to multiple environments, when test resources increase proportionally with the number of environments.
Cluster analysis. When cluster analysis applied upon the $R_{H}$-matrix is used to determine the optimal number of breeding programs, the number of breeding programs (= clusters) should be constrained in such a way that it is related to the break-even $r_{H}$, for example as shown in Figure 6. The challenge is now to link the break-even $r_{H}$ to a method of constraining the number of clusters, for example to stop cluster analysis if each cluster explains a predefined minimum proportion of the total variation in $r_{H}$ in that group of environments ($p_{min}$) (SAS Institute, 2003). When cluster analysis is based on principal components, for example Proc Varclus in SAS 9.1 (SAS Institute, 2003), the proportion of variation explained by one cluster is equal to the proportion of variation explained by the first eigenvalue $\lambda_{1}$. The eigenvalues can be found by solving the characteristic equation $\det(G - \lambda I) = 0$. When assuming equal $r_{H}$ between environments, the first eigenvalue is $\lambda_{1} = 1 + (n - 1)r_{H}$ and the other eigenvalues are $\lambda_{i+1} = 1 - r_{H}$ (e.g., Jackson, 1991). The proportion of variation explained by one cluster ($p_{1}$) is then:
\[ p_1 = \frac{\lambda_1}{n} = \frac{1 + (n-1)r_{\mu}}{n} \]  

(21)

where \( n \) is the number of environments in that cluster. The \( p_{\min} \) is calculated by using the break-even \( r_{\mu} \) in Equation 21.

**Table 6.** Genetic correlations between E1, E2, E3 and E4 used in the example of cluster analysis in Figure 7.

<table>
<thead>
<tr>
<th></th>
<th>E1</th>
<th>E2</th>
<th>E3</th>
<th>E4</th>
</tr>
</thead>
<tbody>
<tr>
<td>E1</td>
<td>1.00</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>E2</td>
<td>0.80</td>
<td>1.00</td>
<td></td>
<td></td>
</tr>
<tr>
<td>E3</td>
<td>0.20</td>
<td>0.45</td>
<td>1.00</td>
<td></td>
</tr>
<tr>
<td>E4</td>
<td>0.30</td>
<td>0.40</td>
<td>0.48</td>
<td>1.00</td>
</tr>
<tr>
<td></td>
<td>symmetric</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**Figure 7.** Schematic representation of using cluster analysis to determine the required number of breeding programs (= 3) in the example given in Table 6 using Proc Varclus in SAS 9.1 (SAS institute, 2003). The \( p_{\min} \) is based on a break-even \( r_{\mu} \) of 0.49 using Equation (21).

Figure 7 shows schematically how cluster analysis can be used to determine the required number of clusters (= breeding programs) in an example of 4 environments with a genetic correlation matrix as shown in Table 6. The first step (Step 1) is to compare \( p_1 \) of a single cluster with \( p_{\min} \). When \( p_1 \geq p_{\min} \), a single breeding program is optimal and one can stop the cluster analysis. When \( p_1 < p_{\min} \), two clusters are formed with cluster analysis. The next step
(Step 2a, 2b) is to compare for each cluster \( p_i \) with \( p_{min} \) updated with respect to \( n \) for that cluster. When both \( p_i \)-values \( \geq p_{min} \), two breeding programs are optimal and one can stop the cluster analysis. In this case, in Step 2b \( p_i < p_{min} \), so that this cluster is split into two clusters. This process (Step 3a, 3b) can be continued when \( p_i < p_{min} \) for a certain cluster, until all clusters satisfy \( p_i \geq p_{min} \). In the example, ultimately, three clusters are formed, indicating that three breeding programs are required to breed for these 4 environments. The proposed cluster analysis may not always give the optimal number of breeding programs, for example, when environments are very different in importance, but cluster analysis is a suitable operational method to determine initially a suitable number of breeding programs in situations with a large number of environments and how these environments can be grouped. Additional simulations are necessary to optimize the number of breeding programs and to optimize the design of these breeding programs, for example the number of bulls tested in each environment.

7.2.3 EFFECTS OF COMPETITION AND GENOMIC SELECTION

7.2.3.1 Competition

In section 7.2.2 and in Chapter 4 break-even \( r_H \) are low, in the range of 0.40 to 0.60, indicating that in most situations a single breeding program with progeny testing in different environments is optimal from a genetic point of view. The aim of this section is to discuss the effects of competition on the break-even \( r_H \).

In dairy cattle breeding, the goal of a breeding organization is to maximize profit from selling semen. Dairy farmers have very diverse breeding goals when selecting bulls to breed their cows (Groen et al., 1993). The challenge of a breeding organization is to have top-ranking bulls in a number of market segments, which may not be accomplished when the breeding program is designed to maximize genetic gain in all environments. Having top-ranking bulls requires not only a high genetic gain (high mean of EBV), but also a high accuracy of the EBV (= high variance of EBV) (Dekkers et al., 1996). \( G \times E \) lowers the accuracy of EBV in environments where less progeny are tested. Consequently, EBV in these environments are regressed to the mean, which results in a lower probability of top-ranking. Therefore, a single breeding program with splitting the total number of progeny over multiple environments and selecting simultaneously for performance in these environments may result in proven bulls that have high EBV for both environments, but not high enough to get in the top-rankings of both environments, when competitors test bulls with an equal total number of progeny in only one environment. The effect of competition on break-even \( r_H \) can be quantified by calculating the probability of having bulls in the top in both environments. To illustrate this, assume a situation with two environments and one competitor that runs two
environment-specific breeding programs. The breeding organization of interest would like to have more bulls in the top 1% than the competitor and can choose between a single breeding program or two environment-specific breeding programs, assuming that the number of bulls tested and the total number of progeny per bull are equal for both breeding organizations. In this situation, the break-even $r_m$ increases from 0.49 to 0.64. With more competitors, the break-even $r_m$ is likely to increase more. This shows that the commercial value of separate breeding programs might be higher than the genetic value. Competition is likely to increase the break-even $r_m$ to 0.70 – 0.80. Development of a framework to calculate break-even $r_m$ in the presence of competition is recommended, for example by following the framework of Dekkers and Shook (1990).

