Estimation of Environmental Sensitivity of Genetic Merit for Milk Production Traits Using a Random Regression Model

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ABSTRACT

The objective of this study was to estimate effects of environmental sensitivity of milk production traits for several environmental parameters and to investigate the impact of combining traits with different environmental sensitivity in an economic index. Variance components and breeding values were estimated for milk, fat, and protein yield, and fat and protein percentage by applying a random regression on values of an environmental parameter for each sire. Fourteen environmental parameters were defined and fitted to data consisting of 151,696 heifers in 6780 herds in The Netherlands with first-lactation records for milk production, somatic cell count, body condition score, and number of inseminations. Milk, fat, and protein yield showed environmental sensitivity in combination with 12 environmental parameters. Herd-year averages of protein, body condition score, age at calving, calving interval, and peak date of calving explained most genotype by environment interaction, mainly resulting from scaling effects. Almost all genetic correlations across environments were 0.99 or higher. Although heterogeneity of genetic variances was considerable, heterogeneity of heritabilities was limited. Scaling had a large effect on the weights of the economic index, but environmental sensitivities of milk, fat, and protein yields were approximately of equal magnitude. Consequently, very little reranking occurred based on the economic index. (**Key words:** environmental sensitivity, environmental parameter, genotype $\times$ environment interaction, random regression model)

Abbreviation key: EP = environmental parameter, ES = environmental sensitivity, G $\times$ E = genotype $\times$ environment interaction, HYS = herd-year-season.

INTRODUCTION

The phenomenon that different genotypes respond differently to changes in their environments is known as genotype $\times$ environment interaction (G $\times$ E) or as differences in environmental sensitivity (ES) of genotypes (Falconer and Mackay, 1996). This interaction can cause reranking of animals across environments or a change of scale, i.e., variance, across environments (Lynch and Walsh, 1998). Traditionally, animal breeders are more concerned about reranking of animals than about differences in scale between environments because differences in scale do not affect the ranking of the animals for the considered trait. However, reranking of animals across environments is limited for milk production traits (Veerkamp et al., 1995b; Cromie, 1999; Calus et al., 2002), although there is evidence that variances and heritabilities vary (Veerkamp et al., 1995b; Cromie, 1999; Calus et al., 2002). Scaling effects can be accounted for in the breeding value estimation model (Meuwissen et al., 1996) and do not influence the ranking of sires, based on a single trait. However, if scaling effects are different for traits that are combined together in an economic index, the relative importance among the traits might change and cause reranking based on this economic index (Namkoong, 1985). In that case it might be more appropriate to include environmental sensitivity in breeding decisions rather than to correct for it in the statistical model.

An environmental parameter (EP) reflects the environment encountered by the animals. An EP can reflect production level of a herd (Veerkamp and Goddard, 1998; Calus et al., 2002; Kolmodin et al., 2002), or other characteristics of the herd, such as average calving interval or average age at calving (Fikse et al., 2003). Describing G $\times$ E for dairy cattle with a covariance function of an EP is recently described for a limited number of EP (Veerkamp and Goddard, 1998; Calus et al., 2002; Kolmodin et al., 2002; Fikse et al., 2003). The use of an EP in a covariance function has the advantage that environments are treated as a continuum, rather than a set of arbitrarily defined groups of the data. The EBV

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of an animal, which is divided into an environment independent and an environment dependent part, is also called reaction norm (Falconer and Mackay, 1996). The simplest form of a covariance function describes the ES of the genotype as a linear function of the EP, but higher order functions are possible. Covariance functions can be estimated by a two-step procedure or by random regression models (Van der Werf et al., 1998).

The objective of this paper is to estimate ES for milk production traits for a range of EP in order to identify those EP that gave most ES and to investigate the effects of ES on reranking in the Dutch economic index (INET) combining milk, fat, and protein yields.

