

Genetic parameters for test-day model with random regressions for production traits of Czech Holstein cattle

L. ZAVADILOVÁ^{1,3}, J. JAMROZIK², L.R. SCHAEFFER²

¹Research Institute of Animal Production in Prague-Uhřetěves, Czech Republic

²Centre for Genetic Improvement of Livestock, Department of Animal and Poultry Science, University of Guelph, Guelph, Canada

³Collaborator, via a fellowship under the Organisation for Economic Co-operation and Development, Biological Resource Management for Sustainable Agriculture Systems

ABSTRACT: Multiple-lactation random regression model was applied to test-day records of milk, fat and protein yields in the first three lactations of the Czech Holstein breed. Data included 9 583 cows, 89 584, 44 207 and 11 266 test-day records in the first, second and third lactation, respectively. Milk, fat and protein in the first three lactations were analysed separately and in a multiple-trait analysis. Linear model included herd-test date, fixed regressions within age-season class and two random effects: animal genetic and permanent environment modelled by regressions. Gibbs sampling method was used to generate samples from marginal posterior distributions of the model parameters. The single- and multiple-trait models provided similar results. Genetic and permanent environmental variances and heritability for particular days in milk were high at the beginning and at the end of lactation. The residual variance decreased throughout the lactation. The resulting heritability ranged from 0.13 to 0.52 and increased with parity.

Keywords: test-day yields; random regression model; genetic parameters; Czech Holstein cattle

Advantages of random regression (RR) test-day models over an approach using 305-day lactation yields are now widely acknowledged. The model for test-day (TD) yields can account more precisely for environmental factors that could affect cows differently during lactation. Random regressions allow for a different shape of lactation curves for each cow. The RR model also allows a cow to be evaluated on the basis of any number of TD records during lactation and it can account for different genetic, permanent environmental and residual variances in the course of lactation.

In the Czech Republic the advantages of test-day model methodology stimulated an increasing interest in the use of original TD measurements

instead of aggregated lactation records and in an implementation of test-day model methodology for the genetic evaluation of cattle. The first step in implementing a routine evaluation with a test-day model is to estimate variance components. Strabel and Misztal (1999) suggested that the estimation of genetic parameters for TD models was much more model dependent in comparison with the lactation model.

The first estimates of variance components for test-day milk yield obtained by RR model were published by Jamrozik and Schaeffer (1997). Random regressions were used for describing genetic effects only. The further development of the variance component estimation by RR model included model-

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ling of permanent environmental effect by random regressions (Van der Werf *et al.*, 1998; Olori *et al.*, 1999; Rekaya *et al.*, 1999; Strabel and Misztal, 1999). Some authors found it important to model the heterogeneity of residual variance across the lactations (Jamrozik and Schaeffer, 1997; Jamrozik *et al.*, 1998; Brotherstone *et al.*, 2000; Jaffrezic *et al.*, 2000).

Parameters obtained in various models and with various data sets showed great variability in both average values and shapes (Misztal *et al.*, 2000). The heritability estimates of the first lactation milk yield for particular DIM resulting from RR models ranged between 0.14–0.19 (Strabel and Misztal, 1999) and 0.31–0.51 (Olori *et al.*, 1999). Some authors reported high heritabilities at the beginning and at the end of lactation (Jamrozik and Schaeffer, 1997; Olori *et al.*, 1999; Kettunen *et al.*, 2000). Other authors found the highest heritabilities in the middle of lactation (e.g. Swalve, 1995; Rekaya *et al.*, 1999; Liu *et al.*, 2000; Pool *et al.*, 2000; Jakobsen *et al.*, 2002; Druet *et al.*, 2003).

The objectives of this study were to estimate (co)variance components of the first three lactation data with single- and multiple-trait random regression models and to characterize some genetic aspects of dairy production in the first three lactations of Czech Holsteins.

MATERIAL AND METHODS

Data consisted of TD records on milk, fat and protein yields (kg) from the first three lactations of Holstein breed. They were extracted for cows calving between 1995 and 1999 from the Czech national milk recording database. All traits were required to be recorded on each test-day between 7 to 305 days in milk (DIM). Age of calving was restricted from 660 to 1 000 days in the first, from 1 020 to 1 420 days in the second and from 1 390 to 1 840 days in the third lactation. Cows with the second or third lactations had to have all their preceding lactations in the data set. Number of TD records per lactation

ranged from 8 to 10. A random selection on herd number was applied to create the final data set. Summary of the data is given in Table 1. Selected subset of data was assumed to be a representative sample from the respective overall population. The decrease in number of lactations from the first to third calving reflected the structure of the cattle population in the Czech Republic, where cows attained on average 2.6 lactations.

Cows were assigned to one of three subclasses for age at calving within lactation and to one of three seasons of calving (February–April, May–September, October–January). This gave nine subclasses of age-season of calving within lactation. Ancestors of cows in the final data set were traced back in pedigree as far as parents were known. The resulted pedigree file included 44 264 animals.

Two types of analyses were set up. Single-trait model for milk, fat and protein involved three-lactation model in which TD yields in the first, second and third lactation were considered as different traits. The multiple-trait model included all the measured traits in the first three parities. The model was assumed to be the same for each parity and trait combination. The model equation was:

$$y_{nkitjl} = \text{HTD}_{ni} + \sum_{m=1}^q \beta_{nkm} z_{tm} + \sum_{m=1}^q a_{njm} z_{tm} + \sum_{m=1}^q p_{njm} z_{tm} + e_{nkitjl}$$

where: y_{nkitjl} = record l on cow j made on day t within herd-test day effect i , for a cow belonging to subclass k for age and season of calving for parity n

HTD_{ni} = fixed herd-test day effect i in parity n

β_{nkm} = fixed regression coefficients specific to subclass k in parity n

a_{njm} = random regression coefficients specific to animal j in parity n

p_{njm} = random regression coefficients specific to permanent environmental (PE) effect of cow j in parity n

e_{nkitjl} = residual effect for each observation

z_{tm} = covariates associated with DIM, assumed to be same for both fixed and random regressions

Table 1. Summary of data

Parity	Number					Mean ± SD		
	Cows	Records	Sires	Dams	HTD	Milk (kg)	Fat (kg)	Protein (kg)
1	9 583	89 584	951	8 863	4 750	18.3 ± 5.83	0.78 ± 0.25	0.60 ± 0.18
2	4 743	44 207	659	4 503	3 392	21.8 ± 8.27	0.92 ± 0.35	0.73 ± 0.12
3	1 532	14 266	367	1 503	1 685	23.0 ± 8.8	0.96 ± 0.38	0.76 ± 0.27

Third-degree Legendre polynomials (with four coefficients) were used for both the fixed and random regressions on the scale from 7 to 305 DIM. Let p_j represent the vector of 12 by 1 (single-trait model) or of 36 by 1 (multiple-trait model) random permanent environmental regression coefficients for cow j with the covariance matrix P . The PE covariance matrix for all cows was $I \otimes P$. For a_j , the vector of 12 by 1 (single-trait model) or of 36 by 1 (multiple-trait model) random regression coefficients for animal j , the covariance matrix was G . $A \otimes G$ was the genetic covariance matrix for all animals with A being the additive relationship matrix. Different residual variances were allowed for different lactations and time periods within lactation, defined as 7 to 45 DIM, 46 to 115 DIM, 116 to 265 DIM and 266 to 305 DIM (Jamrozik *et al.*, 1998). Residual effects on different DIM were uncorrelated both within and between cows. The model used was a special case of Jamrozik *et al.* (1998) for the multiple-lactation, multiple-trait scenario.