7.2.3.2 Genomic selection

Currently, many breeding organizations are implementing marker-assisted selection and genomic selection (Meuwissen et al., 2001) in their breeding programs to enhance selection responses (Boichard et al., 2006; Hybro, 2007; HG, 2007). The question is what the effects of these forms of selection are on optimizing breeding programs in the presence of $G \times E$, for example on the break-even $r_m$.

When knowing environment-specific effects of QTL, EBV can be converted with larger accuracy from one environment to another and this would lessen the need to test sibs and progeny in different environments. A very useful application of QTL information is in two-stage selection schemes. The first selection is based on EBV predicted from genomic information and can be performed just after birth or even after fertilization with embryo-transfer (Meuwissen et al., 2001). The best bulls are progeny tested. The advantage is that fewer bulls need to be progeny tested to achieve the same genetic gain (Schrooten et al., 2005). Because of the much larger population size of bulls in the first selection stage, it is much easier to achieve high selection intensity and a high genetic gain for smaller market segments with a low number of bulls progeny tested. A higher selection intensity will increase the break-even $r_m$ from 0.50 – 0.60 to 0.70 – 0.80 (see Chapter 4). As a result, genomic selection will increase break-even $r_m$, making it worthwhile to split the breeding program into smaller units serving different market segments and creating flexibility in dairy cattle breeding programs. The challenge will be to estimate environment-specific QTL-effects.
7.2.4 EXPLOITING GENETIC VARIATION IN ENVIRONMENTAL SENSITIVITY TO INCREASE ROBUSTNESS

Several theoretical studies have shown that selection for increased production in good environments increases environmental sensitivity (= slope of a reaction norm) (Falconer, 1990; Kolmodin et al., 2003; Van der Waaij, 2004). Analyses of experiments confirm these theoretical findings; for example, American Holsteins have a larger sensitivity in milk production to the level of concentrate feeding than New Zealand Holsteins (Linnane et al., 2004; Horan et al., 2005) and pigs with large growth potential have a larger environmental sensitivity for days to reach market weight than pigs with an average growth potential (Schinkel et al., 1999). Most literature states that this increased environmental sensitivity is undesirable and that the degree of environmental sensitivity should be included in the breeding objective. In this section, the desired direction for environmental sensitivity is discussed. A distinction is made between macro- and micro-environmental sensitivity, which has received little attention (e.g., Kolmodin et al., 2003; Van der Waaij, 2004; Calus, 2006).

Chapters 2, 3 and 4 and section 7.2.2 of this chapter deal extensively with genetic variation in macro-environmental sensitivity, or G × E between herd types, geographic regions, etc. The question whether a single or multiple breeding programs are optimal is equivalent to the question whether to breed for general adaptability to a range of environments, creating generalists, or breeding for special adaptability for a specific environment, creating specialists (Dickerson, 1962). The optimal selection strategies in Chapter 2 and 4 are based on recording relatives in the commercial environments, guaranteeing that animals are bred for good adaptation to these environments. These optimal breeding strategies may lead to increased responsiveness to predictable changes in environment, for example increased concentrate feeding, which can be seen as a desirable increase in environmental sensitivity when the level of performance increases as well (Kolmodin, 2003; Calus, 2006). The negative perception of increased macro-environmental sensitivity by selection is mostly related to the increased health and welfare problems in livestock, especially in unfavorable conditions, because of selection on production. Defining sustainable breeding goals for all environments can prevent further deterioration of health and welfare (e.g., Olesen et al., 2000; Kanis, et al., 2005; Nielsen et al., 2006). This will lead to higher emphasis on health and welfare traits in less favorable environments than in more favorable environments. When breeding programs are optimized according to these environment-specific breeding goals, for example according to 7.2.2.1, breeding programs are automatically optimized for macro-environmental sensitivity. Therefore, breeding organizations can concentrate on genetically improving levels of traits in different environments, instead of concentrating on genetically improving macro-environmental sensitivity itself.
Genetic variation in micro-environmental sensitivity is associated with sensitivity to random unpredictable environmental effects, such as temperature changes, electricity failure, etc. (see also 7.1.2). There are a few reasons in favor of selection for reduced micro-environmental sensitivity: 1) to minimize risk for bad performance, 2) to improve health and welfare, or 3) to increase uniformity of animals. Minimizing risk is especially important for risk-averse farmers that operate in an unpredictable environment, for example organic farms due to limited use of antibiotics and no use of fertilizer. Reduction of micro-environmental sensitivity lowers the risk for very bad or very good performance. For risk averse farmers, very good performance does not outweigh very bad performance. Utility functions can be used to derive economic weights for micro-environmental sensitivity (e.g., Eskridge and Johnson, 1991). Environmental sensitivity is also important to improve health and welfare, because impaired health and welfare under unfavorable environmental conditions should be avoided because of economic and ethical reasons (Sandøe et al., 1999; Neeteson-Van Nieuwenhoven et al., 2006; MacArthur Clarke et al., 2006). Decreasing micro-environmental sensitivity for health and welfare traits would be of interest when the population averages of these traits are at acceptable levels (e.g., Kolmodin, 2003). Increased uniformity of animals or animal products is of relevance if there is a need for homogeneous products, for example in the meat industry (Hammerstedt, 1999; Garnier et al., 2003; Kanis et al., 2006; see Chapter 6). Cases, in which an increase in micro-environmental sensitivity is desirable, are exceptional (see Chapter 6). In most cases, therefore, reduction of micro-environmental sensitivity is desirable and in line with the desire to breed animals that are insensitive (robust) to unpredictable environmental factors (e.g., Knap, 2005).

