Genetic and environmental parameters estimation for milk traits in Slovenian dairy sheep using random regression model

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ABSTRACT: (Co)variance components for daily milk yield, fat, and protein content in Slovenian dairy sheep were estimated with random regression model. Test-day records were collected by the ICAR A4 method. Analysis was done for 38 983 test-day records of 3068 ewes in 36 flocks. Common flock environment, additive genetic effect, permanent environment effect over lactations, and permanent environment effect within lactation were included into the random part of the model and modelled with Legendre polynomials on the standardized time scale of days in lactation. Estimation of (co)variance components was done with REML. The eigenvalues of covariance functions for random regression coefficients were calculated to quantify the sufficient order of Legendre polynomial for the (co)variance component estimation of milk traits. The existing 13 to 24% of additive genetic variability for the individual lactation curve indicated that the use of random regression model is justified for selection on the level and shape of lactation curve in dairy sheep. Four eigenvalues sufficiently explained variability during lactation in all three milk traits. Heritability estimate for daily milk yield was the highest in mid lactation (0.17) and lower in the early (0.11) and late (0.08) lactation. In fat content, the heritability was increasing throughout lactation (0.08–0.13). Values in protein content varied from the beginning toward mid lactation (0.15–0.19), while they rapidly increased at the end of lactation (0.28). Common flock environment explained the highest percentage of phenotypic variability: 27–41% in daily milk yield, 31–41% in fat content, and 41–49% in protein content. Variance ratios for the two permanent environment effects were the highest in daily milk yield (0.10–0.27), and lower in fat (0.04–0.08) and protein (0.01–0.10) contents. Additive genetic correlations during the selected test-days were high between the adjacent ones and they tended to decrease at the extremes of the lactation trajectory.

Keywords: dairy ewes; test-day records; orthogonal Legendre polynomials; heritability; additive genetic correlations

Several test-day models have been proposed for the genetic evaluations of milk traits in animal breeding, where test-day records are directly used, considering both genetic and environmental effects specific to each test-day yield. Test-day records collected during lactation on the same animal were treated as repeated measurements of the same trait (Ptak and Schaeffer, 1993). They constituted longitudinal data and they were mutually dependent. Test-day repeatability models have been widely used for routine evaluations in many countries. Studies on dairy cattle by Danell (1982), Ptak and Schaeffer (1993), Schaeffer and Jamrozik (1996), and Ilatsia et al. (2007), as well as on dairy sheep by Barillet and Boichard (1994), Baro et al. (1994), El-Saied et al. (1998), Brežnik (1999), Serrano et al. (2001), Oravcová et al. (2005), and Komprej et al. (2009) are only some of many studies, where the repeatability model was applied for the genetic parameter estimation of milk traits. Use of the repeatability model assumes a constant variance and genetic correlations of the unity among yields at different stages of lactation (Ptak and Schaeffer, 1993). The model assumes a standard shape of the lactation curve for all animals in the comparative group, while differences in persistency among animals are ignored.

In the last two decades, a random regression model has become the model of choice for the genetic evaluations in animal breeding. The general concept of random regression model has already been described by Henderson (1982). Random regression model fits fixed overall regression on lactation stage, which is the same for all animals in a group. In addition, analysis of test-day records by random regression model allows the shape of the lactation curve to differ among individual animals by including random regression coefficients for each animal (Jamrozik and Schaeffer, 1997). This model accommodates repeated records for traits which change gradually and continually over time, and do not require stringent assumptions about constancy of the variances and correlations. The method allows the estimation of covariance among records obtained in various time intervals (e.g. days, weeks, months) within a given time-scale, including time intervals that were not sampled. Orthogonal polynomials of standardized units of time have been recommended as covariables (Kirkpatrick et al., 1990). Schaeffer and Deckers (1994) were the first researchers who proposed random regression model to model test-day records of milk traits in dairy cattle. Soon afterwards, similar analyses were done in dairy cattle by Jamrozik and Schaeffer (1997), Van der Werf et al. (1998), Olori et al. (1999), Kettunen et al. (2000), Cobuci et al. (2005, 2011), Druet et al. (2005), Zavadilová et al. (2011), and many others. Random regression model was also used for the genetic parameter estimation of milk traits in dairy sheep by Ligda et al. (2000), Kominakis et al. (2001), Horstick et al. (2002), Banos et al. (2005), Cadavez et al. (2011), and even in dairy goats (Breda et al., 2006; Menéndez-Buxadera et al., 2010; Menezes et al., 2011).

The objective of our study was to apply a random regression model and estimate (co)variance components for milk traits (daily milk yield, fat, and protein content) in three dairy sheep breeds in Slovenia, using test-day records.

