

# Additive and Dominance Genetic Variance of Fertility by Method $\mathcal{R}$ and Preconditioned Conjugate Gradient

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## ABSTRACT

The objectives of this study were threefold: 1) estimation of additive and dominance genetic variances for fertility traits for Austrian Simmental and Brown Swiss dairy cattle; 2) use of method  $\mathcal{R}$  and the preconditioned conjugate gradient compared to solving for method  $\mathcal{R}$  by second-order Jacobi iteration; and 3) study of the impact of inclusion of parental subclass effects on solutions for other random effects. Dominance variances were modeled for the inseminated cow and ranged from 0.32 to 1.36% of total variance. These values were similar to values for additive effects, which were approximately 1% of total variance. Convergence was clearly improved with preconditioned conjugate gradient and number of extrapolations reduced. Variance for permanent environment under a model without dominance could be split into a new estimate of permanent environmental variance and parental subclass variance. Solutions for parental subclass dominance effects were approximately proportional to permanent environment effects, but highly dependent on the number of animals contributing dominance relationships, especially full-sibs and three-quarter-sibs. For animals with a lot of dominance information (full-sibs, three-quarter-sibs, cousins), permanent environment and parental subclass dominance effects were nearly independent. Changes in additive effects were negligible, probably because both variances for parental subclass dominance effects and additive genetic effects were very

small compared with residual variance.

(**Key words:** variance component estimation, dominance, fertility)

**Abbreviation key:** PCG = preconditioned conjugate gradient.

## INTRODUCTION

Dairy cattle breeding programs generally stress milk production, but profitability also depends on nonproduction traits, such as physical, fertility, and health traits. Under quota systems as in the European Union, the relative economic importance of these traits is even greater than where quota systems are not used.

Fertility is considered to be one of the most important economic traits in both dairy and beef cattle populations ([Jansen, 1986](#); [Philipsson, 1981](#)). Fertility, to a large degree, determines the number of progeny an individual contributes to the next generation and provides the basis for cow selection ([Thaller, 1998](#)). Better reproduction efficiency has several economic consequences, such as: 1) a reduction in the number of inseminations per conception and of veterinary costs, 2) more control over calving interval, 3) increased milk production per day of herd life, 4) increased meat production, as a consequence of more progeny, 5) decreased culling rate, and 6) increased intensity of selection ([Jansen, 1986](#); [Thaller, 1998](#)). As mentioned by Groen et al. ([1998](#)), fertility and the other functional traits also have an impact on animal welfare and on consumer acceptance of animal products.

Fertility traits can be recorded in several ways ([Thaller, 1998](#)); in Austria, nonreturn rate at 90 d after first inseminations is used. This trait is influenced by both service bull and the inseminated cow ([Jansen, 1986](#)) so that two genetic components have an impact on the success of an insemination. Based on information published by Sreenan and Diskin ([1986](#)) and Zavy ([1994](#)), Van der Lende ([1998](#)) concluded that return to estrus after insemination was more often due to embryonic mortality than fertilization failure. Therefore, the genotype of the embryo could be added as a third component in the analysis of fertility ([Hoeschele, 1991](#)).

The main problem in selection for fertility is the relatively small number of observations available for a given animal compared with the large number required to predict breeding values. This difficulty stems from the low heritability of the trait and properties of the bivariate distribution. Genetic variance computed by usual models is quite low, but only additive components have been taken into account. However, genetic variation can be partitioned into additive and nonadditive components. Nonadditive components may be further divided into dominance variance caused by interaction of the alleles at the same locus and epistatic variance due to interactions among alleles in different loci ([Falconer, 1989](#)). Several authors ([Beckett et al., 1979](#); [Fuerst and Solkner, 1994](#); [Hoeschele, 1991](#); [Philipsson, 1981](#)) suggested that nonadditive genetic variance could be relatively important in fertility traits as these traits show low additive genetic variance. Little use has been made of nonadditive genetic effects in cattle breeding to date, due to difficulties in modeling these effects. Interest in nonadditive effects has increased with recent development of algorithms for large datasets using models with nonadditive genetic components ([Henderson, 1984](#)), rapid inversion of dominance relationship

matrices ([Hoeschele and Van Raden, 1991](#)), and method  $\mathfrak{R}$  computation of variance components ([Misztal, 1997](#)). This interest is also due to datasets that include types of relatives necessary for estimating nonadditive genetic effects, becoming more common.