To reduce micro-environmental sensitivity ($A_v$) by selection, genetic variation in $A_v$ is necessary, but estimates of genetic variation in $A_v$ are still scarce (see Chapters 1 and 5), due to the computational difficulties and the low power to detect genetic variation in micro-environmental sensitivity (= micro-environmental variance; see 7.1.4). When genetic variation in micro-environmental sensitivity is present at levels as reported in literature, reductions in micro-environmental sensitivity of at least 10% of the current micro-environmental sensitivity can be achieved when the relative emphasis on $A_v$ is larger than 50% (see Chapter 5 and 6 for more results). These results show that genetic variation in micro-environmental sensitivity can be exploited to breed animals that are more robust against unpredictable environmental factors. The limiting factor, however, is the availability of estimates of genetic variance in micro-environmental sensitivity in livestock.
7.2.5 RECOMMENDATIONS FOR OPTIMIZATION OF BREEDING PROGRAMS

The conclusions of 7.2 are:
• The break-even $r_H$ is a suitable parameter to use for optimization of breeding programs in the presence of $G \times E$ and breeding goal differences between environments.
• Cluster analysis on a matrix with $r_H$-values between environments is helpful to group a large number of environments into a limited number of clusters and to determine the number of required breeding programs.
• Competition and genomic selection increase the break-even $r_H$ to 0.70 – 0.80. Environment-specific breeding programs are recommended, when $r_H$ is lower than the break-even $r_H$.
• Genetic variation in micro-environmental sensitivity (= genetic heterogeneity of environmental variance) can be exploited to breed animals that are more robust against unpredictable environmental factors, which is of interest to reduce risk, to improve health and welfare and to increase uniformity of animals.

7.3 ACKNOWLEDGEMENTS

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7.4 REFERENCES


General discussion


Chapter 7


APPENDIX

Power of F-test for heterogeneity of variances in selection experiments

The power of a F-test for heterogeneity of variances is (Lynch and Walsh, 1998):

\[
Pr[F_{n-1, n-1, \lambda} > F_{n-1, n-1, [\lambda]}] \approx Pr(U > z_0) \tag{22}
\]

where \(\lambda = R(n-1)/\sigma^2_{P,0}\) is the noncentrality parameter, \(R\) is the total response in phenotypic variance (e.g., difference between the high and low line with divergent selection), \(n\) is number of animals in each sample, \(\sigma^2_{P,0}\) is the phenotypic variance in generation 0, \(U\) is a standard normal, \(z_0 = \frac{\sqrt{(4n-5)B} - \sqrt{2(n-1+\lambda)-A}}{\sqrt{A+B}}\), where \(A = \frac{n+2\lambda}{n+\lambda}\) and \(B = \frac{n-1}{2n-2} F_{n-1, n-1, [\lambda]}\). The power of Equation 22 is compared with the power as calculated with the Equations 14, 17 and 18 in Table A1. The results of both tests are similar. The F-test is more conservative with low selection responses in variance, but less conservative with large responses in variance. It should be noted that Equation 22 does not account for drift, whereas Equations 17 and 18 do account for drift.
Table A1. Comparison of power to detect response to selection in phenotypic variance for different types of selection based on the assumption that variances estimates are normally distributed or that the ratio of variance estimates is F-distributed$^{1,2,3}$.

<table>
<thead>
<tr>
<th>Type of selection$^2$</th>
<th>Direction</th>
<th>Generation</th>
<th>Normal distribution</th>
<th>F distribution</th>
</tr>
</thead>
<tbody>
<tr>
<td>Stabilizing phenotype</td>
<td>One down</td>
<td>1</td>
<td>0.10</td>
<td>0.07</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2</td>
<td>0.16</td>
<td>0.13</td>
</tr>
<tr>
<td></td>
<td></td>
<td>5</td>
<td>0.42</td>
<td>0.52</td>
</tr>
<tr>
<td>Disruptive phenotype</td>
<td>One up</td>
<td>1</td>
<td>0.15</td>
<td>0.13</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2</td>
<td>0.31</td>
<td>0.36</td>
</tr>
<tr>
<td></td>
<td></td>
<td>5</td>
<td>0.84</td>
<td>0.96</td>
</tr>
<tr>
<td>Sib testing 20 half-sibs</td>
<td>Divergent</td>
<td>1</td>
<td>0.22</td>
<td>0.22</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2</td>
<td>0.50</td>
<td>0.61</td>
</tr>
<tr>
<td></td>
<td></td>
<td>5</td>
<td>0.98</td>
<td>&gt;0.99</td>
</tr>
<tr>
<td>Sib testing 20 + 80 half-sibs</td>
<td>Divergent</td>
<td>1</td>
<td>0.50</td>
<td>0.60</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2</td>
<td>0.93</td>
<td>0.98</td>
</tr>
<tr>
<td></td>
<td></td>
<td>5</td>
<td>&gt;0.99</td>
<td>&gt;0.99</td>
</tr>
<tr>
<td>Progeny testing 100 half-sibs</td>
<td>Divergent</td>
<td>1</td>
<td>0.91</td>
<td>0.97</td>
</tr>
</tbody>
</table>

