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Non-additive breed effects on milk production in cattle

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Abstract

Crossbreeding effects on milk production traits of Czech dual-purpose and dairy cattle breeds were estimated. Nearly 370000 cows with known gene proportions from Czech Pied, Ayrshire or Holstein cattle were selected from the national milk recording data base. Single-trait animal models with exact solutions including standard deviations for estimates of fixed effects were calculated for milk, fat and protein yield, fat and protein content. The model of Dickerson including additive, additive maternal, heterotic and recombination effects was used for the part of the animal model describing the crossbreeding effects in all calculations. For milk yield, the additive genetic effect (defined as deviation from Czech Pied cattle) was 850 to 900 kg for Holstein and 240 to 480 kg for Ayrshire. The maternal effects were low and negative. Low significant positive heterotic effects were observed being up to approximately 100 kg for Czech Pied x Holstein. The recombination effects were negative and statistically significant for Czech Pied x Holstein. The results for fat and protein yield were similar to the results for milk yield. For fat and protein content, nearly no statistically significant cross-breeding effects were found.

Introduction

Crossbreeding of indigenous dual-purpose cattle breeds with specialized dairy breeds for increasing milk production has been practiced in many countries and breeding associations all over the world. During this process of breed replacement and upgrading, a great variety of crossbred combinations has been formed. It can be expected that besides of the additive genetic breed effects, heterotic and further non-additive genetic effects will be of importance. These effects may have an impact on the prediction of breeding values. It is therefore necessary to estimate these effects to decide if they can be neglected in the prediction of breeding values or if they should be an integral part of the model for the estimation of breeding values.

Material and methods

For the estimation of potential non-additive genetic effects on milk yield traits in cattle, a sample of cows with known gene proportions was selected from the national milk recording data base. The data were collected between 1985 and 1999. It was demanded that the cows had to belong to one of the following breeds or to any combination between these breeds: Czech Pied cattle, Ayrshire and Holstein. For each cow, the proportion of genes from these three breeds had to be known and to sum up to unity. Furthermore, it was postulated that both parents were known for each cow and that the proportions of genes from individual breeds were also known for the parents. Milk, fat and protein yields as well as fat and protein percenttages were analyzed. The number of records as well as the phenotypic mean and standard deviation for all traits in the first three lactations are given in Table 1. The first lactation was required for the second and third to be used.

In the first lactation, about 30% of all animals were purebred. This proportion declined to about 25% in the third lactation. The proportion of purebred Ayrshire cows was very low in all lactations (around 0.30% of all cows). The vast majority of cows (83, 86 and 89% in the first, second or third lactation, respectively) had at least some genes from the Czech Pied breed. The proportion of cows with genes from the Holstein breed was decreasing from the first to third lactation, the appropriate values being 63, 60 and 57%, respectively. Genes from Ayrshire cattle were present only in about 30% of the cows.

Table 1. Number of records and phenotypic means and standard deviations for all traits

Trait	1st lactation	2nd lactation	3rd lactation
	Number of records		
Milk yield	368652	254682	152943
Milk fat yield	357752	247071	148976
Milk protein yield	205474	154644	103532
	Phenotypic mean and standard deviation (in parentheses)		
Milk yield (kg)	4059 (1315)	4227 (1543)	4372 (1505)
Milk fat yield (kg)	170.0 (55.8)	177.6 (66.5)	184.3 (65.9)
Milk protein yield (kg)	149.7 (48.5)	153.4 (57.0)	152.9 (53.9)
Milk fat percentage (%)	4.17 (0.41)	4.19 (0.49)	4.20 (0.46)
Milk protein percentage (%)	3.33 (0.21)	3.34 (0.22)	3.32 (0.22)

Single-trait animal models were calculated for each trait. The animal models were essentially of the same structure as in DĚDKOVÁ and WOLF (2001):

$$y_{ijkl} = HYS_{ik} + animal_j + b_{1k}AC_{jk} + b_{2k}AC_{jk}^2 + b_{3k}CI_{jk} + b_{4k}CI_{jk}^2 + DO_{kl} + CBE_{jk} + e_{ijkl}$$

where: y_{ijkl} is the observed value of the milk performance trait on animal j in the k^{th} lactation, the i^{th} herd-year-season class and the l^{th} class for days open, HYS_{ik} is the fixed herd-year-season effect, $animal_j$ is the random effect of animal j, AC_{jk} is the calving age for animal j in lactation k, DO_{kl} is days open class l in lactation k, CI_{jk} is the previous calving interval for animal j in lactation k, b_{lk} are regression coefficients (l = 1, …, 4), CBE_{jk} are crossbreeding effects for animal j in lactation k and e_{ijkl} is the random residual effect.