The objectives of this study were to: 1) estimate additive and dominance genetic variances for fertility traits for Austrian Simmental and Brown Swiss dairy cattle; 2) compare method  $\mathfrak{R}$  and the preconditioned conjugate gradient to solving for method  $\mathfrak{R}$  by second-order Jacobi iteration and; 3) determine the impact of inclusion of parental subclass effects on solutions for other random effects.

## MATERIALS AND METHODS

### Data

Data were provided by the Federation of Austrian Cattle Breeders in Vienna from two of the largest Austrian cattle populations, the Simmental of Lower Austria, and the Austrian Brown Swiss population. Data consisted of 393,947 (Simmental) and 360,073 (Brown Swiss) 90-d nonreturn rates, recorded from January 1, 1990 through January 31, 1997. A successful first insemination was coded as 0 (i.e., no return); and failure to conceive from the first inseminations was coded as 1.

The following edits were applied to the data; the days from calving to first insemination had to be between 20 and 200 d, and heifer first insemination had to occur between 420 and 960 d of age. Original pedigrees files consisted of 995,694 and 268,630 Simmentals and Brown Swiss, respectively. The huge size of Simmental pedigree file in comparison with performances file was because the complete Simmental pedigree file for all Austria was obtained and the records were those from a limited part of Austria, Lower Austria.

### Models

The data were analyzed using the following linear animal models. No threshold models were used for two reasons. First, it would have been difficult to accomplish with available computing resources, and second, an objective was to duplicate the official Austrian genetic evaluation model as nearly as possible. Therefore, the estimation of variance components and solutions for additive and dominance effects was first calculated using the current Austrian genetic evaluation model:

$$\text{Model 1:} \quad \mathbf{y} = \mathbf{X}_h \mathbf{h} + \mathbf{X}_m \mathbf{m} + \mathbf{X}_l \mathbf{l} + \mathbf{Z}_p \mathbf{p} + \mathbf{Z}_c \mathbf{c} + \mathbf{Z}_s \mathbf{s} + \mathbf{e}, \quad [1]$$

where  $\mathbf{y}$  = vector of insemination results;  $\mathbf{X}_h$ ,  $\mathbf{X}_m$ , and  $\mathbf{X}_l$  = known matrices relating insemination results to fixed effects;  $\mathbf{h}$  = vector of herd by year of insemination fixed effects;  $\mathbf{m}$  = vector of month of insemination fixed effects;  $\mathbf{l}$  = vector of fixed effects defined for virgin heifers as age at first insemination (16 groups), and for cows as lactation group number (seven groups; lactations 1 to 6 separately, and seventh and later lactations grouped together) by days open (11 groups), giving a total of 93 levels;  $\mathbf{Z}_p$  = known matrix relating insemination results to permanent environment of the inseminated cow random effects;  $\mathbf{p}$  = vector of permanent

environment of the inseminated cow random effects;  $\mathbf{Z}_c$  = known matrix relating insemination results to additive genetic female effects (inseminated cow);  $\mathbf{c}$  = vector of genetic female effects (inseminated cow);  $\mathbf{Z}_s$  = known matrix relating insemination results to additive genetic service bull effects;  $\mathbf{s}$  = vector of additive genetic service bull effects and  $\mathbf{e}$  = vector of residuals.

Thaller (1998) concluded that there was no or a small negative (co)variance between additive genetic effects as assumed in the official Austrian model. This was also the case in our models. This gave the following (co)variance structures in model 1:

$$\text{Var} \begin{bmatrix} \mathbf{p} \\ \mathbf{c} \\ \mathbf{s} \end{bmatrix} = \begin{bmatrix} \mathbf{I}\sigma_p^2 & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{A}\sigma_c^2 & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{A}\sigma_s^2 \end{bmatrix}$$

where  $\sigma_p^2$  is the permanent environment variance,  $\sigma_c^2$  is the additive genetic variance associated with the inseminated cow effect,  $\sigma_s^2$  is the additive genetic variance associated with the service sire effect,  $\mathbf{I}$  is an identity matrix and  $\mathbf{A}$  is the additive relationship matrix.