MATERIALS AND METHODS

Data

The data contained first-lactation test-day records for milk production traits and SCC, date of first calving, date of each insemination, and BCS for 271,606 heifers calving in 1998 and 1999 from 12,347 Dutch dairy herds. A few criteria were used to select the data for the estimation of variance components of milk production traits. Each heifer needed at least five test-day records during the period of 5 to 305 DIM of which at least one was on or after 180 DIM; heifers that calved at an age of less than 640 or more than 1310 d were deleted. These criteria decreased the number to 267,120 heifers in 11,602 herds. Selected animals were deleted if their herd did not meet the criteria of the EP, which are explained later. To calculate EP, for each herd-year a minimum number of four records were needed for calving interval, as this EP was most restrictive, and five records for other EP. A total of 151,696 mostly Holstein-Friesian and Meuse-Rhine-Yssel heifers in 6780 relatively large herds were eventually selected. Each herd-year contained an average of 14 heifers.

In the pedigree file, a maximum of five generations of sires were included, together with the pedigrees of dams of first and second generations of sires and the sires' maternal grandsires. A total of 4769 sires with daughters in the data were identified. Sires had on average 32 daughters. The relationship matrix contained 14,382 animals.

Traits

Five traits were evaluated: average daily milk yield, fat yield, protein yield, fat percentage, and protein percentage. Milk, fat, and protein yield were calculated as the average of the test-day yields between 5 and 305 DIM. Fat and protein percentage were calculated as

the average yield of fat and protein divided by the average milk yield.

Environmental Parameters

Environmental parameters were calculated for each herd-year level, based on calving date. Potentially a large number of EP could be defined, but parameters used here were chosen because they: 1) reflect management and environment, 2) are obtainable from the available data, 3) are continuous rather than categorical, i.e., the parameter is expressed on a scale rather than defined in several classes, and 4) are not too strongly correlated with each other. Each parameter was averaged over all heifers calving in the relevant herd-year. For parameters that reflected traits with more records per lactation, first an average was calculated for each selected animal.

Test-day record parameters. Average protein and SCC were calculated from test-day records in 1998 and 1999. Each SCC test-day record was transformed to a SCS, by $SCS = \log_{10}(SCC)$. Persistency was calculated in two different ways. First, persistency was calculated for each animal from the ratio of milk production on the test-day closest to 60 DIM to milk production on the test-day closest to 240 DIM (Zwald et al., 2001), both in a range of 42 d around those. Second, persistency was taken as the highest test-day milk production of a heifer divided by its average test-day milk production. This last parameter is called relative peak milk yield.

Age at calving and herd size parameters. Average age at calving and number of freshened heifers were calculated over all heifers that calved during the year, regardless how many days they produced. In both years, the change in number of freshened heifers was set to the difference between 1998 and 1999.

Energy balance parameters. Energy balance reflects the ability of management to tune the feed intake to the energy requirements and therefore indicates whether tissue reserves are mobilized or deposited in the cow. Body condition score reflects cumulated energy balance (Chilliard et al., 1991). Body condition score was measured during classification and only once during the first lactation. Average BCS was calculated from all classified heifers in a herd that calved in the same year. Other traits that reflect energy balance are change in fat percentage and fat over protein ratio (De Vries and Veerkamp, 2000). Change in fat percentage was calculated as the difference in fat percentage on the test-day closest to 77 DIM and the test-day closest to 14 DIM (De Vries and Veerkamp, 2000), both in the range from 10 to 100 DIM. Fat over protein ratio was calculated by test day and then averaged across test days.