$^1$ $\sigma_p^2 = 1$, $\sigma_{a_m}^2 = 0$, $\sigma_{a_{km}}^2 = 0.05$, selected proportion = 0.25, number of females = 400, number of males = 100, for stabilizing and disruptive selection numbers of males and females are doubled, because of only one direction of selection.

$^2$ Response was calculated using formulae in Chapter 5; variance of response was calculated with Equation 17 for stabilizing and disruptive selection based on phenotype and with Equation 18 for divergent selection based on family information. Equation 14 was used to calculate the power.

$^3$ Equation 14 was used to calculate the power using a t-test assuming that variance estimates are normally distributed; Equation 22 was used to calculate power using a F-test assuming that the ratio of variance estimates is F-distributed (variance estimates are $\chi^2$-distributed).
Summary
Introduction. Genotype by environment interaction (G × E) is the phenomenon that different genotypes respond differently to changes in the environment. As a consequence, the best genotype in one environment may not be the best genotype in another environment. In other words, G × E may result in reranking of genotypes, indicated by a genetic correlation between environments lower than one. G × E affects opportunities for genetic improvement in breeding programs. Due to globalization of livestock breeding and differentiation of farming systems, it is more and more important to consider G × E in livestock improvement.

G × E can exist between environments that are easy to identify, for example geographic region or organic versus conventional farming systems. Within these environments, G × E can also exist due to fluctuations in weather, feed quality, etc. In other words, genotypes may differ in environmental sensitivity to these within-environment fluctuations. This phenomenon leads to genetic differences in environmental variance, so-called genetic heterogeneity of environmental variance. Genetic heterogeneity of environmental variance gives opportunities to select for increased uniformity and robustness of animals.

The two main objectives of this PhD-research were: 1) to optimize livestock breeding programs with G × E and breeding goal differences between environments (Chapter 2, 3, 4 and 7), and 2) to develop a framework for prediction of selection responses with genetic heterogeneity of environmental variance, and to investigate the use of such genetic heterogeneity in livestock breeding programs (Chapter 5, 6 and 7).

Chapter 2. In this chapter, consequences of G × E between a selection environment (SLE, e.g. nucleus environment) and a production environment (PDE, e.g. commercial farms) were investigated for genetic gain in sib testing and progeny testing schemes. Recording of half-sibs or progeny in PDE limited the loss in genetic gain in PDE. Progeny-testing schemes had less loss in genetic gain than sib-testing schemes. Higher heritability increased the loss in genetic gain, whereas increasing the number of progeny per sire in PDE decreased the loss in genetic gain. Genetic gains for sex-limited and carcass traits were less affected by G × E than traits measured on both sexes. Progeny-testing schemes rather than sib-testing schemes are preferable in situations with low to moderate heritability ($h^2 \leq 0.3$), relative short generation interval of progeny tested sires ($L_{prog}/L_{sub} \leq 1.7$), and moderate to severe G × E interaction between SLE and PDE ($r_g \leq 0.8$).

Chapter 3. In dairy cattle, it is very common to select bulls and cows worldwide, which is called cooperation between breeding programs in this chapter. In this chapter, the objectives were to investigate to which extent G × E limits the possibilities for cooperation between dairy cattle breeding programs operating in different environments, and to quantify the effect of such cooperation on genetic gain. A dairy cattle situation with two breeding programs operating in two environments was simulated. Long-term cooperation between the two breeding programs was possible, when the genetic correlation was higher than 0.8 to 0.9, resulting in up to 15% extra genetic gain. With more intense selection, breeding programs
were less likely to benefit from cooperation. Small breeding programs benefited more from cooperation than did large breeding programs, and cooperation was optimal at lower values (i.e., <0.8) of the genetic correlation.

**Chapter 4.** Dairy cattle breeding organizations tend to sell semen to different parts in the world. The objective of this study was to investigate optimization of dairy cattle breeding programs for two environments with G × E. Breeding strategies differed in 1) including one or two environments in the breeding goal, 2) running either one or two breeding programs, and 3) progeny testing bulls in one or two environments. Breeding strategies were evaluated on average genetic gain of both environments. When both environments were equally important and the genetic correlation was higher than 0.61, a single breeding program with progeny testing all bulls in both environments was optimal. When the genetic correlation was lower than 0.61, it was optimal to have two environment-specific breeding programs progeny testing an equal number of bulls in their own environment only. Ranking of breeding strategies was very sensitive to selection intensity. Environment-specific breeding programs were less appropriate for situations where one of the two environments had a relative importance less than 10 to 20%.