Dominance effects in the inseminated cow were modeled as parental subclass dominance effects (Hoeschele and VanRaden, 1991; Misztal, 1997), which represent the dominance interaction effects between sire and dam of the cow:

$$\text{Model 2:} \quad \mathbf{y} = \mathbf{X}_h\mathbf{h} + \mathbf{X}_m\mathbf{m} + \mathbf{X}_l\mathbf{l} + \mathbf{Z}_p\mathbf{p} + \mathbf{Z}_c\mathbf{c} + \mathbf{Z}_s\mathbf{s} + \mathbf{Z}_f\mathbf{f} + b\Delta + \mathbf{e}, \quad [2]$$

where  $\mathbf{Z}_d$  = known matrix relating insemination results to dominance effects of the female component of fertility;  $\mathbf{f}$  = vector of dominance effect of the female component of fertility;  $b$  = coefficient for the linear regression on inbreeding of the cow;  $\Delta$  = vector of inbreeding coefficients of the cows.

The following (co)variance structures were assumed across random effects in Model 2:

$$\text{Var} \begin{bmatrix} \mathbf{p} \\ \mathbf{c} \\ \mathbf{s} \\ \mathbf{f} \end{bmatrix} = \begin{bmatrix} \mathbf{I}\sigma_p^2 & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{A}\sigma_c^2 & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{A}\sigma_s^2 & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{F}\sigma_f^2 \end{bmatrix}$$

where  $\mathbf{F}$  is the parental subclass dominance relationship matrix and  $\sigma_f^2$  is the parental subclass dominance variance, which is one quarter of the total dominance variance (Hoeschele and VanRaden, 1991; Misztal, 1997).

For all models, the data were prepared with a set of programs developed by Misztal (1997). These programs built the inverse of the parental dominance relationship matrix  $\mathbf{F}$  using the method proposed by Hoeschele and VanRaden (1991), based on animals with records, and only one round of their recurrence equation. All information from full-sib and three-quarter sib families and from cousins linked by the classes was used. Inbreeding was considered in the

construction of the additive relationship matrix **A** as shown by Wiggans et al. ([Wiggans et al., 1995](#)).

## Variance Components Estimation

Estimation of variance components was based on method  $\mathfrak{R}$  ([Reverter et al., 1994](#)), which required simultaneous estimation of BLUP solutions. In fact, after each round of solving algorithm (e.g., second-order Jacobi) on partial and complete data sets, regression factors were computed based on two sets of solutions ([Misztal, 1997](#)). When all regression factors stabilized (changes in regression factors from successive rounds had to be smaller than  $1 \times 10^{-6}$  during three successive rounds), the variance ratio of one random effect was changed. With the new variance ratios, new solutions were computed iteratively until regression factors stabilized again. After each convergence of regression factors, only one variance ratio was updated until all variance ratios had changed once. Then the extrapolation method presented by Misztal ([1997](#)) was used to estimate new variance ratios and the process was started again until all regression factors converged towards  $1 \pm 0.0002$ .

Method  $\mathfrak{R}$  needs efficient algorithms to obtain solutions to large mixed model equations with high precision and in an acceptable time frame. The algorithm based on second-order Jacobi iterations effect by effect used by Misztal ([1997](#)) was compared with a method based on preconditioned conjugate gradient (**PCG**). This method is still relatively unknown and is rarely used in animal breeding because of its greater memory requirements ([Van Vleck and Dwyer, 1984](#)). A modern use of PCG for animal breeding purposes was only recently described by Strandén and Lidauer ([1999](#)). The theory of the preconditioned conjugate gradient can be found in Shewchuk ([1994](#)). In our implementation, the diagonal of the left hand side of the mixed model equations was used as preconditioner matrix.

For variance component estimation for each of the two models, six random samples of half of the data were used. The variance components for every model and population were obtained from averages over all samples. The standard deviation of the six samples was computed and reported as approximate standard error.

## Comparison of Solving Algorithms

To test the efficiency of solving algorithms (second-order Jacobi and PCG), both methods were used to estimate variance components of two test samples using the official model and Simmental data. Due to the difficulty of accurately measuring CPU required for solutions, the numbers of rounds of solving algorithms, time necessary to realize one round of solving algorithm and the numbers of extrapolations required were used to compare algorithms.

In comparison of algorithms, the official model was used with three random effects (model 1). Therefore, regression factors had to converge 4 times before reestimation of new variance ratios (once for initial variance and three for changes in each variance of each random effect). The number of rounds of solving algorithms (second-order Jacobi or PCG) completed to get convergence of regression factors for a given set of variance ratios was highly dependent on convergence of BLUP solutions of the partial and complete data sets.