The terms with the calving interval were included only in the analyses for the 2nd and the 3rd lactation. The term for the crossbreeding effects will be specified in detail below. Nine classes were formed for days open. The classes of the herd-year-season effect were formed as three-month-intervals within herds with 12 records per class on average.

The crossbreeding effects were estimated as regression coefficients. For this purpose, several coefficients will be introduced. Let α_r be the proportion of genes from breed r (r = C, A, H for Czech Pied, Ayrshire and Holstein, respectively). When adding the superscript S or D, the proportion of genes will refer to the sire or dam of the given animal. Furthermore, coefficients δ_{rs} will be needed. Such coefficients designate the probability that at a randomly chosen locus of the given animal one allele is from breed r and the other allele is from breed s. These coefficients can be calculated for the given animal from the gene frequencies in the parents (WOLF et al., 1995):

$$\delta_{rs} = \alpha_r^S \alpha_s^D + \alpha_s^S \alpha_r^D \quad \text{with} \quad r \neq s$$

In each individual j, the proportions of genes from the three breeds sum up to unity:

$$\alpha_{Cj} + \alpha_{Aj} + \alpha_{Hj} = 1$$

For that reason, only two independent additive effects and two independent additive maternal effects could be estimated. In the model used for the calculations, the additive and maternal additive effects for Czech Pied cattle were set to zero. The additive effects for Ayrshire and Holstein were therefore expressed as deviations from Czech Pied cattle.

The model of DICKERSON (1969, 1973) was used in all calculations. Four kinds of crossbreeding effects were included: additive, additive maternal, heterotic and recombination effects. The coefficients for these effects were expressed as given in WOLF et al. (1995). The full model for crossbreeding effects has the following form then:

$$CBE_{jk} = \alpha_{Aj} a_{Ak} + \alpha_{Hj} a_{Hk} + \alpha_{Aj}^{D} m_{Ak} + \alpha_{Hj}^{D} m_{Hk} + \delta_{CAj} h_{CAk} + \delta_{CHj} h_{CHk} + \delta_{AHj} h_{AHk}$$
$$+ (4\alpha_{Cj}\alpha_{Aj} - \delta_{CAj}) r_{CAk} + (4\alpha_{Cj}\alpha_{Hj} - \delta_{CHj}) r_{CHk} + (4\alpha_{Aj}\alpha_{Hj} - \delta_{AHj}) r_{AHk}$$

where: a_{rk} is the additive effect of breed r in lactation k, m_{rk} is the additive maternal effect of breed r in lactation k, h_{rsk} is the heterotic effect for breed combination r x s in lactation k and r_{rsk} is the recombination effect for breed combination r x s in lactation k. The α's and δ's are the coefficients explained above; they are specific for each animal.

Table 2. Additive genetic and residual variances for all traits in the first three parities

Trait	1st lactation	2nd lactation	3rd lactation
	Additive genetic variance		
Milk yield (kg)	156000	198028	243397
Milk fat yield (kg)	239	337	416
Milk protein yield (kg)	123	177	222
Milk fat percentage (%)	0.082	0.109	0.092
Milk protein percentage (%)	0.047	0.048	0.053
	Residual variance		
Milk yield (kg)	401000	569819	651955
Milk fat yield (kg)	800	1190	1398
Milk protein yield (kg)	412	603	695
Milk fat percentage (%)	0.078	0.117	0.094
Milk protein percentage (%)	0.043	0.049	0.049

The genetic parameters for milk, fat and protein yield were approximated from the breed-specific parameters published in DĚDKOVÁ and WOLF (2001) by forming the arithmetic mean from the variance components for Czech Pied and Holstein cattle. They are summarized in Table 2. All calculations were carried out with the PEST program (GROENEVELD et al. 1992). The SMP solver was used to get fixed effects results with standard errors.

Results

The estimates of crossbreeding effects are summarized for yield traits in Tables 3 to 5. The standard deviations of the estimates are given in parentheses. As the estimates are calculated from a large number of observations, an estimate of a crossbreeding effect will be considered to differ significantly from zero if its absolute value is at least twice as large as its standard deviation. As no genes of the Ayrshire breed were present in 66 to 71% of the cows in dependence of the parity, the estimates of crossbreeding effects with the Ayrshire breed had a lower precision (a higher standard error) than the estimates of crossbreeding effects referring to the two remaining breeds.

