

Estimation of Genetic Parameters in a Crossbred Population of Black and White Dairy Cattle

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ABSTRACT

Genetic parameters were estimated using data of cows with variable proportions of genes from two breeds: Dutch Friesian and Holstein-Friesian. The data set contained 92,333 first lactation records (305-d milk production) from 675 young sires and 307,050 records from 202 proven sires.

Data were analyzed using four additive mixed models with genetic groups defined according to 1) breed composition of the cow, 2) breed composition of sire and dam, 3) linear regression on the fraction and Holstein-Friesian genes of the cow, and 4) breed composition of sire. A nonadditive model included a linear regression on breed fraction, heterozygosity, and recombination in the cow's genome.

Estimates for heterosis varied from 2.5% (fat yield) to 0% (protein percentage). Recombination effects varied from -1.9% (protein yield) to 1.5% (fat percentage). Additive models with progeny groups overestimated genetic variance by 6%. Models with sire groups overestimated additive genetic values of imported Holstein-Friesian sires by 33%. Using a nonadditive model, heritability estimates were .38 for milk yield, .80 for fat percentage, and .70 for protein percentage. It was concluded that a nonadditive model was preferable for estimation of genetic variance and prediction of breeding values in crossbred dairy populations.

INTRODUCTION

Numerous estimates of genetic parameters for production traits have appeared in the dairy breeding literature (1, 2, 9, 12, 14, 16, 22, 23). Such focus can be justified because production traits have high economic importance and heritabilities and variances may change due to selection, migration of genes from one population to another, or changing environmental conditions. Recently, genes from North American dairy breeds have been imported to European populations. Genetic parameters should be estimated regularly in such a process of upgrading from data collected in well-organized milk recording schemes.

Genetic parameters for milk production traits were summarized by Maijala and Hanna (12). The average heritability estimates were .27 for first lactation milk yield and .24 for fat yield. Estimates using more sophisticated methods (i.e., REML) showed no major differences for first lactation traits (14, 18). More recently, higher heritabilities were found for data from Canada (2) and from the United States (22). Hill et al. (9) have shown that heritabilities tended to increase with production. Those authors used data mainly from single breed populations and, thus, parameters may not necessarily be valid for upgraded European dairy populations.

Heritability estimates in crossbred populations were adjusted to various degrees for fixed additive effects of breed contributions. Meyer (14) found higher heritability for first lactation milk and fat yield when data from imported Canadian sires were included and breed effects were not accounted for. Other authors accounted for breed of sire but found also high heritabilities in crossbred data (1, 16, 23). Van der Werf et al. (20) found heritabilities of .41 for milk yield and .79 for fat yield after accounting for breed of progeny.

Received November 21, 1988.
Accepted April 21, 1989.

TABLE 1. Distribution of data (%) over sire and dam groups.¹

Group of dam	Group of sire									Total
	1	2	3	4	5	6	7	8	9	
1	24.7	.1	.2	0	5.7	.1	3.2	.9	49.1	84.1
2	NR ²	0	NR	0	NR	0	NR	.2	NR	.2
3	.4	NR	0	NR	.3	NR	.2	NR	1.4	2.2
4	NR	0	NR	0	NR	0	NR	.1	NR	.1
5	1.5	NR	0	NR	.8	NR	.6	NR	8.9	11.9
6	NR	NR	NR	NR	NR	0	NR	.2	NR	.2
7	0	NR	0	NR	0	NR	0	NR	.7	.8
8	NR	NR	NR	NR	NR	0	NR	0	NR	0
9	0	NR	0	NR	0	0	0	0	.4	.4
Total	26.7	.1	.3	0	6.8	.1	4.0	1.4	60.5	100 ³

¹Group number *i* corresponds to $(i - 1) \times 12.5\%$ Holstein-Friesian genes.

²No records.

³100% = 399,383 records.