Total number of rounds necessary to get estimates of variance ratios was dependent on two distinct processes: 1) number of extrapolations (updates of variance ratios) necessary to get variance ratios corresponding to regression factors close enough to 1 and; 2) number of rounds of solving algorithms necessary for convergence of regression factors corresponding to specific variance ratio (during one round of method  $\mathfrak{R}$ , each of the two sets of solutions required one round of second-order Jacobi or PCG). The cumulative number of rounds of solving algorithm was used to compare PCG and second-order Jacobi. The cumulative number of rounds was the sum of rounds of solving algorithm required for convergence of regression factors for each set of variance ratios tested (for which regression factors were computed). If a solving algorithm led to more sets of variance ratios being tested, then the cumulative number of rounds was heavily affected. Finally time to execute a round of iteration with both solving algorithms were compared.

## Changes of Solutions for Random Effects

Inclusion of dominance in genetic evaluation programs could provide more precise estimates of additive genetic effects because of the more precise model. Therefore, in this study solutions for random effects for models 1 and 2 were compared using the variance components estimated. To facilitate comparisons, model 1 was slightly modified to include the same regression on inbreeding ( $b \Delta$ ) as in model 2.

Extending the results from Varona et al. (1998), we can show that if no dominance information comes from the pedigree, permanent environment solutions of model 1 can be split into a parental subclass dominance effect and a new permanent environment effect in model 2. Detailed derivations are in the Appendix. The permanent environment effect of model 2 can be written as:

$$p_2 = \frac{\sigma_{p_2}^2}{\sigma_{p_1}^2} p_1, \quad [6]$$

where  $p_i$  is a solution for permanent environment in model  $i$  and  $\sigma_{p_i}^2$  is the variance for the permanent environment effect in model  $i$ . If no related parental subclass dominance effects exist and the animal has no full-sibs, a similar relationship should exist between parental subclass dominance effects from model 2 and permanent environment effects from model 1 (Appendix):

$$f = \frac{\sigma_f^2}{\sigma_{p_1}^2} p_1, \quad [7]$$

where  $f$  represents a solution for the parental subclass dominance effect of the inseminated cow and  $\sigma_f^2$  is the associated variance.

## RESULTS AND DISCUSSION

### Descriptive Statistics

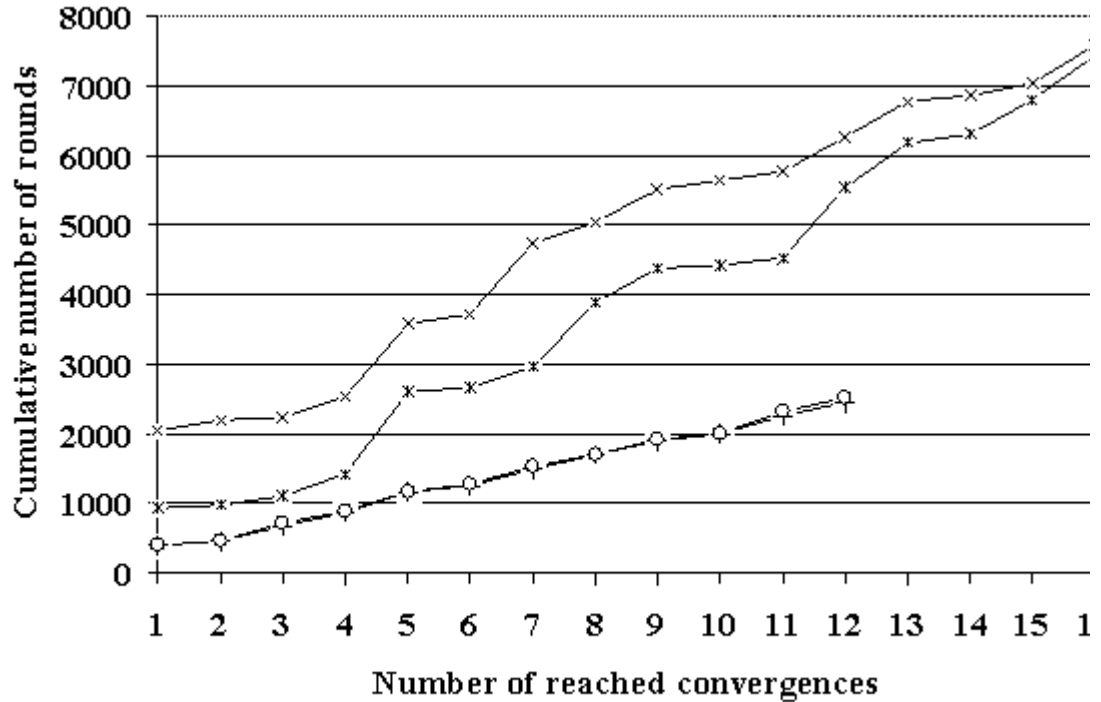
A total of 267,447 (67.9%) inseminations were successful in Simmental breed and 250,239