Bayesian estimation using Gibbs sampling was used to generate variances and covariances from their respective posterior distributions. Blocked sampling with multivariate normal and inverted Wishart distributions was used. For each trait, 55 000 samples were generated and 5 000 burn-in samples were discarded. Estimates of the variance and covariance components were obtained as posterior means of 50 000 samples.

RESULTS AND DISCUSSION

Variances of random regression coefficients for all analysed traits are presented in Table 2 and residual variances are shown in Table 3. Correlations between genetic random regression coefficients in single-trait models ranged from -0.43 to 0.68 . Permanent environmental correlations were in the range from -0.29 to 0.33 . In general, correlations were stronger for the genetic component than for the permanent environmental effect, especially for the single-trait analyses. Genetic and permanent environmental correlations in the multiple-trait model were higher than 0.7 for the same coefficients that described different traits. Genetic and PE correlations between the first coefficients represent the correlations between 305-days lactation yields. They will, therefore, be described later in the paper.

Single- and multiple-trait models provided similar estimates of variance components. The resulting

estimates of heritabilities, genetic and PE correlations followed the general pattern reported in other studies. The basic differences between results from these two types of models were higher variances and heritabilities estimated by the multiple-trait analysis in comparison with single-trait models (Tables 2 and 4). Larger heritability estimates were due to higher values of genetic variances and lower estimates of permanent environmental variances resulting from the multiple-trait model. The multiple- and single-trait models yielded almost the same estimates of residual variances. Further differences between results from different models are reported below.

305-d yield estimates

Variances and heritabilities. Genetic and PE variances were calculated for the whole lactation period from the estimated covariance function coefficients (Jamrozik and Schaeffer, 1997) and they are presented in Table 4. In general, genetic variances increased with parity. Variances of the PE effect went up substantially between the first and subsequent lactations. The differences between the permanent environmental variances in the second and third lactations were small. Residual variances also increased with parity. Consequently, heritability estimates increased, especially from the second to the third lactation. On the contrary, Rekaya *et al.* (1999) using repeatability model found heritabilities for milk (0.30 ; 0.26 and 0.24 for the first, second and third lactation, respectively) and protein (0.28 ; 0.26 and 0.24 for the first, second and third lactation, respectively) that tended to be lower for later lactations. This was due to a proportionally lower increase in genetic variance with lactation number than in the present study. Using an animal model for aggregated 305-days yields in the first three lactations of Czech Holsteins, Dědková and Wolf (2001) reported almost the same values of heritabilities (0.28 – 0.30 ; 0.24 – 0.25 ; 0.25 – 0.27) for milk, fat and protein, respectively.

The highest heritabilities were obtained for milk yield while the lowest heritabilities were found for fat yield. This was in agreement with other studies (e.g. Rekaya *et al.*, 1999; Jakobsen *et al.*, 2002). Lidauer *et al.* (2003) published heritabilities of 0.30 ; 0.22 ; 0.23 for milk, fat and protein yield in the first lactation, respectively. Jakobsen *et al.* (2002) reported higher heritabilities (0.42 ; 0.37 ; 0.36) for 305-day production of milk, fat and protein in

Table 2. Variances of random regression coefficients (RRC) for genetic and permanent environmental effects for milk, fat (*1 000) and protein (*1 000) yield (posterior SD in brackets)

RRC	Single-trait model			Multiple-trait model		
	Lactation I	Lactation II	Lactation III	Lactation I	Lactation II	Lactation III
Genetic effects						
Milk						
1	3.21 (0.27)	4.36 (0.69)	7.30 (0.87)	3.64 (0.34)	5.73 (0.61)	8.28 (1.16)
2	0.77 (0.08)	2.77 (0.24)	2.54 (0.49)	0.84 (0.07)	2.67 (0.19)	2.75 (0.32)
3	0.32 (0.03)	0.45 (0.07)	1.10 (0.20)	0.35 (0.03)	0.48 (0.06)	1.02 (0.18)
4	0.11 (0.02)	0.20 (0.03)	0.29 (0.06)	0.12 (0.01)	0.25 (0.03)	0.42 (0.04)
Fat						
1	4.60 (0.48)	7.55 (1.20)	11.36 (1.50)	5.69 (0.06)	9.85 (0.99)	15.20 (0.18)
2	1.65 (0.17)	5.12 (0.46)	4.92 (0.82)	1.68 (0.14)	5.14 (0.39)	5.16 (0.70)
3	0.53 (0.07)	0.89 (0.15)	1.72 (0.33)	0.69 (0.07)	0.98 (0.14)	0.20 (0.03)
4	0.23 (0.04)	0.37 (0.06)	0.53 (0.11)	0.26 (0.03)	0.44 (0.04)	0.94 (0.11)
Protein						
1	2.67 (0.27)	4.42 (0.70)	7.06 (0.81)	3.00 (0.27)	5.48 (0.62)	7.58 (1.10)
2	0.88 (0.09)	3.03 (0.26)	2.86 (0.52)	0.97 (0.08)	2.88 (0.21)	2.94 (0.36)
3	0.40 (0.04)	0.46 (0.08)	1.12 (0.21)	0.42 (0.04)	0.52 (0.07)	1.16 (0.19)
4	0.13 (0.02)	0.25 (0.04)	0.39 (0.08)	0.15 (0.02)	0.31 (0.03)	0.55 (0.06)
Permanent environmental effects						
Milk						
1	6.20 (0.24)	10.15 (0.60)	10.15 (0.60)	7.16 (0.16)	9.37 (0.53)	10.26 (1.11)
2	1.16 (0.06)	1.48 (0.19)	2.35 (0.41)	4.98 (0.06)	1.60 (0.15)	2.27 (0.26)
3	0.38 (0.03)	0.83 (0.07)	0.53 (0.16)	0.36 (0.03)	0.82 (0.07)	0.66 (0.13)
4	0.16 (0.02)	0.22 (0.04)	0.28 (0.07)	0.15 (0.02)	0.17 (0.03)	0.20 (0.04)
Fat						
1	10.79 (0.41)	18.96(1.05)	20.96 (1.67)	10.35 (0.05)	17.97 (0.09)	19.14 (1.79)
2	2.25 (0.14)	3.29 (0.38)	4.56 (0.72)	2.32 (0.13)	3.48 (0.33)	4.96 (0.62)
3	0.88 (0.07)	1.35 (0.16)	1.16 (0.28)	0.78 (0.07)	1.44 (0.15)	1.42 (0.23)
4	0.31 (0.04)	0.36 (0.07)	0.41 (0.10)	0.32 (0.03)	0.49 (0.06)	0.55 (0.09)
Protein						
1	6.09 (0.23)	10.16 (0.60)	11.20 (0.90)	5.90 (0.23)	9.50 (0.54)	11.11 (1.11)
2	1.36 (0.07)	1.64 (0.20)	2.51 (0.44)	1.32 (0.07)	1.82 (0.16)	2.60 (0.29)
3	0.42 (0.03)	0.94 (0.08)	0.63 (0.17)	0.41 (0.04)	0.90 (0.07)	0.71 (0.13)
4	0.20 (0.02)	0.25 (0.04)	0.29 (0.07)	0.18 (0.02)	0.22 (0.03)	0.25 (0.04)