Models for estimating additive genetic variance and heritabilities from data of crossbred populations usually do not include nonadditive effects. Heterosis and recombination effects are considered to be small for milk production traits (13). However, not accounting for these nonadditive effects may cause upward bias in the estimation of additive genetic parameters (19). Elzo and Famula (4) proposed a general strategy to estimate sire effects, accounting for fixed additive and nonadditive breed effects. Other models proposed for analysis of crossbred populations were intended to estimate effects of breed differences, heterosis, and recombination (6, 10). However, random genetic effects within breed groups were ignored.

The objectives of this paper were to estimate additive and nonadditive genetic parameters for milk production traits in a crossbred population. Models accounting differently for fixed additive and nonadditive breed effects were compared. Differences in estimates of genetic parameters from subpopulations were investigated.

MATERIALS AND METHODS

First lactation records on 305-d milk, fat, and protein yield were obtained from the Dutch Cattle Syndicate (NRS). Records were sampled from Black and White heifers freshening between August 1983 and September 1986. Records had been previously adjusted for month of calving, and incomplete lactations of 90 d or more had been extrapolated to 305 d according

to the methods described by Wilmink (24). Data on the following seven traits were obtained for each cow; milk yield (kg), fat yield (kg), protein yield (kg), fat percentage, protein percentage, fat protein-corrected milk (FPCM, kg) (11), and carrier (milk-fat-protein, kg).

Crossbred AI sire progeny of the Dutch Friesian (FH) and the Holstein-Friesian (HF) breed were used. Breed composition (% HF genes) was known for all sires and their progeny. Editing of data included checks on age at calving (21 to 32 mo) and on breed codes of sire and progeny. Total number of valid records was 451,261.

Heifers were considered to belong to the sire's first group of daughters when the sire was younger than 70 mo at the start of their lactation. Young sires were included that had a minimum of 75 progeny distributed over at least 50 herds. Omission of young sires was mostly due to not having a complete first batch of daughters within the period considered. Therefore, elimination was assumed to be unrelated to sire's genetic merit. In total, 92,333 records from 675 young sires were selected.

Records of proven sires improve connectedness in the data and therefore contribute to more accurate estimation of the herd-year-season effects and the within sire variance (21). Therefore, records of herdmates of young bull's progeny were also included in the analysis. Herdmates were required to descend from proven sires that were older than 80 mo at time of initiation of lactation and had a minimum of

TABLE 2. Distribution of number of sires over genetic groups.¹

Sires	Group of sire									Total
	1	2	3	4	5	6	7	8	9	
Base	32	0	0	0	0	0	0	0	61	93
Young	174	2	10	1	127	4	111	35	211	675
Proven	98	0	0	0	9	0	2	1	92	202

¹Group number i corresponds to (i - 1)*12.5% Holstein-Friesian genes.

100 daughters in 75 herds. Herdmate records of 307,050 heifers from 202 proven sires were added to the dataset.

Nine genetic groups were defined according to percentage of HF genes at intervals of 12.5%. The distribution of progeny over groups of sire and groups of dam is expressed in Table 1. The distribution of sires over genetic groups is expressed in Table 2. Male ancestry was known for young sires, which consisted of 93 base animals.

MODELS FOR ANALYSIS

Several grouping strategies can be followed to attempt to account for fixed genetic effects of subpopulations (19). Four additive models that varied in their definition of genetic groups were considered. A nonadditive model (NA) also was considered, which accounted for interactions between breed groups due to effects of heterosis and recombination loss.

Model A1 was an additive model with grouping according to fraction of HF genes in the progeny from which the records originated (g_p). The model was described as:

$$y_{ijklmn} = hys_{in} + b_{1n} (A_{ijklm} - \bar{A}.....) + b_{2n} (A_{ijklm} - \bar{A}.....)^2 + m_{jn} + g_{pkn} + s_{ln} + e_{ijklmn}[1]$$

where:

- y_{ijklmn} = observation ijklm for the trait n (n = 1,...,7),
- hys_{in} = the fixed effect of herd-year-season class i for the trait n (i = 1,...,62,605). Two seasons were distinguished per herd-year: February to August and September to January,

- A_{ijklm} = the calving age (months) of cow ijklm,
- $\bar{A}.....$ = the mean calving age,
- b_{1n} = the linear regression coefficient of age for the trait n,
- b_{2n} = the quadratic regression coefficient of age for the trait n,
- m_{jn} = the fixed effect of the month j of calving class for the trait n (j = 1,...,12),
- g_{pkn} = the fixed effect of the progeny group class k for the trait n; group referring to percentage of HF genes (k = 1,...,9),
- s_{ln} = the effect of the sire l for the trait n. Effects of young sires were considered random while proven sires were treated as fixed effects,
- e_{ijklmn} = the random residual effect for the trait n associated with the cow ijklm.