(69.5%) in Brown Swiss. For both breeds, there were cows inseminated until lactation 16. Average time between calving and first insemination was 72.6 d (SD 28.2 d) for Simmental and 83.3 d (SD 31.9 d) for Brown Swiss. Mean age at first insemination on heifers was 613 d (SD 83.2 d) in Simmental breed and 690 d (SD 92.5 d) in Brown Swiss.

Random effect classes for both breed and different models are given in [Table 1](#). After editing and deleting redundant information, the pedigree files included 623,816 (Simmental) and 242,070 (Brown Swiss) animals, respectively. The larger number of animals for Simmental can be explained by the fact that original Simmental files contained pedigrees for all Austria (records were limited to Lower Austria only) and that our algorithm to select animals has kept some noncontributive animals. This was no major problem for method  $\mathfrak{R}$  as noncontributive animals do not affect regressions. The programs used to built the inverse of the parental dominance relationship matrix  $\mathbf{F}$  using the method proposed by Hoeschele and VanRaden ([Hoeschele and VanRaden, 1991](#)), however, eliminated these animals and therefore the numbers for parental subclasses were very similar (405,156 for Simmental and 462,430 for Brown Swiss).

**Table 1.** Number of levels for random effects in Simmental and Brown Swiss.

Random effect	Brown Swiss	Simmental
Permanent environment of the cow	132,709	143,138
Male/female additive genetic	242,070	623,817
Parental subclass of the cow	462,430	405,156



**Figure 1.** Cumulative number of rounds in regard with the number of the corresponding update ratios with secant method (Jacobi limited to first 16 updates). Sample 1: Jacobi x, Preconditioned gradient +; Sample 2: Jacobi \*, Preconditioned conjugate gradient o.

### Comparison of Solving Algorithms

Times to execute one round of second-order Jacobi or of PCG were comparable: one round of PCG lasted approximately 1.09 times longer than one round of second-order Jacobi. [Figure 1](#) shows the cumulative number of rounds necessary to get convergence of regression factors for two samples of Simmental data using the two different solving algorithms for the BLUP solutions: second-order Jacobi and PCG. [Table 2](#) shows the evolution of estimated variances during the first three extrapolations. For all test runs, initial variance ratios were 47 for all random effects corresponding to 2 % of total variance. Method  $\mathfrak{R}$  values (regression factors) converged at least twice as fast with the PCG method. The number of total rounds to get convergence of  $\mathfrak{R}$  values close to one was much smaller for PCG (2780 and 2871 rounds) than for second-order Jacobi (8350 and 27,146 rounds). Note that results shown in [Figure 1](#) are truncated. This difference was also due to higher number of extrapolations necessary to get final variance ratios (3 and 3 vs. 4 and 13), especially for the second sample, for which the second-order Jacobi had convergence problems. [Table 2](#) shows that after three extrapolations, variance ratios for PCG were virtually equal to the final estimates (accurate to two decimal places). Even so, among all the samples used for variance components estimation, with PCG too, some extrapolations led repeatedly to variance ratios that were very close to final estimates but failed



to converge, therefore increasing the number of rounds necessary. The results from this study indicated that the use of PCG with the method  $\mathcal{R}$  procedure instead of second-order Jacobi method is recommended because of substantial savings in computing time.

**TABLE 2.** Comparison of variances (in % of total variance) using computations with preconditioned conjugate gradient (PCG) or second-order Jacobi for permanent environment, male and female genetic effects for two samples of Simmental of Lower Austria.