the first lactation. Estimates of Dědková and Wolf (2001) were 0.30; 0.24; 0.25.

Covariances and correlations. Table 5 contains genetic, PE and residual covariances and correla-

tions between yields calculated on lactation basis for all the analysed traits. The strongest genetic and PE covariances were found between the first and second lactations resulting from single-trait

Table 3. Estimates of residual variances for milk, fat (*1 000) and protein (*1 000) yields (posterior SD in brackets)

Days in milk	Single-trait model			Multiple-trait model		
	Lactation I	Lactation II	Lactation III	Lactation I	Lactation II	Lactation III
Milk						
7–45	6.96 (0.15)	12.90 (0.39)	16.39 (0.89)	7.17 (0.16)	13.17 (0.40)	16.35 (0.89)
46–115	4.49 (0.06)	7.79 (0.14)	9.32 (0.32)	4.52 (0.06)	7.86 (0.15)	9.41 (0.32)
116–265	3.47 (0.03)	5.01 (0.06)	5.95 (0.14)	3.46 (0.03)	4.98 (0.06)	5.94 (0.14)
266–305	3.68 (0.11)	3.58 (0.18)	3.39 (0.37)	3.66 (0.10)	3.55 (0.18)	3.48 (0.37)
Fat						
7–45	22.11 (0.51)	48.41 (1.43)	60.57 (3.13)	22.29 (0.49)	47.83 (1.37)	59.78 (3.00)
46–115	16.16 (0.20)	33.37 (0.57)	36.00 (1.13)	16.10 (0.20)	33.42 (0.57)	36.16 (1.12)
116–265	10.86 (0.09)	16.50 (0.20)	19.30 (0.42)	10.80 (0.09)	16.19 (0.20)	18.64 (0.40)
266–305	9.72 (0.28)	10.24 (0.51)	10.82 (1.02)	9.80 (0.27)	10.46 (0.48)	9.71 (0.88)
Protein						
7–45	6.77 (0.16)	13.20 (0.41)	15.08 (0.90)	6.81 (0.16)	13.21 (0.41)	14.71 (0.86)
46–115	5.17 (0.06)	9.39 (0.17)	12.06 (0.40)	5.29 (0.07)	9.44 (0.17)	12.14 (0.40)
116–265	4.61 (0.03)	6.58 (0.08)	7.88 (0.18)	4.61 (0.04)	6.58 (0.08)	7.85 (0.17)
266–305	4.88 (0.14)	5.35 (0.26)	4.94 (0.51)	4.89 (0.13)	5.20 (0.24)	4.70 (0.46)

models. The highest genetic correlations obtained by the multiple-trait analysis occurred between the successive lactations (the first and second, the second and third). These values were lower than those

estimated by Dědková and Wolf (2001) or Rekaya *et al.* (1999).

The divergent trends of yield traits were observed when covariances from single- and multiple-trait

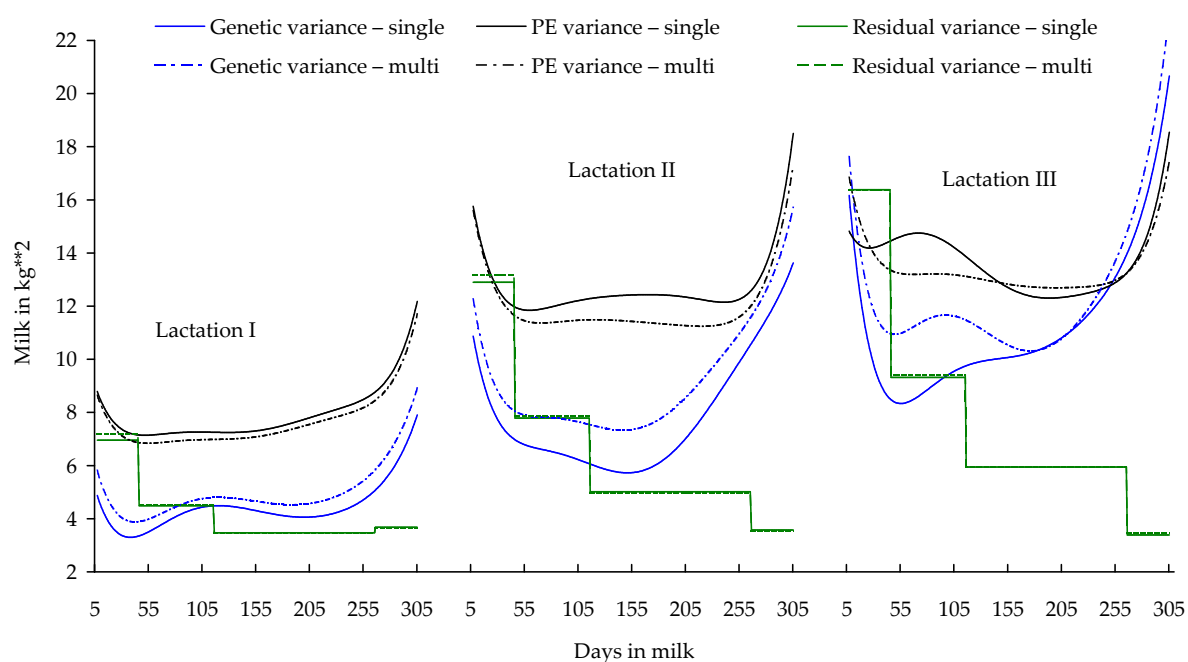


Figure 1. Estimates of variances in lactations – milk yield

Table 4. Estimates of genetic variances, variances of permanent environmental effect (PE), residual variances and heritabilities (h^2) for 305-day milk, fat and protein yields