MATERIAL AND METHODS

Test-day records of three dairy sheep breeds (Bovec – B, Improved Bovec – IB, and Istrian Pramenka – IP) were used for the analysis. Data were provided by the Slovenian breeding programme for small ruminants and collected according to the ICAR regulations by the A4 method (ICAR, 2005). Only test-day records with known daily milk yield (DMY), fat (FC), and protein content (PC) at the same time were used. Records collected between days 5–244 of lactation were required. Only lactations with at least three test-day records were included into the analysis. Test-day yields below 50 g of DMY and outside the range of 1.5–18% for FC, and 2.0–13% for PC were discarded. Records with parity exceeding 10 were excluded from the data set. Finally, 38 983 test-day records from 3068 ewes (1957 B, 486 IB, and 625 IP) in 36 flocks were analyzed (Tables 1 and 2).

A pedigree file contained 3534 animals of all three breeds and it was set up using all the available relationships among animals (Table 1). Breed B represented the majority of the animals (2244), the rest of the animals belonged to breeds IB and IP (677 and 720, respectively). Since some animals from B and IB breeds coincided, the sum of animals across breeds was not equal to 3534. There was 66% (2346) of the animals with at least one ancestor known. The rest (1188) were base animals with both ancestors unknown.

Descriptive statistics for the observed milk traits was done using SAS software (Statistical Analysis System, Version 8.2, 2001) and is shown in Table 2 on the selected day of lactation. The average DMY was the highest at the beginning of lactation (2073 g). It was decreasing during lactation period to 492 g at the end of lactation. The overall average DMY was 1022 g. Standard deviation for DMY was also the highest at the beginning of lactation (1017 g) and it was declining during the stage of lactation (to 273 g). The average FC was increasing during lactation period from 4.53 to 7.95%. The overall average FC was 6.62%. Standard deviation for FC was also increasing in the meantime, so it was the highest at the end of lactation (1.70%). Also, the average PC was increasing from the beginning (4.71%) to the end of lactation period (6.64%). The overall average PC was 5.51%. As in FC, standard deviation for PC was the highest at the end of lactation and it amounted to 1.19% at day 196 of lactation.

The random regression analysis was performed for all breeds together due to the low number of observations in breeds IB (5982) and IP (6414). DMY, FC, and PC (y_{ij}) were modelled with a single-trait animal random regression model (Equation 1):

$$y_{ij} = \mathrm{F} + \sum_{m=0}^{k_\gamma - 1} \gamma_{im}\phi_m(t_{ij}) + \sum_{m=0}^{k_\alpha - 1} \alpha_{im}\phi_m(t_{ij}) + \sum_{m=0}^{k_\lambda - 1} \kappa_{im}\phi_m(t_{ij}) + \sum_{m=0}^{k_\mathrm{f} - 1} \lambda_{im}\phi_m(t_{ij}) + \varepsilon_{ij} \qquad (1)$$

where:

y_{ij} = j^{th} record of the i^{th} animal
F = fixed part of the model
γ_{im} = random regression coefficients of the common flock environmental effect
ϕ_m = polynom of the m^{th} order for time t_{ij}
t_{ij} = j^{th} month of lactation on the standardized time scale from +1 to –1
α_{im} = additive genetic effect of animal
κ_{im} = permanent environment effect over lactations
λ_{im} = permanent environment effect within lactation
ε_{ij} = residual

Fixed part of the model (F) was already used in the previous study by Komprej et al. (2009). It contained the effect of breed with three levels and the season of lambing with 63 levels. Days in lactation, nested within breed, parity, and litter size as a number of born lambs were treated as covariates. The modified Ali-Schaeffer's lactation curve (Ali and Schaeffer, 1987) with four regression coefficients was used to model days in lactation. Instead of constant 305, a constant of 150 was used because lactation in sheep usually ends earlier than in cows. For parity and for litter size, simple quadratic and linear regressions were used. The permanent environment effect over lactations accounted for the repeated measurements on the same animals all over lactations, while the permanent environment effect within lactation accounted for the repeated measurements on the same animal, but within lactation. Random effects were fitted as a random regression on days in lactation, using orthogonal Legendre polynomials (LG) on standardized time scale t_{ij}. Thus, days in lactation were transformed into values from –1 to +1 (Equation 2):

$$t_{ij} = -1 + 2\left(\frac{t_x - t_{\min}}{t_{\max} - t_{\min}}\right) \qquad (2)$$

where:

t_{ij} = transformed number of the days in lactation
t_x = number of the days in lactation
$t_{\min}$ = minimum number (5th day) of the days in lactation
$t_{\max}$ = maximum number (244th day) of the days in lactation

Legendre polynomials from the first (LG1) to the fourth (LG4) order were fitted.