The additive genetic effect for milk yield was around 850 to 900 kg for the Holstein breed compared with the appropriate effect of the Czech Pied breed (Table 3). Ayrshire had a positive additive genetic effect for milk yield too, but its value was lower (240 to 480 kg). Especially in Ayrshire, the value of the additive effect decreased with parity. The maternal effects for milk yield were negative and considerably lower in their value both for Holstein and Ayrshire. Low but significant positive heterotic effects were observed as a rule. Expressed in per cent of the population mean, they were between 1% and 5%. A heterotic effect near 100 kg (approximately 2% of the population mean) was estimated for the most important combination Czech Pied x Holstein. The estimates of the recombination effect were negative (with one exception). They were statistically significant for Czech Pied x Holstein in all parities and for Czech Pied x Ayrshire in the first parity.

Table 3. Estimates of crossbreeding effects with standard errors (in parentheses) for milk yield (kg)

Type of effect	Breed or breed combination	1st lactation	2nd lactation	3rd lactation
additive	Czech Pied (C)	0	0	0
	Ayrshire (A)	477 (57)	325 (76)	240 (98)
	Holstein (H)	909 (22)	849 (28)	846 (37)
maternal additive	C	0	0	0
	A	-52 (23)	-58 (30)	-80 (40)
	H	-99 (12)	-95 (17)	-104 (23)
heterosis	C x A	52 (23)	50 (31)	136 (41)
	C x H	90 (9)	94 (13)	79 (18)
	A x H	111 (34)	82 (47)	217 (63)
recombination effect	C x A	-118 (43)	-75 (56)	-91 (71)
	C x H	-207 (21)	-227 (30)	-148 (42)
	A x H	-200 (185)	-52 (265)	193 (356)

Table 4. Estimates of crossbreeding effects with standard errors (in parentheses) for milk fat yield (kg)

Type of effect	Breed or breed combination	1st lactation	2nd lactation	3rd lactation
additive	Czech Pied (C)	0	0	0
	Ayrshire (A)	23.9 (2.5)	16.4 (3.4)	13.0 (4.4)
	Holstein (H)	36.9 (0.9)	35.2 (1.3)	35.5 (1.7)
maternal additive	C	0	0	0
	A	-1.9 (1.0)	-2.1 (1.4)	-3.9 (1.8)
	H	-4.4 (0.5)	-3.8 (0.8)	-4.3 (1.1)
heterosis	C x A	1.8 (1.0)	1.0 (1.4)	4.8 (1.9)
	C x H	4.6 (0.4)	4.6 (0.6)	4.0 (0.8)
	A x H	4.9 (1.5)	4.4 (2.1)	8.0 (2.9)
recombination effect	C x A	-4.3 (1.8)	-1.3 (2.5)	-0.9 (3.2)
	C x H	-8.1 (0.9)	-9.5 (1.4)	-4.8 (1.9)
	A x H	-5.4 (8.0)	-7.2 (12.0)	-1.8 (16.4)

The results for fat yield and protein yield (Tables 4 and 5) were very similar to the results for milk yield. Holstein showed a fat yield approximately 35 kg higher and a protein yield approximately 25 kg higher than Czech Pied cattle. In Ayrshire, the additive genetic effect for fat yield decreased from 24 kg in the first lactation to 13 kg in the third lactation; similarly, the additive genetic effect for protein yield decreased from 11 to 5 kg, the effects in the second and third lactation not being statistically significant. All estimates of heterotic effects were positive (between 1% and 8% of the population mean); all estimates of recombination effects were negative. All heterotic effects for the combination Czech Pied cattle x Holstein were statistically significantly different from zero and had a value of about 4 kg (between 2 and 3 % of the population mean) both for fat and protein yield. Likewise, all recombination effects for this combination were statistically significant taking values in the range from -4 kg to -10 kg.