	Single-trait model			Multiple-trait model		
	Lactation I	Lactation II	Lactation III	Lactation I	Lactation II	Lactation III
Milk						
Genetic	286 899	388 849	651 679	325 678	511 468	739 739
PE	554 110	906 820	939 167	533 754	836 989	916 295
Residual	123 979	183 462	216 578	123 982	183 462	217 149
h^2	0.30	0.30	0.36	0.33	0.33	0.39
Fat						
Genetic	411.1	675.2	1 016.2	508.4	881.2	1 360.2
PE	965.1	1 694.7	1 872.1	925.0	1 606.4	1 710.0
Residual	394.0	649.0	746.6	391.1	1 061.7	722.5
h^2	0.23	0.22	0.28	0.28	0.25	0.36
Protein						
Genetic	238.9	395.1	630.7	267.8	489.2	676.9
PE	544.1	907.6	1 000.8	527.5	848.4	992.6
Residual	157.5	233.5	277.1	157.6	233.1	275.5
h^2	0.25	0.26	0.33	0.28	0.31	0.35

models were compared. For milk and fat yield, genetic covariances between lactations were higher for multiple-trait analysis than for single-trait analysis

while the covariances of permanent environmental effects were smaller. For protein yield, genetic covariances between lactations were smaller for

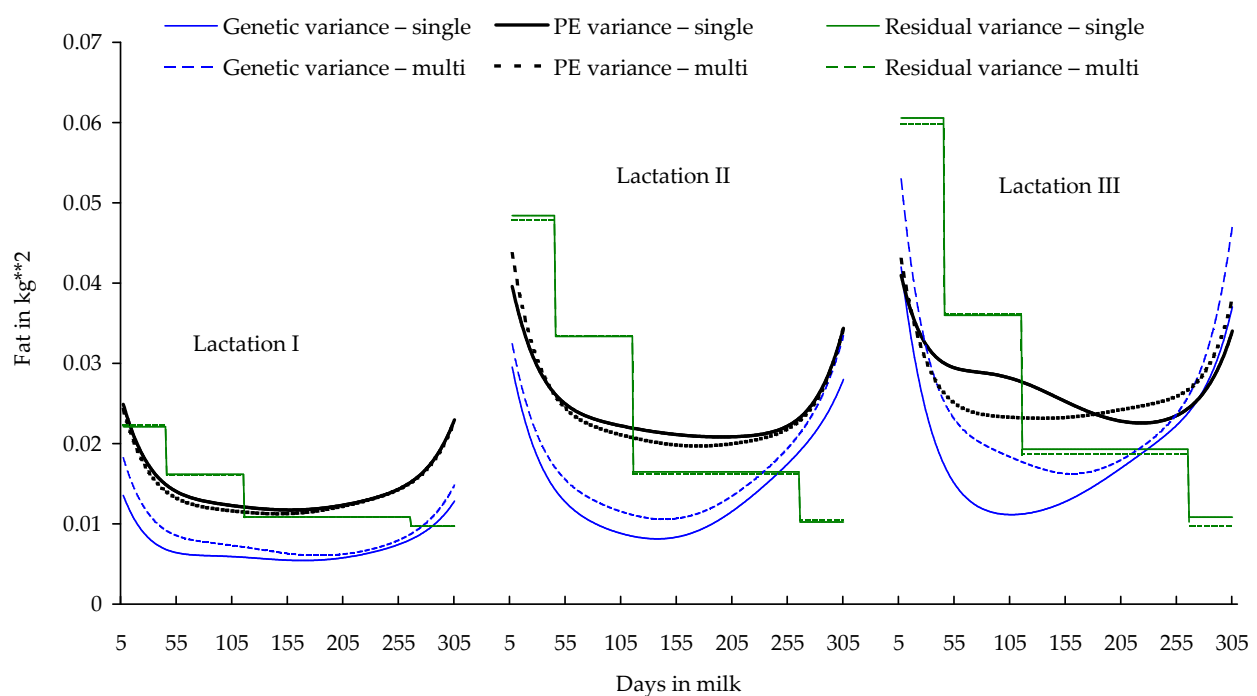


Figure 2. Estimates of variances in lactations – fat yield

Table 5. Estimates of genetic and permanent environmental (PE) covariances, genetic correlations (r_g) and permanent environmental correlations (r_{pe}) between 305-day milk, fat and protein yields

	Single-trait analyses			Multiple-trait analysis		
	Lactation I–II	Lactation I–III	Lactation II–III	Lactation I–II	Lactation I–III	Lactation II–III
Milk						
Genetic	277 247	314 465	390 937	313 662	298 102	461 145
PE	299 293	319 692	475 102	285 952	343 251	451 903
r_g	0.83	0.72	0.73	0.77	0.61	0.75
r_{pe}	0.42	0.44	0.51	0.43	0.49	
Fat						
Genetic	412.2	439.1	610.3	506.3	526.0	797.4
PE	583.4	677.0	1 022.8	547.4	625.6	941.8
r_g	0.78	0.68	0.74	0.76	0.63	0.73
r_{pe}	0.46	0.50	0.57	0.45	0.50	
Protein						
Genetic	312.7	340.7	531.1	262.1	232.9	419.3
PE	245.4	250.7	370.1	531.5	349.6	501.0
r_g	0.80	0.65	0.74	0.72	0.55	0.73
r_{pe}	0.45	0.46	0.56	0.46	0.48	0.54

the multiple-trait model than for single-trait model while the permanent environmental covariances showed the opposite behaviour.

Daily yield estimates

Genetic, PE and residual variances and heritabilities were calculated for particular days in milk (Jamrozik and Schaeffer, 1997) to demonstrate changes along the lactation trajectory. Estimates of variances are presented in Figures 1, 2, 3 for milk yield, fat yield and protein yield, respectively. Heritabilities are shown in Figures 4, 5, 6 for lactation I, II and III, respectively.

Genetic variances. Generally, genetic variances were high at the beginning and at the end of lactation. The flattest shapes were observed for the first lactation. The lowest values and decreasing trend of genetic variance in early days in milk were noticed for all traits. The rapid increase of genetic variance occurred at the last trimester of the second and third lactation. Genetic variances for fat yield (Figure 2) followed a little different pattern with a stronger decrease at the beginning of lactation.