**Chapter 5.** In this chapter, a framework was developed for prediction of breeding values and selection responses in mean and environmental variance in the presence of genetic heterogeneity of environmental variance. Both means and environmental variances were treated as heritable traits. Breeding values and selection responses were predicted with little bias using linear, quadratic and cubic regression on individual phenotype, or using linear regression on the mean and within-family variance of a group of relatives. To standardize results in the literature and to facilitate comparisons to ‘conventional’ traits, a measure of heritability was proposed for environmental variance. Although a large amount of information is necessary to accurately estimate breeding values for environmental variance, response in environmental variance can be substantial, even with mass selection. The methods developed allow use of the selection index framework to evaluate breeding strategies that simultaneously change the mean and the variance of traits.

**Chapter 6.** The objective of this study was to investigate the use of genetic heterogeneity of environmental variance in breeding programs, for example in situations where it is not only worthwhile to change the mean, but also the variability of traits by selection. The framework developed in Chapter 5 was used to predict genetic gain. Genetic parameters were obtained from the literature. Economic values for mean and variance were derived for some standard non-linear profit equations, e.g. for traits with an intermediate optimum. Responses in environmental variance were large, in some cases more than 10% of the current environmental variance. Progeny testing schemes were more efficient than sib testing schemes in decreasing environmental variance. With optimum traits, selection pressure shifted gradually from the mean to the variance when approaching the optimum and most
economic gain was initially due to change in mean. Genetic improvement of uniformity is particularly of interest for traits where the current population mean is near an intermediate optimum.

Chapter 7. In the first part of this chapter, models to account for G × E and genetic heterogeneity of environmental variance were reviewed. A combined model was proposed to link both phenomena. It was shown that datasets with groups of at least 100 progeny per sire are necessary to estimate genetic heterogeneity of environmental variance with sufficient power. Alternatively, divergent selection experiments based on 100 progeny per sire could be used to show response to selection in phenotypic variance in the presence of genetic heterogeneity of environmental variance.

In the second part of this chapter, it was shown that the genetic correlation between breeding goals (\( r_{HI} \)) is a suitable parameter to use for optimization of breeding programs in the presence of G × E and breeding goal differences between environments. Single breeding programs are recommended to split into environment-specific breeding programs when \( r_{HI} \) is lower than 0.7 – 0.8. Genetic heterogeneity of environmental variance, rather than G × E between macro-environments, can be exploited to breed animals that are more robust against unpredictable environmental fluctuations.

**Main conclusions of this thesis.**

1. Recording of sib or progeny information in the production environment reduces the loss in genetic gain due to G × E between selection environment and production environment.
2. It is recommended to split breeding programs into environment-specific breeding programs when the genetic correlation between environments is lower than 0.7 – 0.8.
3. Genetic heterogeneity of environmental variance can be used to increase uniformity and robustness of animals.
Samenvatting
Samenvatting

In deze sectie heb ik mijn promotieonderzoek in lekentaal samengevat. Deze samenvatting is vooral bedoeld voor mensen die minder bekend zijn met het vakgebied Fokkerij en Genetica. Een wetenschappelijke samenvatting is te vinden in de Engelstalige summary.

Inleiding

Het doel van fokkerij is om de erfelijke aanleg van dieren te verbeteren. Bij landbouw­huisdieren gaat het hierbij om erfelijke aanleg te verbeteren van kenmerken die invloed hebben op het economische resultaat van veehouderijbedrijven, bijvoorbeeld het verhogen van melkproductie in melkkoeien, het verhogen van groei in varkens en vleeskuikens, of het verhogen van eiproductie in leghennen. Het verbeteren van de erfelijke aanleg van dieren gebeurt door de genetisch beste dieren te selecteren en deze vervolgens te paren om de volgende generatie te fokken.

Tegenwoordig wordt de erfelijke aanleg van dieren geschat met statistische computerprogramma’s, die gegevens van het dier zelf en zijn familieleden zo goed mogelijk gebruiken om de erfelijke aanleg van het dier te schatten. De erfelijke aanleg wordt uitgedrukt in een fokwaarde: dat is een getal dat aangeeft of het dier qua erfelijke aanleg boven of onder het populatiegemiddelde ligt. In het geval van een stier is de fokwaarde vooral gebaseerd op gegevens van dochters; in het geval van koeien is de fokwaarde gebaseerd op de eigen prestatie(s) en de prestaties van ouders, dochters en andere familieleden.

Aan de hand van fokwaardes worden de beste dieren uitgekozen als ouders van de volgende generatie. De structuur om genetische verbetering van een populatie te bewerkstelligen wordt een fokprogramma genoemd. De doelstelling van een fokprogramma is vaak om de genetische vooruitgang te maximaliseren gegeven de randvoorwaarden. Maximalisatie van genetische vooruitgang kan door optimalisatie van een aantal zaken, zoals het aantal te selecteren ouders, het totale aantal selectiekandidaten, het aantal te testen nakomelingen per vader of moeder en het moment van selectie. Grofweg bestaan er twee typen fokprogramma’s: bij varkens en kippen worden dieren veelal geselecteerd op basis van (half)broer-zus gegevens, terwijl bij melkkoeien stieren worden geselecteerd op basis van nakomelingen.