Calving and insemination parameters. Calving interval is the period between first and second calving. The number of inseminations required for a successful second calving was estimated during first lactation. The herd calving pattern was represented by peak date of calving and distribution of calving dates over the year. The peak date of calving shows the date around which the heifers are calving and the distribution of the calving dates shows whether the heifers are calving near that date or throughout the whole year. Average day of calving can be calculated by numbering each day of the year from 1 to 365 and obtaining the average of the renumbered calving dates (Zwald et al., 2001). A disadvantage of this method is that a nonequal distribution of calving during a year, e.g., if the peak date of calving does not fall on July 1st, leads to an underestimation or an overestimation of the peak date of calving. Here, a slightly different procedure is used. The peak date of calving is calculated by iteratively repeating the following procedure: 1) calculate the average of calving dates (Zwald et al., 2001) and 2) define a maximal time period in the same calendar year with the average of step 1 as central point. For instance, with an average calving date of d 140, the new period ranges from d 0 to 280. If the period became shorter than 182 d, it was expanded over the borders of the calendar year. Insemination data from 1997 and 2000 were available to make this expansion feasible. The time period in step 1 is in the first iteration the calendar year and in later iterations the period defined in step 2 in the previous iteration. Steps 1 and 2 are repeated until the average day of calving no longer changes. The converged average day of calving is considered to be the peak date of calving. For a few herds, two peaks of calving in a year made convergence impossible. If convergence had not occurred after 1000 iterations, the average day of calving of all 1000 iterations was taken. Values for 1999 were adjusted by subtracting 365 d to come to the same standard as in 1998. The distribution of calving dates during the year was calculated by the use of an interval of 182 d and one of 365 d, both centered on the peak date of calving. The distribution of calving dates was calculated as the ratio of the number of calving dates in the short interval to the number of calving dates in the long interval.

Estimating Variance Components and Environmental Sensitivity

Variance components were estimated by using a sire model. Environmental sensitivity was modeled by applying a random regression for each sire, representing its EBV, on values of an EP for the herds in which his daughters were producing. A fixed linear and qua-

dratic regression for age at calving was included, as was a fixed effect to account for herd-year-season (HYS) groups. Furthermore, a fixed polynomial was also applied to the EP, to account for the average effect in each environment. An HYS effect was not fully covered by the herd-year effect. In each situation, only one EP was used for both the random regression for sires and the fixed regression for herd-year. The residual variance was calculated for 10 equally sized groups, based on increasing EP, to include heterogeneous residual variances in the model.

The HYS groups were defined by a method that optimizes the composition of HYS groups based on the calving dates and intervals between consecutive calving dates in a herd (Crump et al., 1997). Initially, the criteria of a maximum period of 91 d and a minimum of five animals per HYS group were applied. If some animals were not assigned to an HYS group based on these criteria, they were forced to join one by relaxing the criterion for the maximum period. The same was applied to animals from groups that had fewer than five animals, to force them to join another HYS group. The applied model was:

$$Y_{ijklmnoq} = \mu + HYS_i + \gamma_0 * AGE_j + \gamma_1 * (AGE_j)^2 + \sum_{k=0}^{10} \beta_k P_{km} + \sum_{l=0}^S \alpha_{ln} P_{lm} + E_{ijklmnoq}$$

where:

$Y_{ijklmnoq}$ is the performance of heifer q ,

μ is the average performance over all animals,

HYS_i is the effect of herd-year-season group i ,

γ_0 and γ_1 are coefficients of linear and quadratic fixed regression on age at calving j in days, respectively,

AGE_j is age at calving in days of heifer q ,

β_k is coefficient k of a fixed regression on element k of the orthogonal polynomials of all environments,

P_{km} is element k of the orthogonal polynomial resembling an environmental parameter of environment m ,

α_{ln} is coefficient l of the random regression on the orthogonal polynomials of all environments of the daughters for sire n ,

P_{lm} is element l of the orthogonal polynomial resembling an environmental parameter of environment m , s is the largest significant coefficient l of the random regression, and

$E_{ijklmnoq}$ is the residual effect of heifer q in environment m within group of environments o ($o = 1, 2, \dots, 10$).

The order of the polynomials for the fixed regression on an EP was arbitrarily set to 10 in each situation. For the random regression, the order of the polynomial was increased per combination of trait and EP until the extra added components of the next order did not

significantly improve the fit of the model or the variance of the extra component was zero. The log likelihood ratio test (Kirkpatrick et al., 1990) was used to compare the fit of two models with consecutive orders of polynomials.

The sire variances for values of an EP are calculated as $\Phi S \Phi'$, where Φ is a matrix with polynomial coefficients for a value of the EP on each row and S is an $n \times n$ matrix, where n is the highest order of the polynomial + 1, with variances of each random regression coefficient on the diagonal and covariances between the random regression coefficients on the off-diagonals. The residual variance was calculated for 10 different groups. Residual covariances between groups were assumed to be zero. Covariances between sire and residual effects were assumed to be zero and not taken into account.