Several authors e.g. Rekaya *et al.* (1999), Pool *et al.* (2000), Druet *et al.* (2003) found the highest genetic variance in mid-lactation and lower estimates at the beginning and at the end of lactation. Our results were in line with those obtained by Olori *et al.* (1999) and Jakobsen *et al.* (2001), who reported an increasing genetic variance towards the end of lactation.

Permanent environmental and residual variances. Permanent environmental variances for milk yield (Figure 1), fat yield (Figure 2) and protein yield (Figure 3) were higher than the corresponding genetic variances. The shapes of PE variance curves showed a similar pattern like the shape of genetic variance. The largest differences between the shapes of genetic and permanent environmental variances were in protein yield in the second and third lactations (Figure 3). In general, residual variances (Figures 1–3) decreased with days in milk.

Shapes of PE variance curves obtained in this study were in agreement with Rekaya *et al.* (1999) and Pool *et al.* (2000). Permanent environmental and residual variances in their study (summed together) showed higher values at the beginning and at the end of lactation. Decreasing values of

Table 6. Estimates of genetic correlations (*100) between yields on selected days in milk for multiple-trait (above diagonal) and single-trait models (below diagonal)

Days in milk	Lactation I						Lactation II						Lactation II					
	15	45	125	205	265	305	15	45	125	205	265	305	15	45	125	205	265	305
Milk																		
15		86	47	43	34	20		89	46	18	0	-10		86	45	37	27	14
45	83		83	65	44	30	89		76	33	8	0	86		80	51	28	18
125	45	84		86	59	42	43	74		76	49	36	34	73		77	45	30
205	42	66	86		89	68	8	21	68		91	71	27	47	81		86	62
265	30	41	57	88		92	-10	-7	36	90		92	21	25	47	86		90
305	12	24	38	62	92		-20	-16	24	74	94		9	11	24	59	90	
Fat																		
15		90	49	44	34	19		92	44	12	2	-2		91	45	34	27	14
45	89		79	58	38	25	93		71	26	11	10	93		74	46	33	26
125	47	78		81	51	34	39	66		74	53	93	32	60		78	55	41
205	39	53	79		86	61	4	15	69		92	74	13	28	81		87	59
265	24	27	47	87		90	-6	-2	44	92		93	13	22	62	90		88
305	3	10	28	61	90		-12	-5	35	75	93		9	20	46	66	90	
Protein																		
15		80	43	17	2	-9		88	43	17	2	-9		82	33	32	24	8
45	79		80	57	31	16	87		75	28	5	0	82		75	45	23	14
125	32	80		80	46	27	36	70		71	44	33	16	63		73	41	26
205	39	61	80		85	60	7	15	65		90	71	18	38	79		86	59
265	28	32	44	84		91	-7	-9	37	92		92	17	22	51	89		89
305	9	13	24	60	92		-17	-15	28	77	94		6	10	32	65	91	

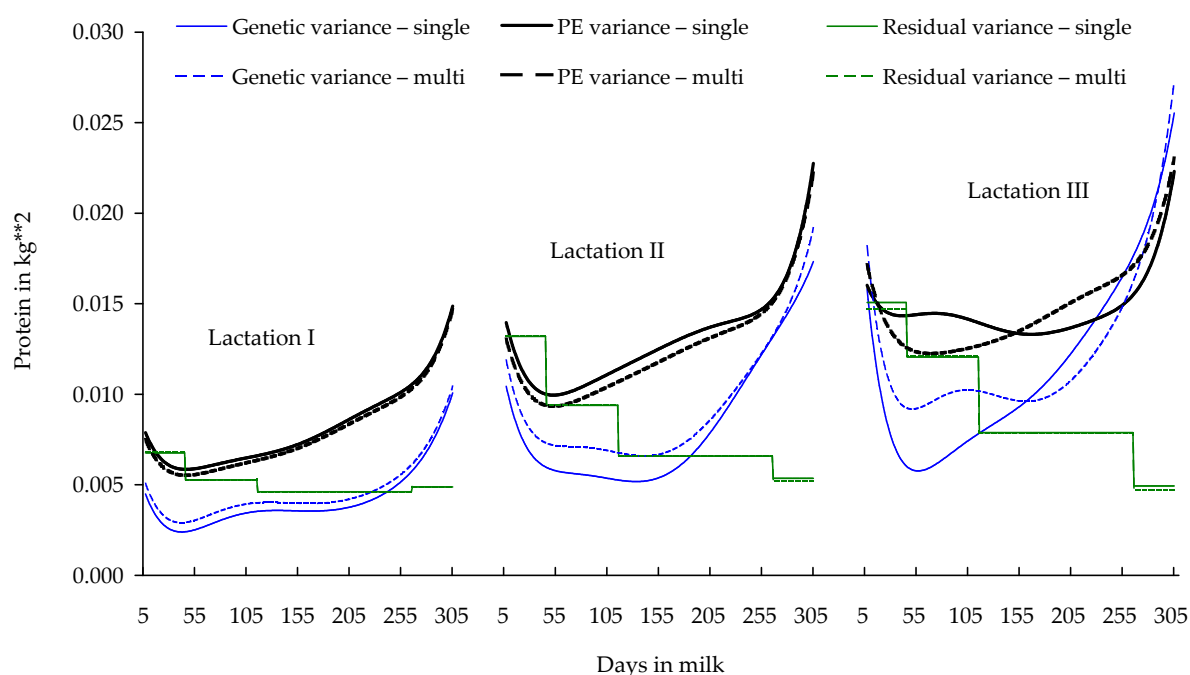


Figure 3. Estimates of variances in lactations – protein yield

Table 7. Estimates of genetic (above diagonal) and permanent environmental (below diagonal) correlations (*100) from the multiple-trait model

	Milk I	Milk II	Milk III	Fat I	Fat II	Fat III	Protein I	Protein II	Protein III
Milk I		77	61	71	50	38	92	66	51
Milk II	43		75	49	69	45	70	93	68
Milk III	49	52		40	54	75	54	69	94
Fat I	90	40	47		76	63	77	53	44
Fat II	36	91	45	45		73	54	77	60
Fat III	40	51	91	50	56		40	51	82
Protein I	97	43	49	92	41	45		72	55
Protein II	42	97	48	43	93	55	46		72
Protein III	44	50	97	48	48	93	48	54	

residual variance throughout the lactation with a slight increase at the end of lactation were found by Druet *et al.* (2003). Jakobsen *et al.* (2002) reported a highly increasing residual variance at the end of lactation.

Heritabilities. Heritabilities for daily yields for particular days in milk are presented in Figures 4, 5, 6 for lactation I, II and III, respectively. They followed shapes similar to genetic variances, with the lowest heritabilities in the early stage of lactation, an increase afterwards, and the highest values at the end of lactation.