Hieronder staan definities van enkele belangrijke begrippen in de fokkerij, die hierna terugkomen in de beschrijving van mijn promotieonderzoek:

- Genetische vooruitgang = de verbetering van het populatiegemiddelde door selectie, bijvoorbeeld toename in de gemiddelde melkproductie van melkkoeien door fokkerij;
- Variantie = statistische maat voor de spreiding/variatie van een kenmerk;
- Fenotypische variantie = totale variantie; een gedeelte van de variantie komt door erfelijke verschillen (= genetische variantie) en een gedeelte

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door niet-erfelijke verschillen (= milieuvariantie), bijvoorbeeld als gevolg van verschillen in leefomgeving;

- Erfelijkheidsgraad = gedeelte van de totale variantie (= fenotypische variantie) verklaard door erfelijke verschillen, getal tussen 0 en 1;
- Genetische correlatie = maat voor de genetische relatie tussen twee kenmerken, getal tussen -1 en 1;
- Fokwaarde = getal dat de erfelijke aanleg van een dier weergeeft, waarvan de helft wordt doorgegeven aan een nakomeling;
- Fokdoel = omschrijving van de belangrijkheid en richting waarin een aantallen kenmerken verbeterd moeten worden door selectie;
- Index = gewogen som van fokwaardes van verschillende kenmerken, waarbij de gewichten bepaald worden door de mate van belangrijkheid van de kenmerken in het fokdoel;
- Milieu = leefomgeving, de omstandigheden waarin een dier presteert.

Dit proefschrift

Dit proefschrift gaat over de ontwikkeling van methoden om fokprogramma’s te optimaliseren bij genotype-milieu interactie en genetische verschillen in milieuvariantie. Genotype-milieu interactie betekent dat dieren verschillend reageren op milieuoostandigheden, oftewel dat er een wisselwerking is tussen erfelijke aanleg en leefomgeving. Genetische verschillen in milieuvariantie kunnen optreden doordat dieren genetisch verschillen in heftigheid van reactie op schommelingen in milieu, bijvoorbeeld schommelingen in weer en voerkwaliteit. Het is belangrijk om genotype-milieu interactie zorgvuldig mee te nemen in fokprogramma’s, terwijl genetische verschillen in milieuvariantie mogelijkheden bieden om te fokken op een grotere uniformiteit (dus voor dieren meer op elkaar lijken).

**Genotype-milieu interactie.** Genotype-milieu interactie vereist verschillen in milieuoostandigheden. Voorbeelden zijn bedrijven met een ander management, bijvoorbeeld biologische of gangbare bedrijven, of bedrijven in verschillende landen, bijvoorbeeld Nederland of Nieuw-Zeeland. Door het optreden van genotypemilieu interactie is het genetisch beste dier in het ene milieu misschien niet het genetisch beste dier in een ander milieu. Dit kan betekenen dat de beste stier in Nieuw-Zeeland minder geschikt is voor Nederland. Hierdoor ontstaan rangordeverschillen tussen stieren, bijvoorbeeld op basis van de fokwaarde voor melkproductie. Rangordeverschillen door genotype-milieu interactie treden op wanneer de genetische correlatie tussen milieus kleiner is dan 1.0 voor een bepaald kenmerk, bijvoorbeeld melkproductie. De genetische correlatie wordt lager naarmate de milieus meer verschillen, maar is in de meeste gevallen hoger dan 0.5, of zelfs hoger dan 0.8. Als gevolg van rangordeverschillen door genotype-milieu interactie kunnen verschillende of
zelfs verkeerde dieren geselecteerd worden. Dit kan gevolgen hebben voor genetische vooruitgang in fokprogramma’s.

DeHoofdstukken 2, 3 en 4 behandelen het effect van genotype-milieu interactie op genetische vooruitgang vanuit een verschillend perspectief. Genotype-milieu interactie kan bijvoorbeeld voorkomen tussen het selectiemilieu op teststations, en het productiemilieu bij de veehouder (Hoofdstuk 2). Deze situatie komt veel voor in de pluimvee- en varkensfokkerij. Er zijn twee mogelijkheden om genetische vooruitgang in het productiemilieu op peil te houden: 1) het selectiemilieu zoveel mogelijk gelijk houden aan het productiemilieu of 2) dieren in het selectiemilieu selecteren op basis van informatie van halfbroers/halfzusjes of nakomelingen in het productiemilieu. Het verlies aan genetische vooruitgang is het kleinste door te selecteren op informatie van nakomelingen in het productiemilieu.

In Hoofdstuk 2 wordt uitgegaan van één productiemilieu, maar in werkelijkheid kunnen er meerdere productiemilieus zijn. Sperma van fokstieren wordt bijvoorbeeld verkocht aan veehouders in verschillende landen of met verschillende managementstijlen. De vraag rijst dan of maximale genetische vooruitgang in die verschillende milieu wordt gehaald met één fokprogramma of met meerdere fokprogramma’s. Een belangrijke uitkomst van dit proefschrift is dat één fokprogramma optimaal is wanneer de genetische correlatie hoger is dan 0.7 – 0.8 (Hoofdstuk 4 en 7). Als de genetische correlatie lager is, zijn meerdere fokprogramma’s nodig. Als één fokprogramma optimaal is, wordt de hoogste genetische vooruitgang gehaald wanneer dochters van proefstieren in meerdere milieu worden getest. Bestaande fokprogramma’s kunnen genetische vooruitgang vergroten door ook stieren en koeien te selecteren uit andere milieu, bijvoorbeeld waar concurrenten opereren, wanneer de genetische correlatie hoger is dan 0.8 – 0.9 (Hoofdstuk 3).