Several criteria can be defined to rank EP based on the given amount of GxE. In this study, we used the absolute change in sire variances between 25 and 75% of the environmental scale as an indicator of change in sire variance across environments and therefore of the given amount of GxE. To check the results of the random regression model, a multitrait model was applied for selected combinations of traits and EP. The program ASREML (Gilmour et al., 2002) was used for all analyses.

Economic Index

The Dutch INET is an economic index that includes milk, fat, and protein yield and is calculated as $INET = -0.08 \times EBV(\text{milk yield}) + 1 \times EBV(\text{fat yield}) + 6 \times EBV(\text{protein yield})$. The INET was used to investigate the effects of ES on the combination of milk, fat, and protein yields. First, the INET was calculated based on

the results of the described model. No base adjustments in the index were made, i.e., average breeding values were not adjusted based on the average of the whole current population. Secondly, the economic weight was readjusted to real economic weights in a few environments. The correlated response of selection in a different environment is:

$$CR_Y = r_{XY} \times (\sigma_Y/\sigma_X) \times R_X \text{ (Falconer and Mackay, 1996),}$$

where CR is the correlated response in environment Y, r_{XY} is the genetic correlation between environment X and Y, σ_X and σ_Y are genetic standard deviations in environments X and Y, and R_X is the response of selection in environment X. The adjustment factor of the weights of the INET is then equal to $r_{XY} \times (\sigma_Y/\sigma_X)$. If no reranking occurs or adjustment is for scaling effects only, i.e., $r_{XY} = 1$, this reduces to (σ_Y/σ_X) .

RESULTS

Environmental Parameters

Mean and range for the environmental parameters is given in Table 1 based on 151,696 heifers in 6780 herds. Herds differed considerably for the EP, for example, average protein ranged from 0.46 kg of protein per day to 1.21 kg of protein per day, average age at calving from 672 to 1028 d and herd size from 5 to 270 numbers of heifers calving. Correlations among all EP ranged from -0.43 to 0.45 but were generally weak. Strongest correlations were found for pairs of EP that were calculated from the same traits, such as EP defined on production traits and defined on the number of freshened heifers in a herd. As peak date of calving is one of the newly defined EP and had a considerable effect, the

Table 1. Mean, standard deviation, coefficient of variation and range of all environmental parameters.

Environmental parameter	Mean	SD	CV (%)	Minimum	Maximum
Average protein (kg/d)	0.84	0.09	10.7	0.46	1.21
Fat/protein	1.26	0.05	4.1	1.02	1.51
SCS	2.55	0.99	38.8	-5.74	5.54
Persistency	1.10	0.04	3.6	0.99	1.47
Relative peak milk yield	1.23	0.05	3.7	1.09	1.57
Age at calving (d)	797	39	4.9	672	1028
Number of animals	22.73	16.22	71.3	5	270
Change in number of animals ¹	3.95	9.35	237	-40	71
BCS (thin-fat: scale 1-9)	4.75	0.66	13.8	2.18	7.50
Change in fat percentage (%) ²	-0.20	0.26	-125.6	-1.53	1.33
Calving interval (d)	388	27.1	7.0	316	605
Number of inseminations	1.33	0.25	19.0	1.00	3.50
Peak calving date (d) ³	232	78	22.4	-108	434
Distribution of calving dates	0.41	0.18	44.9	0.00	1.00

¹In both years the difference between 1998 and 1999 is used.

²The difference in fat percentage on the test day closest to 77 DIM and the test day closest to 14 DIM.

³-108 means d 257 of the year before, 434 means d 69 of the next year.

Figure 1. Distribution of the numbers of animals with a peak date of calving in a certain month for both 1998 (□) and 1999 (■).

number of animals with peak date of calving in a certain month is shown for both years (Figure 1). This illustrates that most herds have their heifers calving in the autumn, although this is less clear for 1999 than for 1998.