Estimates of heritabilities obtained in different studies with random regression models were very heterogeneous (Misztal *et al.*, 2000), concerning both the magnitude and the shape of heritability curves. Several authors (e.g. Swalve, 1995; Rekaya *et al.*, 1999; Liu *et al.*, 2000; Jakobsen *et al.*, 2002; Druet *et al.*, 2003) observed the highest heritabilities in the middle of lactation and lower heritabilities at the beginning and at the end of lactation. Brotherstone *et al.* (2000) obtained heritabilities at their lowest during the first 14 days of lactation, stable values during most of lactation, and slightly

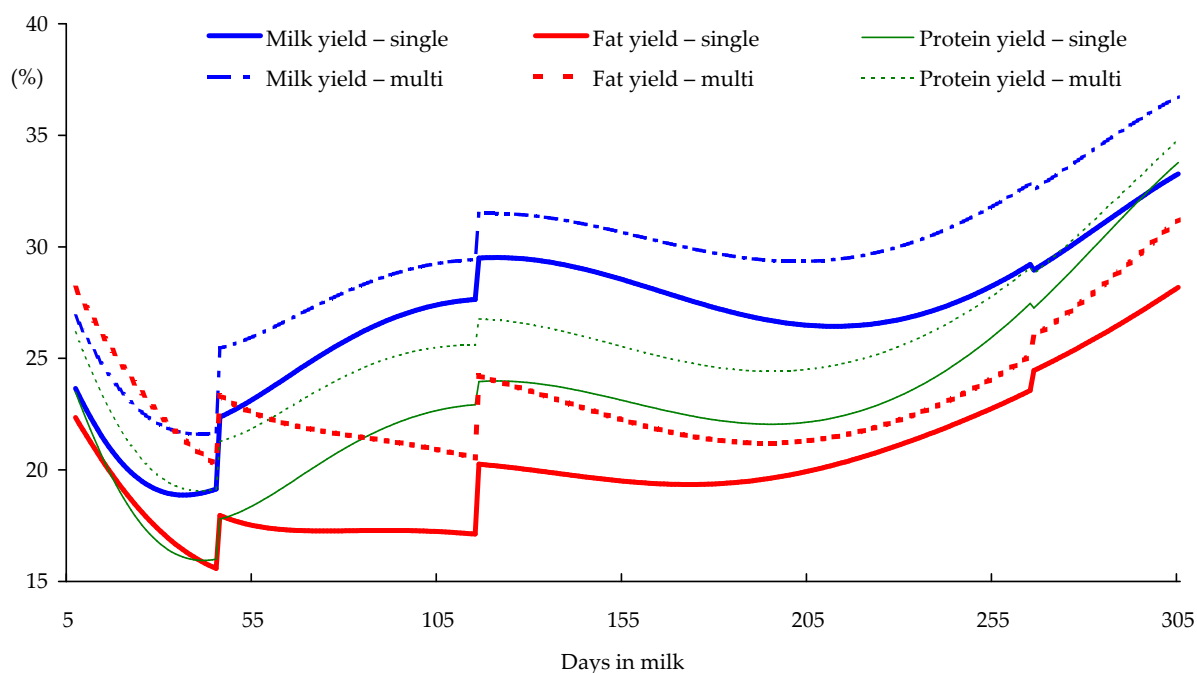


Figure 4. Heritabilities in lactations I

lower values towards the end of lactation. Similarly, Strabel and Misztal (1999) found that heritability for milk yield was low at the peak of lactation, increased toward the middle lactation, and then dropped to rise again at the end of lactation.

Shapes of heritability curves obtained in this study were previously observed for Finnish Ayrshire by Kettunen *et al.* (2000). They reported the highest estimates of heritability during early and late lactation. Heritabilities increasing with days in milk were also reported by Olori *et al.* (1999).

Values of heritability estimates ranged from 0.13 to 0.52. They showed a wide variability in comparison with other studies. Brotherstone *et al.* (2000) reported heritabilities ranging from 0.08 to 0.18. Heritabilities found by Druet *et al.* (2003) were in the range from 0.16 to 0.39. Strabel and Misztal (1999) observed heritabilities for milk (0.16–0.19 and 0.10–0.16 for first and second lactation, respectively), fat (0.11–0.16 and 0.11–0.22 for first and second lactation, respectively) and protein yields (0.10–0.15 and 0.06–0.15 for first and second lactation, respectively).

Contrary to our study, Liu *et al.* (2000) reported lower heritabilities for later lactations than for the first one, and no evident difference in heritability was observed between the second and third lactation. Guo *et al.* (2002) showed that the heritability

decreased across parities. On the contrary, higher (but lower than in the present study) estimates for all yield traits for the second lactation were obtained by Strabel and Misztal (1999) when compared with first lactation.

Shapes of heritabilities for protein yield and for fat yield showed a similar pattern like those for milk yield but the lowest values of heritability for fat yield were recorded later in lactation (around 100 DIM) than those for milk or protein yield (around 45 DIM). Milk yield had the highest heritability among the three production traits. That was in agreement with Strabel and Misztal (1999) and Liu *et al.* (2000).

Covariances and correlations

Estimates of genetic correlations between selected days in milk for milk, fat and protein yields are given in Table 6. Correlations between yields on days that were close together were higher compared to those for days that were farther apart. Some of the early yields in the second lactation were slightly negatively correlated with daily yields on later DIM. The reason for low values of genetic correlations can be a poorer fit of the function at the beginning and at the end of the second lactation.