**Genetische verschillen in milieuvariantie.** Een voorbeeld van genetische verschillen in milieuvariantie is bijvoorbeeld dat de variatie tussen dochters van de ene stier groter is dan de variatie tussen dochters van een andere stier. Bijvoorbeeld de dochters van stier A produceren tussen 7500 en 8500 kg melk per lactatie met een gemiddelde van 8000 kg, terwijl de dochters van stier B tussen 7000 en 9000 kg produceren ook met een gemiddelde van 8000 kg. Stier B heeft dus meer uitblinkers en tegenvallers dan stier A. Deze eventueel genetische verschillen kunnen misschien gebruikt worden om dieren te fokken die meer op elkaar lijken en dus uniformer zijn, doordat ze minder heftig reageren op veranderingen in leefomgeving.

De Hoofdstukken 5 en 6 gaan over hoe genetische vooruitgang voorspeld kan worden in de aanwezigheid van genetische verschillen in milieuvariantie en hoe deze verschillen gebruikt kunnen worden om te fokken op een grotere uniformiteit en robuustheid van dieren. Er is een methode ontwikkeld om fokwaardes en genetische vooruitgang te voorspellen wanneer er verschillen in milieuvariantie zijn. Genetische verschillen in milieuvariantie is te vergelijken met een kenmerk met een lage erfelijkheidsgraad. Door selectie op een kleinere milieuvariantie kan de gemiddelde milieuvariantie per generatie met 5 tot 10% verkleind
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worden. Selectie op een kleinere milieuvariantie en dus een grotere uniformiteit is vooral interessant bij kenmerken met een optimum. Dit betekent dat hoge en lage waardes minder gewenst zijn, maar gemiddelde waardes meer gewenst zijn. Het is dan belangrijk om zoveel mogelijk dieren dicht in de buurt van het optimum te hebben. Voorbeelden van optimumkenmerken zijn bepaalde vleeskwaliteitskenmerken, eigewicht of melksnelheid.

Algemene discussie. In het eerste stuk van dit hoofdstuk wordt een samenvatting gegeven van kwantitatief genetische modellen voor genotype-milieu interactie en genetische verschillen in milieuvariantie. Een gecombineerd model wordt gebruikt om te laten zien dat beide fenomenen eenzelfde biologische achtergrond kunnen hebben. Om genetische verschillen in milieuvariantie te kunnen schatten zijn databestanden nodig waarbij 50 vaderdieren minimaal 100 nakomelingen hebben. Om te laten zien dat deze genetische verschillen bestaan en gebruikt kunnen worden in de fokkerij, kan een selectie-experiment uitgevoerd worden waarbij wordt gefokt op zowel een grotere als een kleinere uniformiteit.

In het tweede stuk van dit hoofdstuk wordt gediscussieerd hoe fokprogramma’s geoptimaliseerd kunnen worden als er naast genotype-milieu interactie ook fokdoelverschillen tussen milieus bestaan of wanneer er een zeer groot aantal milieus is. Ook wordt bediscussieerd hoe genotype-milieu interactie en genetische verschillen in milieuvariantie gebruikt kunnen worden om dieren te fokken die robuuster zijn voor schommelingen in milieu.

Belangrijkste conclusies van dit proefschrift:

1. Het meten van nakomelingen of (half)broers of zusjes in het productiemilieu kan het verlies aan genetische vooruitgang door genotype-milieu interactie tussen selectiemilieu en productiemilieu reduceren.
2. Het wordt aanbevolen om fokprogramma’s te splitsen in milieuspecifieke fokprogramma’s als de genetische correlatie tussen milieus lager is dan 0.7 – 0.8.
3. Genetische verschillen in milieuvariantie kunnen gebruikt worden om uniformiteit en robuustheid van dieren te vergroten.
Publications

Refereed scientific journals

Congress proceedings

**Popular articles and other reports**


Dankwoord

Op het moment dat ik dit schrijf, is het vier jaar geleden dat ik begon als AIO (= assistent in opleiding) bij de leerstoelgroep Fokkerij en Genetica. Ik kreeg de mogelijkheid om onderzoek te gaan doen naar optimalisatie van fokprogramma’s in aanwezigheid van genotype-milieu interactie. Prof. Dr. Ir. Johan van Arendonk had financiële middelen om mij aan te stellen op dit project bij de leerstoelgroep Fokkerij en Genetica en Dr. Ir. Piter Bijma had ideeën en schreef ze op in een onderzoeksplan. Ik had al enige ervaring opgedaan met het schatten van genotype-milieu interactie tijdens mijn afstudeervak en het leek me dan ook een uitdaging om grondig te onderzoeken welke consequenties genotype-milieu interactie voor fokprogramma’s heeft. Met veel plezier heb ik vier jaar lang onderzoek gedaan op dit gebied. Ik ben Johan en Piter dan ook zeer dankbaar voor de geboden mogelijkheden.

Allereerst wil ik Piter bedanken voor de goede begeleiding tijdens deze vier jaar. Je gaf me veel vrijheid en het vertrouwen om zelfstandig die dingen te onderzoeken die ik leuk vond. Je hielp goed bij het onderscheiden van hoofd- en bijzaken. Je soms prikelende opmerkingen zorgden ervoor dat ik dingen nog eens extra ging bestuderen, wat het begrip en resultaat ten goede kwamen. Je vele opmerkingen op conceptartikelen kwamen de duidelijkheid ten goede. Ook wil ik Bart bedanken, omdat jij een soort uitlatklep voor mij was. Op informele wijze bespraken we mijn onderzoek of discussieerden we over ontwikkelingen in de fokkerij. Samen met de andere leden van de begeleidingscommissie, Roel en Johan, hebben we met zijn vijven vele bijeenkomsten gehad. We hadden soms felle discussies. Ook begrepen jullie niet altijd precies wat ik wilde of had gedaan. Vaak moesten conceptartikelen op de ‘kop’, wat niet echt mijn lievelingsklusse was. Desalniettemin heb ik onze discussies altijd als zeer waardevol ervaren. Graag wil ik jullie alle vier: Piter, Johan, Roel en Bart, bedanken voor jullie bijdragen. Ik heb er veel van geleerd!