Significant reaction norms were found in 50 out of 70 combinations of traits and EP. The highest estimable and significant order of the polynomial is given for each combination of traits and EP in Table 2. Milk, fat, and protein yield each had significant reaction norms in combination with 12 EP. These three traits generally showed the same order of significant polynomials for a given EP. Fat and protein percentage had significant reaction norms in combination with 6 and 8 EP.

Environmental Sensitivity

The EP for the environments at 25, 50, and 75% of the data based on the increasing environmental scale

were used to calculate sire variances and heritabilities for these environments for milk, fat, and protein yield. The results for the sire variances calculated for 305 d are shown in Table 3. The heritabilities were comparable across environments for all combinations of traits and EP.

Environmental parameters were ranked on decreasing absolute change in sire variances between 25 and 75% on the scale of the EP, indicating decreasing G×E for milk, fat, and protein yield (Table 4). For the trait protein yield, average protein, BCS, calving interval, age at calving and persistency were the most important EP (Figure 2). Age at calving and calving interval showed the same pattern of sire variance, which decreased by a third across the environmental scale. The sire variance showed the most curvilinear relationship with average protein. For average protein and BCS, the sire variances doubled across the environmental scale. For the EP average BCS, the sire variances for milk, fat, and protein yield are shown in Figure 3. The environmental scale in Figure 3 resembles the interval of the mean EP $\pm$ two standard deviations. The sire variances are following a similar pattern across the environmental scale.

The genetic correlation between a trait in the environment at 25% and the same trait at 75% of the data on the environmental scale were calculated for the model with the highest significant order for the given combination of trait and EP. The combination of the trait protein and the EP fat over protein ratio gave a genetic correlation of 0.96 (SE = 0.009). All other correlations were 0.99 or higher (SE ranging from 0.000 to 0.004). The multitrait model (results not shown) gave comparable results to those of the random regression model.

Table 2. The number of the highest estimable and significant ($P < 0.05$) polynomial order¹ of the combination of the environmental parameter in the row and the trait in the column.

Environmental parameter	Traits				
	Milk	Fat	Protein	Fat %	Protein %
Average protein	2	2	2	2	2
Fat/protein	2	2	3	2	0
SCS	2	2	2	0	1
Persistency	2	2	2	0	0
Relative peak milk yield	1	2	1	0	2
Age at calving	1	1	1	1	2
Number of animals	2	1	2	1	2
Change number of animals	2	2	2	0	0
BCS	2	2	2	1	1
Change in fat percentage	0	0	0	0	1
Calving interval	2	1	1	1	0
Number of inseminations	1	2	1	0	0
Peak calving date	3	2	1	1	0
Distribution of calving dates	0	0	0	0	1

¹A zero means that the first order polynomial is not significant.

Table 3. Sire variances in kg² per 305 d at 25, 50, and 75% on the scale of the environmental parameters, for all combinations of environmental parameters and the traits milk, fat, and protein yield that showed a significant environmental sensitivity.

Environmental parameter	Milk			Fat			Protein		
	25%	50%	75%	25%	50%	75%	25%	50%	75%
Average protein	116,598	131,872	142,291	169.9	189.8	203.8	92.4	107.8	119.5
Fat/protein	118,942	118,923	118,039	168.7	170.5	171.8	96.9	95.9	94.3
SCS	116,095	114,979	117,118	165.9	169.0	175.8	91.9	91.6	95.1
Persistency	114,532	118,291	122,291	164.4	169.8	175.5	91.7	94.9	99.0
Relative peak milk yield	118,439	117,388	116,625	172.9	172.6	170.9	94.2	94.3	95.2
Age at calving	123,295	118,942	114,049	177.0	171.5	165.5	103.1	97.1	90.2
Number of animals	117,202	116,905	116,942	165.6	166.8	169.0	93.3	93.4	93.8
Change number of animals	119,379	117,063	114,644	166.6	167.8	169.8	96.1	93.8	91.7
BCS	109,639	120,505	127,984	154.3	174.8	189.2	85.4	97.3	106.1
Calving interval	124,533	115,965	109,100	176.7	170.7	164.2	102.7	96.3	89.4
Number of inseminations	115,072	116,653	119,537	166.7	168.6	172.3	92.0	93.8	97.0
Peak calving date	112,881	118,264	120,046	154.7	164.6	172.1	89.5	94.0	96.2