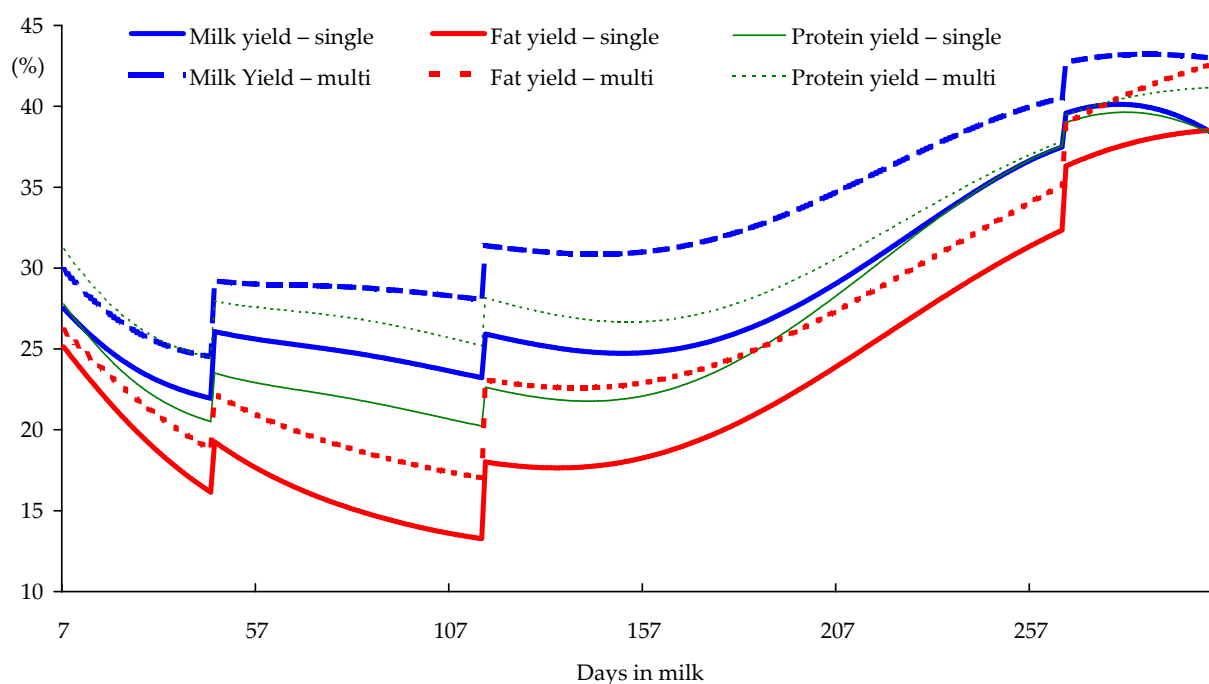


Figure 5. Heritabilities in lactations II

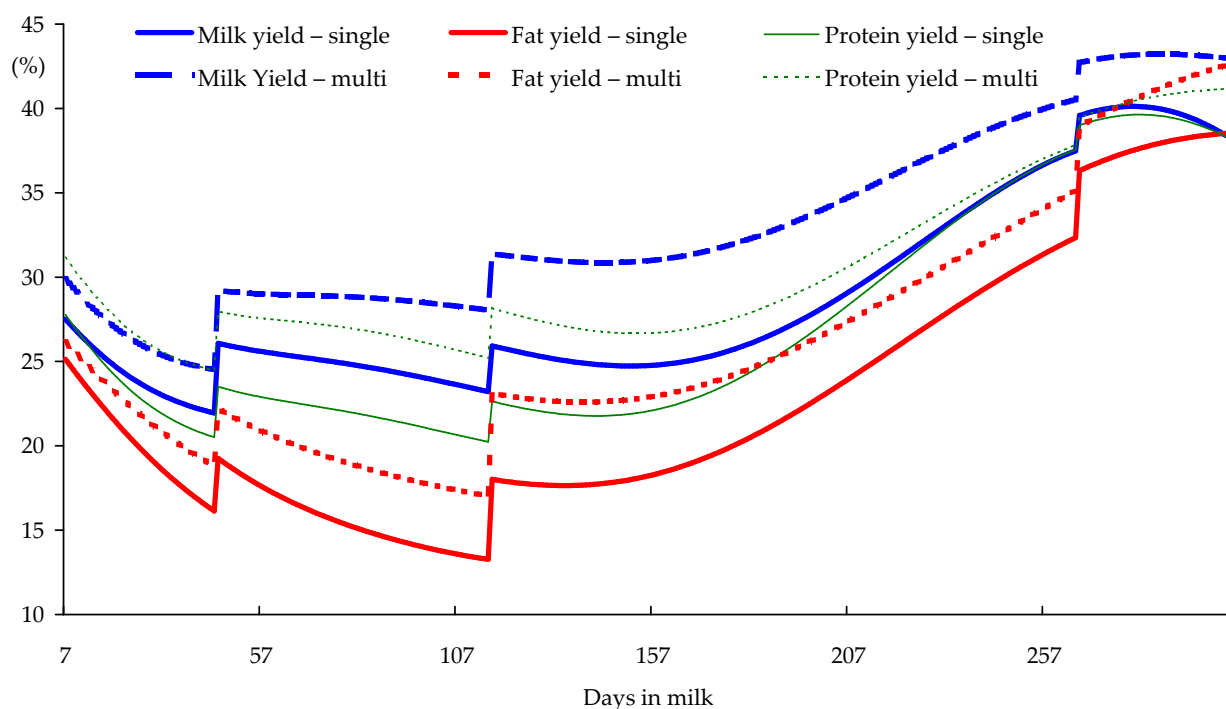


Figure 6. Heritabilities in lactations III

Jakobsen *et al.* (2002) found in general that genetic correlations were high between the individual test-days and 305-day production with an exception for the correlation between day 5 and 305 for fat yield. Strabel and Misztal (1999) reported the lowest correlations between TD recorded at the beginning of lactation and at the very end, values around zero were found for second lactation fat yields and first lactation protein yields. Jamrozik and Schaeffer (1997) and Rekaya *et al.* (1999) obtained negative genetic correlations between yields in early and late lactation when modelling the lactation with parametric curves and not accounting for changes in PE effects during lactation. The lactation curve functions (Wilmink, Ali-Schaeffer and mixed log function) showed an inability to model the association between yields in early and late lactation stages, resulting in negative genetic correlations between the two ends of lactation (Liu *et al.*, 2000). This problem was also reported by Brotherstone *et al.* (2000). Pool *et al.* (2000) recommended using a fourth-degree Legendre polynomial for both the genetic and permanent environmental effects because it seems to fit the genetic and permanent environmental (co)variances successfully.

The genetic and permanent environmental correlations between milk, fat and protein yields calcu-

lated on lactation basis from multiple-trait analysis are presented in Table 7. The genetic correlations between milk yield and protein yield were higher than those between milk and fat yields. Genetic correlations between milk yield in the first, second and third lactation along the lactation trajectory are given in Figure 7. The figures indicated a higher genetic correlation between milk and protein yield than between milk and fat yield. These findings are in agreement with Jamrozik *et al.* (1998) and Jakobsen *et al.* (2002).

CONCLUSIONS

Estimates of genetic parameters for milk, fat and protein yield of Czech Holstein population corresponded to published results for other Holstein breeds. The resulting estimates of (co)variances, heritabilities, genetic and permanent environmental correlations followed the general pattern reported in other studies. (Co)variance components for regression coefficients estimated in this study can be used in random regression test-day model for genetic evaluation of dairy cattle in the Czech Republic.