Extrapolation	Sample 1						Sample 2					
	Second order Jacobi			PCG			Second order Jacobi			PCG		
	PE <sup>1</sup>	M <sup>2</sup>	F <sup>3</sup>	PE	M	F	PE	M	F	PE	M	F
Starting values	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00
1	2.16	1.00	1.38	1.91	1.01	1.45	4.85	1.01	0.98	3.92	0.99	1.08
2	2.24	0.76	1.24	2.29	0.74	1.25	3.28	0.88	0.82	2.98	0.89	0.82
3	2.20	0.75	1.21	2.18	0.74	1.23	2.82	0.89	0.83	2.81	0.89	0.82
Final variances	2.19	0.74	1.22	2.18	0.74	1.23	2.80	0.90	0.84	2.81	0.89	0.82

<sup>1</sup> Permanent environment variance expressed in % relative to total variance.

<sup>2</sup> Male additive genetic variance expressed in % relative to total variance.

<sup>3</sup> Female additive genetic variance expressed in % relative to total variance.

## Variance Components

Results for variance components are given in [Table 3](#). Additive variance was extremely small, only approximately 1% of total phenotypic variance, stressing on the importance of better control of the environment of inseminated cows to get higher nonreturn rate. Fixed effects had the major impact on insemination results. However, variation among breeding values, especially for sires, seemed to indicate that selection is possible. Effects of interactions of alleles were estimated using the **F** matrix (parental subclass dominance relationships) so that parental subclass dominance variance estimates were obtained. To obtain dominance variance estimates, parental subclass dominance variance had to be multiplied by four ([Hoeschele and VanRaden, 1991](#)). Analysis of variance components between different models confirmed some earlier results ([Fuerst and Sölkner, 1994](#); [Hoeschele, 1991](#)). In Brown Swiss, dominance variance of the cow was estimated as 1.36% of total variation, which is slightly higher than the additive variances. In Simmental, estimated dominance of the cow was around 0.32% of total phenotypic variance. Fürst and Sölkner ([1994](#)) and Hoeschele ([1991](#)) found similar results to those in Brown Swiss, where dominance effects were one to two times additive genetic variation. These values were high in comparison with additive effects, but expressed as percentage of total phenotypic

variance, they were extremely low. Except for clones, only a quarter of dominance effects could be used in breeding schemes ([Hoeschele and VanRaden, 1991](#)) because only parental subclass dominance effects could be predicted. However, the possibility of using a random effect showing a quarter or more of the additive variance could still be an important gain for mating programs (e.g., in the population, for three-quarter sibs families:sire/maternal-gransire) or for correcting the breeding values (e.g., in a nucleus program, in fullsibs families).

**TABLE 3.** Variances expressed in % of total variance ( $\pm$  empirical SE computed as the SD of the 6 samples) of random effects for the two models in Simmental and Brown Swiss populations.

The original variance of the permanent environment of the cow (model 1) was approximately equal to the new variance of the permanent environment of the cow plus the parental subclass dominance variance (1/4 of the dominance of the cow) so that residual variance was not changed. This was consistent across samples. [Misztal et al. 1997](#)) found similar results for stature traits with a permanent environment effect. When dominance effects were not included in the model, dominance variance was included in the permanent environment variance estimates. In this way, no additional variation was explained by the model and the additive values should not have been significantly affected. This point was quite logical because the dominance effect of a cow is permanent during her life. Failing to specify that this part of the variation was due to dominance effects, then the model associates these differences with permanent environment effects.

Approximate standard errors obtained from observed standard deviation of the results from the six samples were lower for additive and permanent environment variances than for dominance variances. Clearly, less information is available to estimate the dominance variance.

### **Changes of Solutions for Random Effects**

Permanent environment, female genetic additive, and dominance solutions were analyzed for

cows with records. For these animals, differences between additive solutions from model 1 (with the same inbreeding coefficients as for model 2) and 2 were rather small (Table 4). Although average differences were small, some changes were still important with up to 1/8 of a standard-deviation of additive solutions.

**TABLE 4.** Differences between solutions for additive genetic female effects of model without and with parental subclass dominance effects of the inseminated cow for cows with records in Brown Swiss and Simmental cattle.