Model A1 was referred to as additive progeny group model. The model can be written in matrix notation as:

$$y = Xb + Qg_p + Zs + e \quad [2]$$

where **b** is a vector of fixed environmental effects, **g_p** is a vector of genetic effects of the progeny group, **s** is a vector of sire effects, and **e** is a vector of residual effects. Design matrices for fixed effects, group effects, and sire effects are **X**, **Q**, and **Z**, respectively. The matrices **Z'** and **s'** were partitioned into [**Z**₁:**Z**₂] and [**s**₁:**s**₂], where **Z**₁ and **Z**₂ are matrices relating records to proven (s₁) and young sires (s₂), respectively.

First moments for model A1, treating s₁ sires as fixed, are:

$$E(y) = Xb + Qg_p + Z_1s_1 \quad [3]$$

Model A2 is a parent group model. It can be written as:

$$y = Xb + Q_1g_s + Q_2g_d + Zs + e \quad [4]$$

with g_s and g_d being additive genetic effect of sire group and dam group and Q_1 and Q_2 design matrices for sire and dam group, respectively. Model A3 was a model with a linear regression of performance on the fraction HF genes of the progeny:

$$y = Xb + b_1p_p + Zs + e \quad [5]$$

where p_p is a vector with the fraction HF genes for each animal and b_1 is the regression of y on breed composition of the animal making the record. It should be noted that models A1, A2, and A3 account for additive genetic differences between crossbred groups.

Model A4 was an additive sire group model,

$$y = Xb + Q_1g_s + Zs + e. \quad [6]$$

This model is used in many countries for sire evaluation.

Expectations for y were similar to Model [3] for Models A2, A3, and A4, except for the second term, which was replaced by $Q_1g_s + Q_2g_d$, b_1p_p , and Q_1g_s , respectively.

The NA model was defined as,

$$y = Xb + b_1p_p + b_2h + b_3r + Zs + e, \quad [7]$$

where b_2 and b_3 are regressions on vectors with coefficients for heterozygosity effect (h) and recombination effect (r) for each animal (3, 19). Additive genetic differences between crossbred groups were accounted for by a linear regression on the breed composition of the progeny making the record.

The expectation of y under model NA, treating s_1 as fixed, is:

$$E(y) = Xb + b_1p_p + b_2h + b_3r + Z_1s_1$$

The dispersion matrix of y , treating s_1 as fixed, was for each model:

$$\text{var}(y) = Z_2 AZ_2' \sigma_s^2 + I_n \sigma_e^2 \quad [9]$$

with $\text{var}(s_2) = A\sigma_s^2$, $\text{var}(e) = I_n \sigma_e^2$ and $\text{cov}(e, s_2) = 0$. The matrix A contains additive genetic relationships between the young sires. The vector s_2 was extended to include base animals (sires and maternal grandsires of the young bulls). Sire variances and covariances were assumed to be homogeneous across populations.

Variance components were estimated by REML. A univariate procedure was used for analysis of each trait. For estimation of genetic correlations between traits, a multivariate REML procedure was used. Computations were made feasible by transforming the data to canonical variates was possible, because design matrices were the same for each trait (15). Sampling errors for the variances were approximated using the estimates as true values. Sampling errors for the genetic parameters were derived from a linear approximation using Taylor series expansion (14). Breeding values of sires were computed from mixed model solutions for fixed additive genetic effects (groups or regression) and from predicted sire effects.

RESULTS AND DISCUSSION

Estimation of Nonadditive Genetic Parameters

Overall mean and solutions for heterosis and recombination effects for each trait from model NA are in Table 3. Estimates for heterosis were small but significant for yield traits (about 2.5%). When considering the genetic distance between the DF and the HF breed, estimates for heterosis were in agreement with other estimates described in literature (5, 13). Estimates for milk composition traits were smaller than 1%.