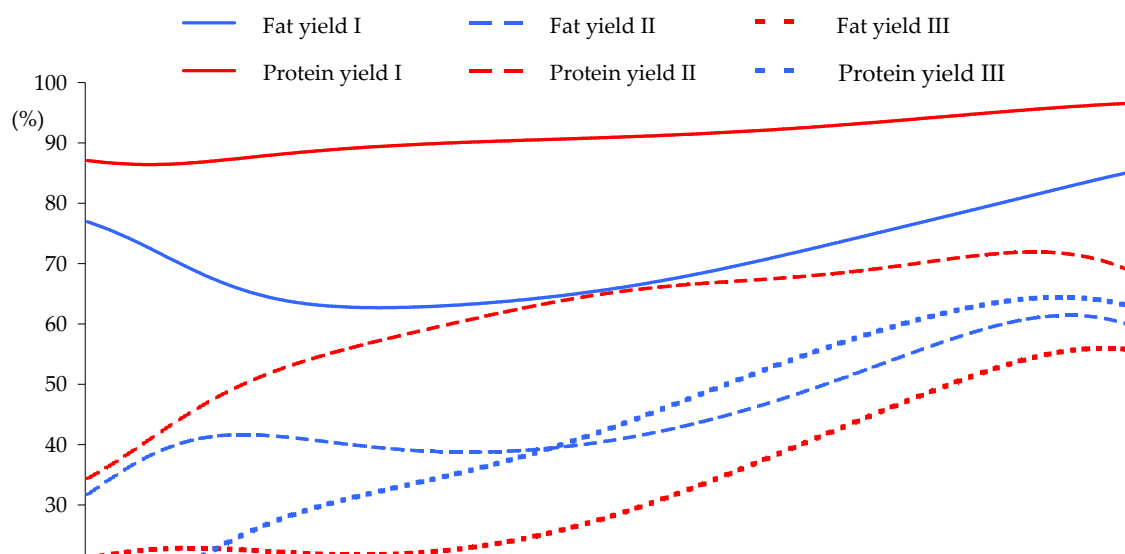


Figure 7. Genetic correlations between milk yield in the first lactation and fat or/and protein yield in the first, second and third lactation

The current evaluation system in the Czech Republic ignores the associations between milk, fat and protein. For the present, the suggested random regression test-day model will be restricted to a single-trait three-lactation model because the computing requirements for a multiple-trait test-day random regression model are still enormous. However, the power of computers is continuously increasing, suggesting that this situation may be of limited duration and the estimated genetic parameters for the multiple-trait model could be used in the future genetic evaluation system.

REFERENCES

- Brotherstone S., White I.M.S., Meyer K. (2000): Genetic modelling of daily milk yield using orthogonal polynomials and parametric curves. *Anim. Sci.*, 70, 407–715.
- Dědková L., Wolf J. (2001): Estimation of genetic parameters for milk production traits in Czech dairy cattle populations. *Czech J. Anim. Sci.*, 46, 292–301.
- Druet T., Jaffrézic F., Boichard D., Ducrocq V. (2003): Modeling lactation curves and estimation of genetic parameters for first lactation test-day records of French Holstein cows. *J. Dairy Sci.*, 86, 2480–2490.
- Guo Z., Lund M.S., Madsen P., Korsgaard I., Jensen J. (2002): Genetic parameter estimation for milk yield over multiple parities and various lengths of lactation in Danish Jerseys by random regression models. *J. Dairy Sci.*, 85, 1596–1606.
- Jaffrézic F., White I.M.S., Thompson R., Hill W.G. (2000): A link function approach to model heterogeneity of residual variances over time in lactation curve analyses. *J. Dairy Sci.*, 83, 1089–1093.
- Jakobsen J.H., Madsen P., Jensen J., Pedersen J. Christensen L.G., Sorensen D.A. (2002): Genetic parameters for milk production and persistency for Danish Holsteins estimated in random regression models using REML. *J. Dairy Sci.*, 85, 1607–1616.
- Jamrozik J., Schaeffer L.R. (1997): Estimates of genetic parameters for a test day model with random regressions for yield traits of first lactation Holsteins. *J. Dairy Sci.*, 80, 762–770.
- Jamrozik J., Schaeffer L.R., Grignola F. (1998): Genetic parameters for production traits and somatic cell score of Canadian Holsteins with multiple trait random regression model. In: *Proc. 6th WCGALP*, Armidale, 303–306.
- Kettunen A., Mäntysaari E.A., Poso J. (2000): Estimation of genetic parameters for daily milk yield of primiparous Ayrshire cows by random regression test-day models. *Livestock Prod. Sci.*, 66, 251–261.

- Lidauer M., Mäntysaari E.A., Strandén I. (2003): Comparison of test-day models for genetic evaluation of production traits in dairy cattle. *Livestock Prod. Sci.*, 79, 73–86.
- Liu Z., Reinhardt F., Reents R. (2000): Estimating parameters of a random regression test day model for first three lactation milk production traits using the covariance function approach. *Interbull Bulletin No. 25*, 74–80.
- Misztal I., Strabel T., Jamrozik J., Mäntysaari E.A., Meuwissen T.H.E. (2000): Strategies for estimating the parameters needed for different test-day models. *J. Dairy Sci.*, 83, 1125–1134.
- Olori V.E., Hill W.G., McGuirk B.J., Brotherstone S. (1999): Estimating variance components for test day milk records by restricted maximum likelihood with a random regression animal model. *Livestock Prod. Sci.*, 61, 53–63.
- Pool M.H., Janss L.L.G., Meuwissen T.H.E. (2000): Genetic parameters of Legendre polynomials for first parity lactation curves. *J. Dairy Sci.*, 83, 2640–2649.
- Pool M.H., Meuwissen T.H.E. (2000): Reduction of the number of parameters needed for a polynomial random regression test day model. *Livestock Prod. Sci.*, 64, 133–145.
- Rekaya R., Carabaño M.J., Toro M.A. (1999): Use of test day yields for the genetic evaluation of production traits in Holstein-Friesian cattle. *Livestock Prod. Sci.*, 57, 203–217.
- Strabel T., Misztal I. (1999): Genetic parameters for first and second lactation milk yields of Polish Black and White cattle with random regression test-day models. *J. Dairy Sci.*, 82, 2805–2810.
- Swalve H.H. (1995): Test day models in the analysis of dairy production data – a review. *Arch. Tierzucht*, 38, 591–612.
- Van der Werf J.H.J., Goddard M.E., Meyer K. (1998): The use of covariance functions and random regressions for genetic evaluation of milk production based on test day records. *J. Dairy Sci.*, 81, 3300–3308.

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Corresponding Author

Ing. Ludmila Zavadilová, CSc., Research Institute of Animal Production in Prague, P.O.Box 1, 104 01 Prague-Uhřetěves, Czech Republic
Tel. +420 2 67009574, fax +420 2 67710779, e-mail: dedkova.ludmila@vuzv.cz