Breed	Model	Mean (x 100)	SD (x 100)	Minimum (x 100)	Maximum (x 100)
Brown Swiss	Model 1	0.59	1.93	-5.53	9.97
	Model 2	0.59	1.92	-5.59	10.02
	Differences	0.00	0.03	-0.12	0.25
Simmental	Model 1	0.04	1.99	-6.29	8.19
	Model 2	0.03	1.99	-6.24	8.20
	Differences	0.00	0.03	-0.16	0.09

**TABLE 5.** Differences between solutions for permanent environment effects of model without and with parental subclass dominance effects of inseminated cow in Brown Swiss and Simmental cattle.

Breed	Model	Mean (x 100)	SD. (x 100)	Minimum (x 100)	Maximum (x 100)
Brown Swiss	Model 1	0.00	1.52	-8.06	8.16
	Model 2	0.00	1.26	-6.67	6.75
	Differences	0.00	0.26	-1.39	1.41
Simmental	Model 1	0.00	1.78	-7.68	9.73
	Model 2	0.00	1.72	-7.40	9.42
	Differences	0.00	0.06	-0.31	0.33

As expected (equation [6]) there was a strong relation between permanent environment solutions from model 1 and model 2. (Table 5) For both breeds the theoretical equation was confirmed using a regression of model 2 solutions on those of model 1: for Brown Swiss  $p_2 = 0.83 p_1$  (theoretical value 0.830) and for Simmental  $p_2 = 0.97 p_1$  (theoretical value 0.965), and both coefficients of determination ( $r^2$ ) were 0.99.

A similar relationship was suspected between parental subclass effects and original (model 1) permanent environment effects. Again regressions were used to confirm the relationships in the

data. For Brown Swiss it was  $\mathbf{f} = 0.17 \mathbf{p}_1$  (theoretical value 0.170 assuming  $\sigma_{\mathbf{f}}^2 = \sigma_{\mathbf{p}_1}^2 - \sigma_{\mathbf{p}_2}^2$ , 0.148 using observed parental subclass variance), and for Simmental it was  $\mathbf{f} = 0.03 \mathbf{p}_1$  (theoretical value 0.035, respectively 0.031). However, this relation did not fit for all animals:  $r^2$  was 0.64 and 0.32 in Brown Swiss and Simmental, respectively. The Appendix provides the theoretical basis for the strict relationship between  $\mathbf{f}$  and  $\mathbf{p}_1$  and explains why it is broken when parental subclass relationships exist and more than one animal is in a parental subclass.

Jacquard (1974) discussed the importance of relationships for the estimation of dominance variance. For this study, contribution to dominance relationship matrix and, therefore, the parental subclass matrix were represented approximately through the sum of the number of full-sibs plus a quarter of the number of three-quarter-sibs for a given animal. Indeed, these animals were those that contribute most. With these contributions, relations between parental subclass effects and permanent environment effects were analyzed for different contribution classes (Table 6). The more full-sibs and three-quarter-sibs an animal had, the more the parental subclass effects were independent of the permanent environment effects. In fact, for animals without any dominance relationships, it was not possible to make a clear distinction between permanent environment effect and parental subclass effect as they were always associated. Therefore, dominance solutions were proportional to permanent environment solutions (from first and second model as they were also proportional to each others), according to their respective variance.

**TABLE 6.** Coefficients of determination from regression of the parental subclass dominance effects in model 2 on the permanent environment effect of model 1 by a function of the approximate contribution to the dominance relationship matrix (**D**) among animals.

Approximate contribution to <b>D</b> <sup>1</sup>	Brown Swiss		Simmental	
	Number of records	Coefficient of determination	Number of records	Coefficient of determination
1	97,028	0.85	72,673	0.84
1.01 to 1.99	19,379	0.54	20,738	0.49
2.00 to 2.99	10,911	0.36	14,003	0.32
3.00 to 3.99	2386	0.26	7883	0.22
4.00 to 4.99	1062	0.17	4354	0.16
5.00 to 7.49	1292	0.17	8783	0.14
7.51 to 9.99	323	0.15	4957	0.10
10.00 to 14.99	328	0.36	5345	0.06
15.00 to 24.99	/	/	2934	0.04
25.00 and more	/	/	1468	0.03

<sup>1</sup>Approximate contribution to dominance matrix = number of full-sibs + 0.25 \* number of three-quarter-sibs.