Estimates for effect of recombination were negative and smaller than heterosis (Table 3). Heterosis was assumed to represent dominance effects and half of additive by additive effects, whereas the recombination effect represented half of the additive by additive effects (19). Literature values for recombination loss often are not significant (13) or are significant but small (5). The recombination effect for fat per-

TABLE 3. Estimates of heterosis, recombination effects, with standard errors and overall means for milk production traits.

Trait	Heterosis	SE	Recombination	SE	Mean
Milk yield	122.9	5.4	-101.2	13.5	5299
FPCM ¹	136.93	5.1	-75.93	12.8	5502
Carrier	112.44	5.0	-95.72	12.6	4891
Fat yield	5.959	.22	-1.325	.55	229.6
Protein yield	4.367	.17	-3.457	.42	178.4
Fat %	.013	.003	.0640	.006	4.34
Protein %	.001	.001	-.0056	.003	3.37

¹FPCM = Fat protein-corrected milk.

centage was positive, which resulted from a smaller recombination effect for fat yield in comparison with milk yield. The heterosis for fat percentage was smaller than the recombination effect, which implies that the dominance effect of fat percentage was negative.

Estimates for nonadditive parameters and their low standard errors were consistent and in agreement with analysis of data simulated (19), using a distribution over sire and dam groups similar to that described in this study. Low sampling errors might have been due to the use of regression to estimate heterosis, recombination, and breed effects. Regression was used rather than interactions between subclass effects, which have larger sampling errors. Results showed that it was feasible to obtain reliable estimates of crossbreeding effects from field data. Although the distribution of data over crossbred groups was unbalanced, many combinations were represented with considerable amounts of data.

Comparison of Models for Milk Yield

Estimates of variance components and heritability for milk yield are in Table 4 for each model. Van der Werf and de Boer (19) have shown by simulation that all models give similar results in absence of nonadditive effects. With Models A1 and A3, however, nonadditive effects caused inflated estimates for sire variance and heritability. Results from the NA model were assumed to be unaffected by NA genetic effects (20).

The overestimation of σ_s^2 and h^2 was 6% using Model A1. Simulation results, using a sire group by dam group structure as expressed in Table 1, showed an overestimation of σ_s^2 by

2.5% when heterosis was 5% and recombination loss was -5% (19). In a simulated structure with increased heterozygosity of dams, bias increased dramatically to 19%. In the data of this study, young sires (random) were mated to relatively more F1 dams, which explains the significant bias in spite of low levels of heterosis and recombination loss. Estimates for the residual component differed only slightly for all models. In accordance with sire variance, heritability was biased upward for Models A1 and A3.

Estimates for additive genetic differences between crossbred groups and average breeding values of sires within groups are shown in Table 5. To make solutions comparable over models, groups with 0% HF were restricted to 0 for each model and solutions of sire and dam groups were multiplied by 2. For Models A3 and NA, additive genetic differences between groups were derived from the estimated regression on corresponding HF percentage.

TABLE 4. Estimates of sire variance (σ_s^2), residual variance (σ_e^2), and heritability (h^2) for first lactation milk yield (kg) with different models.

Model	σ_s^2 ¹	σ_e^2 ²	h^2 ³
A1	49,525	443,285	.402
A2	45,586	443,438	.373
A3	53,351	443,473	.430
A4	45,647	443,986	.373
NA	46,553	443,320	.380

¹Approximated SE varied from 2968 kg² (A4) to 3422 kg² (A3).

²Approximated SE were 1082 kg² for each model.

³Approximated SE were .02 for each model.

TABLE 5. Estimates of fixed additive genetic effects and average breeding value for sires of crossbred groups from different models (milk yield).