In the autumn of 2005, I got the opportunity to visit Prof. Bill Hill at the University of Edinburgh in Scotland for 3.5 months. The period in Scotland has opened my eyes for more fundamental research. I would like to express my gratitude to Bill for hosting me and being an excellent supervisor. It was an honour to work with you. We had many interesting discussions about the research, which ultimately resulted in two nice papers about breeding for uniformity. After I returned to the Netherlands, we had many e-mail contacts. You were surprisingly quick with giving comments and suggestions on my manuscripts to improve not only the contents, but also the quality of English. At this place, I would like to thank also Bernardo, Bill, Ian, Jean-Alaine, Jules, Lutz and Xu-Sheng for the wonderful discussions about quantitative genetics and other subjects during coffee breaks. Bernardo, Jean-Alaine and Jules thanks also for the enjoyable conversations at Kings Buildings, in pubs, or during trips.
I would like to thank Line Buch for carrying out a small research project for your MSc in the spring of 2006. You studied breeding goals of the Holstein breed in Canada, Denmark, The Netherlands, and New Zealand and estimated genetic correlations between these breeding goals. The project was a nice practical example of calculating genetic correlations between breeding goals in different countries.

Behalve mijn begeleiders, wil ik ook Mario, Wytze en Liesbeth bedanken voor de leuke en leerzame discussies over genotype-milieu interactie en robuustheid. Verder wil ik Sijne van der Beek, Henk Geertsema, Egbert Knol, Erwin Koenen, Chris Schrooten en Addie Vereijken bedanken voor discussies over genotype-milieu interactie, uniformiteit en fokprogramma’s. Mijn dank ook voor alle mensen die deelnamen aan de Quantitative Discussion Group bijeenkomsten. We hebben vele interessante onderwerpen behandeld. Ook mijn kamergenoten Tony, Ansku, Koen en vooral Birgitte, die ongeveer 3,5 jaar mijn kamergenoot was, wil ik bedanken voor het creëren van een prettige sfeer. Birgitte, bedankt ook voor de leuke gesprekken over broilers, Denemarken of iets anders. Verder wil ik alle collega’s en oud-collega’s van de leerstoelgroep Fokkerij en Genetica bedanken voor de prettige sfeer in de groep, zowel tijdens het werk op Zodiac als tijdens congressen, cursussen of iets anders.

Sinds januari 2004 maak ik deel uit van de kwantitatieve werkgroep van het robuuste legkip project in samenwerking met Hendrix Genetics in Boxmeer. Op die manier ben ik vanaf het begin betrokken geweest bij de opzet en uitvoering van zowel proeven om genetische parameters te schatten voor uitval door kannibalisme bij legkippen, als bij het pilot selectie-experiment om uitval door kannibalisme te reduceren. Esther, Koen, Laura, Jeroen, Patrick, Addie en Piter, bedankt voor de vele discussies over robuustheid, kannibalisme, ‘associative effects’ en proefopzet. Ik heb het project altijd ervaren als een mooie aanvulling op mijn eigen project.

Bastaan en Bart, mijn hartelijke dank dat jullie me willen bijstaan als paranimf bij de verdediging van mijn proefschrift. Ook wil ik mijn vrienden, familie, (oud-)bestuursleden en leden van de PJO afd. Enschede en andere bekenden bedanken voor de getoonde belangstelling voor mijn onderzoek.

Tot slot, wil ik mijn vader, moeder en zus Marieke ontzettend bedanken voor jullie niet aflatende steun en belangstelling voor wat ik deed, al ging het waarschijnlijk vaak boven jullie pet. Juist dat vormde voor mij altijd een uitdaging om de dingen zo te vertellen dat jullie ze snapten. Verder wil ik Marieke ook bedanken voor de kritische opmerkingen op enkele stukken van dit proefschrift.

Han
Curriculum vitae

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**Subtotal In-Depth Studies** 23

## Professional Skills Support Courses

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**Subtotal Professional Skills Support Courses** 10

## Research Skills Training

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**Subtotal Research Skills Training** 2

## Didactic Skills Training

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**Subtotal Didactic Skills Training** 8

## Management Skills Training

<table>
<thead>
<tr>
<th>Activity Description</th>
<th>Year</th>
<th>Credits</th>
</tr>
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<tbody>
<tr>
<td>Organisation of seminars and courses</td>
<td>2004-2005</td>
<td></td>
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<tr>
<td>WIAS Science Day</td>
<td>2005</td>
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<tr>
<td>Retraite ABG</td>
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<td>Membership of boards and committees</td>
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<td>Faciliteitcommissie ABG</td>
<td>2003-2007</td>
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<td>WIAS theme Food Security and Quality</td>
<td>2004</td>
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<td>WAPS</td>
<td>2005</td>
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**Subtotal Management Skills Training** 10

## Education and Training Total (minimum 30)

73

* one ECTS credit equals a study load of approximately 28 hours
The pictures on the cover page of this thesis were kindly provided by:

CRV Holding BV, Arnhem                  dairy cow
Hendrix Genetics BV, Boxmeer             laying hen
TOPIGS BV, Helvoirt                      sow