Economic Index

The overall economic value for milk, fat, and protein yield, called INET, was calculated on the scale of the EP average BCS for the 10 sires with the highest number of daughters in the data (Figure 4). These bulls are not representative for all bulls in the population, but they represent the breeding bulls that are widely used by dairy farmers. The INET increases with increasing average BCS, and little reranking happened. The sire with the highest change of INET shows an INET of 65 Euros for herds, with an average BCS of 3.5 and an INET of 120 Euros for herds with an average BCS of 6.0.

Based on the scaling effects of milk, fat, and protein yield across environments, the economic weights in the INET formula were adjusted. The results for the EP average BCS are shown in Table 5. The change of the economic weights with the change of the EP clearly illustrates the effect of scaling.

Table 4. Environmental parameters ranked per trait for decreasing absolute change of the sire variances between 25 and 75% on the environmental scale.

Environmental parameter	Traits		
	Milk	Fat	Protein
Average protein	1	2	1
Fat/protein	11	11	10
SCS	10	7	9
Persistency	5	6	5
Relative peak milk yield	9	12	11
Age at calving	4	5	4
Number of animals	12	9	12
Change number of animals	7	10	8
BCS	2	1	2
Calving interval	3	4	3
Number of inseminations	8	8	7
Peak calving date	6	3	6

DISCUSSION

Environmental Parameters

Herds were required to have at least four records for calving interval and at least five records for all other EP in order to be selected. This criterion led to a substantial loss of data. However, it ensured that small herds with very few informative animals were not taken into account. The data from such herds might be biased by the small numbers and from the fact that their genetic composition is more likely to be nonrandom. The edited data still contained herds that differed considerably for EP, indicating that data editing did not discard certain types of herds, apart from small ones.

Figure 2. Sire variance of protein yield in kg² for average protein (protein) (●), BCS (■), calving interval (▲), age at calving (□), and persistency (○) given the deviation of the mean environmental parameter in standard deviations.

Figure 3. Sire variances for 305 d milk/1000 (●), fat (■), and protein yield (▲) as a function of the average BCS per herd-year.

Twelve EP gave significant reaction norms for milk, fat, and protein yield. Results for six of these parameters for milk yield were reported in literature. Significant ES for the EP herd size, relative peak milk yield, persistency, and age at first calving were found (Fikse et al., 2003), but no significant reaction norms for the EP fat over protein ratio and calving interval were found in that study. Average protein and BCS showed the highest ES based on our definition. Average protein is proven to be a useful EP before (Calus et al., 2002; Kolmodin et al., 2002). These results indicate that adjusting for heterogeneous variances in the genetic evaluation model might be possible by using EP.

The situation in which the EP is calculated based on the evaluated trait needs some attention. The fact that EP are calculated as phenotypic averages within a herd implies that the breeding values are partly based on

Figure 4. The Dutch total economic value for milk, fat, and protein yield (INET) in Euros of the 10 sires with the highest number of daughters in the data, as function of the average BCS per herd-year.

Table 5. Economic values (in Euros) for 305-d milk, fat, and protein yield in the INET formula, for different values of the environmental parameter average BCS.

BCS	Milk	Fat	Protein
3.5	-0.068	0.82	4.90
4.0	-0.074	0.90	5.36
4.5	-0.078	0.97	5.79
5.0	-0.082	1.03	6.19
5.5	-0.084	1.07	6.49
6.0	-0.087	1.10	6.74

the breeding values of sires of the cows producing in a herd. Kolmodin et al. (2002) suggested that this may not be a problem, but no extensive evidence was given. In the case of random use of sires across environments, this will probably not be a problem, as the average breeding value will be zero, but the precise implication of including the evaluated trait in the calculation of the EP is not clear yet.