Model	Group effect						Average sire breeding value		
	50% HF ¹		75% HF		100% HF		50% HF	75% HF	100% HF
	SE	SE	SE	SE	SE	SE			
A1	298	4	346	6	432	20	326	356	753
A2-sires ²	434	11	582	13	904	7	367	531	900
A2-dams ²	135	8	280	27	304	37			
A3	154	3	231	5	308	6	368	524	874
A4 ²	437	11	585	13	906	7	371	534	902
NA	265	5	397	7	530	10	302	408	680

¹HF = Holstein-Friesian.

²Solutions for sire and dam groups were multiplied by 2.

Solutions for 50% HF and 100% HF groups were relatively higher with Models A2 and A4 than with other models. Compared to the NA model, breed differences were overestimated by 70% using sire group solutions. Differences between dam groups were small using model A2. Neither sire group nor dam group solutions from an additive model could be interpreted as representing half of additive genetic differences between subpopulations. Group solutions from the additive progeny group Model A1 were more in agreement with the NA model. The 50% HF progeny group was overestimated and the 100% HF progeny group was underestimated. Results from Table 5 agreed with previously reported results from simulation (19).

Estimates of breeding values were similar for additive Models A2, A3, and A4 (Table 5). Average estimated breeding values of sires from those models were higher than estimates from model NA; by about 20% for 50% HF sires and about 30% for 100% HF sires. The progeny group model underestimated 75% HF sires, whereas 100% HF sires were overestimated by 10%.

Breed difference between HF and FH was estimated at 530 kg with model NA, whereas differences between breeding values of sires averaged 680, i.e., random effects of 100% HF sires were positive after correcting progeny records for fixed additive and nonadditive genetic effects. The mean of effects of 100% HF sires was about five times its standard deviation. This may have been caused by assortative mating of young 100% HF bulls or by favorable treatment of their progeny. Such effects would

be confounded with sire group effects in Models A2 and A4. Models with sire groups gave lower estimates for the sire variance than the NA model (Table 4).

Estimation of Additive Genetic Parameters for all Traits

Variance components and heritability of each trait from model NA are in Table 6. Estimates were corrected for fixed effects of breed and for interaction between breeds. Within trait parameters from single-trait models differed only slightly (<.2%) from estimates from a multivariate procedure. Heritability for milk yield was higher than that given by Majala and Hanna (12) and somewhat higher than more recent estimates (1, 16, 22). Heritabilities for milk composition traits were substantially higher than most literature values given for

TABLE 6. Estimates of sire variance (σ_s^2), residual variance (σ_e^2), and heritability (h^2) for milk production traits with a nonadditive model.

Trait	σ_s^2	σ_e^2	h^2	SE
Milk yield	46,553	443,320	.380	.02
FPCM ¹	34,941	400,893	.321	.02
Carrier	42,264	389,960	.391	.02
Fat yield	74.84	753.8	.361	.02
Protein yield	37.87	422.9	.329	.02
Fat %	.024	.0965	.799	.03
Protein %	.0046	.0216	.701	.03

¹Fat protein-corrected milk.

TABLE 7. Estimates of phenotypic (above diagonal) and genetic (below diagonal) correlations for milk production traits with a nonadditive model.

	Milk (kg)	FPCM	Carrier	Fat (kg)	Protein (kg)	Fat %	Protein %
Milk, kg944	.999	.796	.929	-.388	-.409
FPCM, ¹ kg	.883932	.947	.960	-.075	-.190
Carrier, kg	.999	.861776	.920	-.417	-.432
Fat, kg	.583	.889	.548853	.237	-.057
Protein, kg	.868	.927	.851	.722	. . .	-.192	-.052
Fat, %	-.515	-.062	-.550	.393	-.222580
Protein %	-.524	-.189	-.551	.059	-.035	.657	. . .

¹Fat protein-corrected milk.

single breeds. However, heritability estimates for milk yield and fat percentage were very similar to those from a crossbred population of Holstein Friesian × European Friesian cows (1).

Estimates for genetic and phenotypic correlations between traits are in Table 7. Genetic correlations agreed with literature values, except for the correlation between milk yield and fat yield, which was lower in this study, and between milk yield and milk composition traits, which were more negative than most values in literature. Correlations were quite similar to those found by Boichard and Bonaiti (1).