The relationship between parental subclass effects and permanent environment effects could explain low changes in additive values. Indeed, most of animals came from parental families with no ties to other records (Table 6); therefore, their corrected phenotypic deviation in models 1 and 2 were nearly identical, with small resulting changes in additive values. For those animals coming from bigger parental families, changes were generally also small because parental subclass effects were rather limited due to the low parental dominance variance.

## CONCLUSIONS

Use of PCG in method  $\mathfrak{R}$  show better and faster convergence than the second-order Jacobi algorithm. The PCG solver should, therefore, be preferentially used.

Estimated dominance variances were low and therefore dominance effects at this time showed low potential for use in selection for fertility traits. However, in Brown Swiss, dominance variance was larger than additive variances. Dominance variance entered the permanent environment variance when dominance effects were not included in the model. The potential use of a threshold model might have increased relative genetic variances. Additional research is required to evaluate this possibility. Relaxing the assumption that male-female covariance was zero could also increase genetic variances.

Changes in additive solutions from inclusion of dominance in a model were rather small. In fact, to get large differences between additive solutions by including a dominance effect, dominance variance would have to be higher and animals of interest would need to have numerous full-sibs and three-quarter-sibs. Indeed, permanent environment effects were totally confounded with parental subclass dominance effects as long as no dominance information (full-sibs, three-quarter-sibs, cousins) was available to allow separation.

In situations with substantial dominance variance and many animals with numerous full-sibs and three-quarter-sibs, dominance could be utilized in mating systems. Reliable prediction of parental subclass dominance effects methods would be essential.

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## APPENDIX

The only difference between model 1 (modified to include the regression on inbreeding) and model 2 is the addition of the parental subclass dominance effect. First denote  $n$  as the number of records of an animal and  $\sum y^*$  as the sum of its records adjusted for all fixed and additive genetic effects. Consider now the situation where the animal is alone in its parental subclass that is also independent from other parental subclasses. The following equations gives the estimates of the parental subclass dominance and permanent environment effects:

$$\begin{bmatrix} n + \frac{\sigma_e^2}{\sigma_f^2} & n \\ n & n + \frac{\sigma_e^2}{\sigma_{p_2}^2} \end{bmatrix} \begin{bmatrix} f \\ p_2 \end{bmatrix} = \begin{bmatrix} \sum y^* \\ \sum y^* \end{bmatrix}, \quad [3]$$

where  $\sigma_f^2$  is the parental subclass dominance effect variance,  $\sigma_{p_2}^2$  is the permanent environment effect variance in model 2 and  $\sigma_e^2$  is the residual variance. If the first equation is subtracted from the second, the following result is obtained :

$$f = \frac{\sigma_f^2}{\sigma_{p_2}^2} p_2 \quad . \quad [4]$$

Equation [4] holds as long as we can write the linear system in [3]. Therefore, as soon as more than one animal is in a dominance subclass or the dominance subclass is related to other dominance subclasses through the parental dominance relationship matrix the formula is no longer exact.

Under the conditions for equation [3] and if we assume that the estimates of fixed and additive effects are approximately equal in models 1 (adjusted for inbreeding) and 2, we can write:

$$\left( n + \frac{\sigma_e^2}{\sigma_{p_1}^2} \right) p_1 = \sum y^* \quad . \quad [5]$$

Next, assume that the residual variance  $\sigma_e^2$  is constant and, then, by equating the second equation of [3] and equation [5] we find:

$$nf + \left( n + \frac{\sigma_e^2}{\sigma_{\mathbf{p}_2}^2} \right) p_2 = \left( n + \frac{\sigma_e^2}{\sigma_{\mathbf{p}_1}^2} \right) p_1.$$

After substituting  $f$  as given in [4] and after considering  $\sigma_f^2 = \sigma_{\mathbf{p}_1}^2 - \sigma_{\mathbf{p}_2}^2$  we obtain:

$$p_2 = \frac{\sigma_{\mathbf{p}_2}^2}{\sigma_{\mathbf{p}_1}^2} p_1 \quad [6]$$

and after combining [4] and [6]:

$$f = \frac{\sigma_f^2}{\sigma_{\mathbf{p}_1}^2} p_1. \quad [7]$$

Equation [7] holds as long as there is no more than one animal is in a dominance subclass or the dominance subclass is not related to other dominance subclasses. Therefore the deviation

$f - \frac{\sigma_f^2}{\sigma_{\mathbf{p}_1}^2} p_1$  is a function of the dominance information in  $f$ .