It is tempting to suggest that significant scaling effects shown for some of the EP, might be a result of the association with yield, because generally an increasing level of production also leads to increasing variance. In this study, both BCS and calving interval showed changing sire variances with increasing values of the EP (Table 3), and BCS and calving interval had correlations of 0.19 and -0.01 with average protein. However, herds with an average BCS of four and herds with an average BCS of six, both had an average 305-d protein production of 250 kg, indicating that only limited effect can be expected from the low correlation between protein yield and BCS. Still, it illustrates the problem of interpreting EP, and the need to consider multiple EP simultaneously.

Body condition score gave considerable scaling effects. Body condition score reflects cumulated energy balance (Chilliard et al., 1991). It was reported (Cromie, 1999) that defining environments based on the amount of concentrate fed causes scaling effects that are comparable to scaling effects if environments are defined on average protein. These results support the suggestion of others (Calus et al., 2002; Kolmodin et al., 2002) that feed intake and feed supply are important parameters in relation to environmental sensitivity of genetic merit for milk yield.

Environmental Sensitivity

Environmental sensitivity was defined by Falconer (1990) as the difference between phenotypic values of a genotype or a population in two environments, divided by the difference of the means of all individuals in both environments. In our study, ES is defined at a popula-

tion level as the variance in reaction norms of genotypes.

Genetic correlations of a trait across environments were high, indicating that reranking hardly occurred across environments, as was expected from literature (Calus et al., 2002; Kolmodin et al., 2002; Fikse et al., 2003). However, sire variances showed considerable scaling effects for a number of the EP. At the same time, heritabilities were comparable across environments, indicating that scaling effects for environmental and sire variances were comparable. Heterogeneous heritabilities for comparable models were reported, but in these studies the heterogeneity of residual variances was not taken into account (Calus et al., 2002; Kolmodin et al., 2002). If heterogeneity of sire variances is accommodated in the model, but heterogeneity of residual variance is not, the presence of scaling effects is likely to cause heterogeneity of heritabilities.

Herds with high protein, high persistency, young age at calving, high BCS, short calving intervals, and calving peak in the fall or winter appeared to have the highest genetic variance for milk, fat, and protein yield. This means that herds that have one or more of these characteristics are more likely to benefit more from the use of bulls with high genetic merit and the use of expensive high genetic merit bulls is more easily justified in those herds. At the same time, selection of animals on those herds will be more effective when there is an insufficient correction for heterogeneous variances in the breeding value estimation.

Economic Index

The economic value of a trait was affected if the trait showed large scaling effects. If scaling effects are different among traits, the relative importance of these traits in an economic index can change (Namkoong, 1985). The economic index might give different selection responses depending on herd environment, and therefore reranking across environments might occur. This might reduce the total benefit of selection based on this economic index. In this study, the economic values of the traits in the index were only adjusted for scaling effects. Genetic correlations among environments of the adjusted economic values (Table 5) ranged from 0.93 to 0.99. Taking these into account would cause greater differences across environments. As shown here, reranking based on INET will be small, for a number of reasons. First, the scaling effects of milk, fat, and protein yield are comparable across environments. Second, the genetic correlations among these three traits are high and therefore the economic index is relatively insensitive for changes in economic values (Veerkamp et al., 1995a). However, if other traits are included in the

economic index, with scaling effects that are independent from those of production traits, the scaling effects could cause considerable reranking based on the economic index (Namkoong, 1985). This clearly indicates that scaling effects might be of importance in animal breeding programs.

CONCLUSIONS

Herds with high protein, high persistency, young age at calving, high BCS, short calving intervals, and calving peak in the fall or winter, have higher variances for the yield traits and are therefore expected to benefit more from the use of bulls with high genetic merit and selection of animals based on those herds will be more effective. Scaling effects for milk, fat, and protein yield were considerable, but comparable, indicating that no large differences of environmental sensitivities among these traits were found on a population level. Therefore, reranking based on economic index was limited. The absence of reranking based on a single trait does not necessarily mean that G×E is not important and scaling effects can easily be accounted for by adjusting the data. As more reproduction and health traits are included in total merit indices, further research is needed to explore the ES of these traits.

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