The lower correlation between milk yield and fat yield agreed with the more negative correlation between milk yield and the ratio of fat to milk. The correlation between milk yield and the ratio of protein to milk was more negative due to a relatively higher genetic variability for milk yield. Phenotypic correlations were lower between milk and fat yield and higher between milk yield and milk composition traits.

Estimation of Genetic Parameters from Subpopulations

Because variance among sires may not be equal for different breed groups, the data set was divided into subsets according to breed composition of the sire. Three subsets with progeny from 174 young FH sires in set I, from 127 young 50% HF sires for set II, and from 211 young HF sires for set III were analyzed. Herdmate records from proven sires were used in each subset, irrespective of breed composition. Progeny within subset were not necessarily from identical subpopulations because dams were from different breed groups. The NA

model was used to correct for possible bias due to nonadditive effects.

Estimates of sire variance and heritabilities in subpopulations are given in Table 8. Sire variances for milk yield, carrier yield, fat yield, and composition traits were significantly larger in subset III than in other subsets. Standard errors on heritabilities in subset III varied from .03 to .07. Results suggested that variances and heritabilities were not equal for the different populations. However, heritabilities from subset III were also higher than recent estimates from North American and Canadian HF populations (2, 22). Variances and heritabilities from subsets I and II better matched literature values. Differences between subsets were relatively small for protein yield and FPCM.

Breed differences between subsets were partly confounded with other effects. Progeny from 100% HF sires freshened more in later years. They also might have performed in herds with better management. Residual variance was 375,194 for subset I and 476,706 for subset III. Allowing for differences in scale, there was still a clear distinction between sire variance from subsets I and III. Increase in genetic variation has been correlated with level of production (9) or with herd type (16).

Overestimation of sire effects of 100% HF bulls increases the estimate for sire variance. Differences between subsets might have been caused by assortative mating and preferential treatment of progeny of the young bulls from subset III. However, models with sires nested within groups (A2 and A4) also showed high heritabilities. Another bias might have arisen from selection of young bulls based on pedigree indexes. This type of selection is not accounted for when information of sires' ancestors is not included in the analysis (17).

TABLE 8. Estimates of sire variance and heritability for milk production traits from subsets of data with progeny of sires with 0% Holstein-Friesian, 50% HF, and 100% HF genes (model NA).

Trait	Heritability			Sire variance		
	0% HF	50% HF	100% HF	0% HF	50% HF	100% HF
Milk, kg	.339	.307	.444	34,743	35,960	59,499
FPCM, ¹ kg	.331	.280	.332	31,136	29,535	38,842
Carrier, kg	.341	.313	.463	30,601	32,245	54,865
Fat, kg	.332	.307	.384	57.24	61.42	85.55
Protein, kg	.358	.288	.336	36.23	32.23	41.35
Fat, %	.490	.570	1.00	.0106	.0164	.0338
Protein, %	.507	.582	.852	.0029	.0038	.0058

¹Fat protein-corrected milk.

Although single-trait selection would have reduced genetic variation (17), the estimated variance among the 100% HF sires was larger than in the American HF population. In contrast to sires from subsets I and II, sires from subset III descended from imported cows or were imported themselves. Breeding values for imported sire may have been extreme either for milk yield or fat percentage, which are negatively correlated. As a result, genetic variance among imported sires would have been increased for each trait. Methods to account for selection occurring prior to the formation of the base population (7, 8) could be particularly important for populations that import sires.

CONCLUSION

Small effects of heterosis and recombination were shown for Holstein Friesian × Dutch Friesian crosses. Nevertheless, differences between a nonadditive model and additive models were substantial for estimates of breed differences, genetic parameters, and breeding values across breeds. The use of nonadditive models was therefore warranted for analysis of crossbred populations.

Estimates of genetic parameters differed from known values, in particular for milk and fat yield, fat percentage, and protein percentage. Analyses of subpopulations revealed higher genetic variances for data from progeny of imported sires. More research is needed to determine to what extent variances among imported sires are biased by selection on pedigree.

ACKNOWLEDGMENTS

The authors acknowledge Karin Meyer for the use of her REML programs and Brian Kennedy for helpful suggestions.

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