Table 5. Estimates of crossbreeding effects with standard errors (in parentheses) for milk protein yield (kg)

Type of effect	Breed or breed combination	1st lactation	2nd lactation	3rd lactation
additive	Czech Pied (C)	0	0	0
	Ayrshire (A)	11.0 (2.5)	7.5 (3.1)	4.8 (3.8)
	Holstein (H)	26.7 (0.9)	25.4 (1.1)	23.5 (1.4)
maternal additive	C	0	0	0
	A	-1.8 (1.0)	-0.2 (1.3)	-0.6 (1.6)
	H	-4.0 (0.5)	-3.3 (0.7)	-3.0 (0.9)
heterosis	C x A	2.3 (1.1)	1.6 (1.4)	4.5 (1.7)
	C x H	3.8 (0.4)	4.6 (0.5)	2.5 (0.7)
	A x H	3.5 (1.6)	2.2 (2.0)	6.6 (2.5)
recombination effect	C x A	-2.6 (1.8)	-3.3 (2.3)	-2.9 (2.7)
	C x H	-7.0 (0.8)	-7.9 (1.2)	-4.2 (1.6)
	A x H	-13.9 (7.9)	-4.0 (10.9)	-7.5 (14.2)

When analysing fat and protein content, nearly no statistically significant crossbreeding effects were found. The absolute value of all effects was smaller than 0.2%. In protein content, Holstein had a significant negative additive breed effect of about -0.15% in all parities. Gene-rally it can be stated that fat and protein content are nearly independent from the breed or crossbreeding combination.

Discussion

The additive breed effects estimated in this analysis were expected because of the biological and production differences between the two dairy breeds (Holstein and Ayrshire) and the dual-purpose breed (Czech Pied cattle). Especially the higher milk production of the Holstein breed was confirmed in several crossbreeding experiments and population analyses (ROBISON et al. 1981; ERICSON et al. 1988; PEDERSEN and CHRISTENSEN 1989; AHLBORN-BREIER and HOHENBOKEN 1991; DĚDKOVÁ and CHRENEK 1994; GROSSHANS et al. 1994; ELZO et al. 2004). The estimates of additive effects for protein content traits, even if partially non-significant, in favour of the Czech Pied breed are consistent with higher milk fat and protein percentage in Czech Pied cattle than in Holstein.

The negative additive maternal effects for yield traits are to the disadvantage of both dairy breeds with respect to Czech Pied cattle. The negative maternal effect means that the daughters of Holstein or Ayrshire cows had a reduced milk yield. By contrast to the additive effect, the published estimates of maternal effects for the Holstein breed are not consistent. ROBISON et al. (1981) estimated positive maternal effects in milk yield for Holstein in comparison with Ayrshire and Brown Swiss. But in two more recent papers (AHLBORN-BREIER and HOHENBOKEN 1991; DĚDKOVÁ and CHRENEK 1994) negative values were found as well. The results of DĚDKOVÁ and CHRENEK (1994) were obtained when analyzing the upgraded population of Slovak Pied cattle which is closely related to the Czech cattle population.

There is some evidence in the literature for heterotic effects for milk yield traits in dairy cattle (ROBISON et al. 1981; GRAML and PIRCHNER 1984; ERICSON et al. 1988; PEDERSEN and CHRISTENSEN 1989; AHLBORN-BREIER and HOHENBOKEN 1991; DĚDKOVÁ and CHRENEK 1994; GROSSHANS et al. 1994; CHRENEK et al. 1998; VAN RADEN and SANDERS 2003; ELZO et al. 2004). The estimated values were in the range from 3 to 7% of the parental mean. The heterotic effects estimated in the present investigation were rather near the lower border of this range.

The recombination effects for milk yield traits were relatively large and negative for all breed combinations. Fortunately, only a minor proportion of the estimated recombination effect will be expressed in crossbreed cows. Similarly high estimates of recombination losses were reported by PEDERSEN and CHRISTENSEN (1989), GROSSHANS et al. (1994), CHRENEK et al. (1998) for temperate climatic conditions and by KHALIL et al. (2000) and DEMEKE et al. (2004) for tropical climatic conditions. The negative values of the recombination effects are in accordance with the theory that a break of favourable epistatic interactions between genes is expected by the recombination process during meiosis when the crossed breeds are selected for a long time in different directions (DICKERSON 1969, 1973). Consistent with our study, published heterosis for milk fat or milk protein percentage was small and clustered around zero, as might be expected for traits that have a high heritability (ROBISON et al. 1982; GRAML and PIRCHNER 1984; ERICSON et al. 1988; AHLHORN-BREIER and HOHENBOKEN 1991; DĚDKOVÁ and CHRENEK 1994).

Summarizing the results and the discussion, it can be stated that besides of the additive genetic breed effects significant non-additive genetic effects on milk yield traits were observed. Though it will not be the aim actively to exploit these non-additive effects in a breeding programme, they do exist in upgrading programmes and should be taken into account in the models for breeding value estimation as proposed by BROTHERSTONE and HILL (1994) to ensure correct ranking of bulls for purebred and crossbred matings.

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