In matrix notation the model was presented as follows (Equation 3):

$$y = \mathbf{X}\beta + \mathbf{Z}_\gamma\gamma + \mathbf{Z}_\alpha\lambda + \mathbf{Z}_\kappa\alpha + \mathbf{Z}_\lambda\lambda + \varepsilon \qquad (3)$$

where:

y = vector of observations on DMY, FC, and PC
$\mathbf{X}, \mathbf{Z}_\gamma, \mathbf{Z}_\alpha, \mathbf{Z}_\kappa, \mathbf{Z}_\lambda$ = incidence matrices for fixed and random effects: flock-test-month, additive genetic, permanent environment over lactations, and permanent environment within lactation, respectively
β = vector of unknown parameters for fixed effects
$\gamma, \alpha, \kappa, \lambda$ = vectors of unknown parameters for random regression coefficients of common flock environment effect, additive genetic effect, permanent environment effect over lactations, and permanent environment effect within lactation effects, respectively
ε = vector of residuals

Usual assumptions to model were applied. Expected values of observations were equal to $\mathbf{X}\beta$ (Equation 4), and expected values for all random effects were equal to zero. (Co)variances for random effects of common flock environment ($\mathbf{K}_\gamma$), additive genetic effect ($\mathbf{K}_\alpha$), permanent environment over lactations ($\mathbf{K}_\kappa$), permanent environment within lactation ($\mathbf{K}_\lambda$), and residuals ($\mathbf{R}_\varepsilon$) compose phenotypic (co)variances (Equation 5). Equations 6 and 7 describe covariance matrix structure for the individual random effect. Matrices $\mathbf{I}_\gamma$, $\mathbf{I}_\kappa$, and $\mathbf{I}_\lambda$ are the identity matrices for common flock environment effect, permanent environment effect over lactations, and permanent environment effect within lactation. Levels were assumed to be uncorrelated for trivial random effects, while for additive genetic effect, the relationship among levels is shown in the matrix **A**. Measurements are correlated within levels for the individual random effects, what is shown from the (co)variance structure in matrices $\mathbf{K}_{0\gamma}$ for common flock environment

Table1. Pedigree structure by breeds

Breed	Total	B	IB	IP
Ewes	3068	1957	486	625
Pedigree	3534	2244	677	720
Non-base	2346	1458	500	440
Base	1188	786	177	280

B = Bovec breed, IB = Improved Bovec breed, IP = Istrian Pramenka breed effect, $\mathbf{K}_{0\alpha}$ for additive genetic effect (Equation 7), $\mathbf{K}_{0\kappa}$ for permanent environment effect over lactations, and $\mathbf{K}_{0\lambda}$ for permanent environment effect within lactation. Matrix $\mathbf{R}_{0i}$ is a diagonal matrix, where index i indicates matrices for residuals. The matrix for residuals is a direct sum of $\mathbf{R}_{0i}$ matrices due to records with missing test-days along the lactation. Sign ⊗ is the Kronecker's product and $\Sigma^{\oplus}$ is the direct sum. Residuals from different animals were additionally assumed to be independent and normally distributed.

$$E(y) = \mathbf{X}\beta \tag{4}$$

$$V = \mathrm{var}(y) = \mathbf{Z}_{\gamma}\mathbf{K}_{\gamma}\mathbf{Z}_{\gamma}' + \mathbf{Z}_{\alpha}\mathbf{K}_{\alpha}\mathbf{Z}\alpha_{\gamma}' + \mathbf{Z}_{\kappa}\mathbf{K}_{\kappa}\mathbf{Z}_{\kappa}' + \mathbf{Z}_{\lambda}\mathbf{K}_{\lambda}\mathbf{Z}_{\lambda}' + \mathbf{R} \tag{5}$$

$$\mathrm{var}\begin{bmatrix}\gamma\\ \alpha\\ \kappa\\ \lambda\\ \varepsilon\end{bmatrix} = \begin{bmatrix}\mathbf{K}_{\gamma} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0}\\ \mathbf{0} & \mathbf{K}_{\alpha} & \mathbf{0} & \mathbf{0} & \mathbf{0}\\ \mathbf{0} & \mathbf{0} & \mathbf{K}_{\kappa} & \mathbf{0} & \mathbf{0}\\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{K}_{\lambda} & \mathbf{0}\\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{R}_{\varepsilon}\end{bmatrix} =$$

$$= \begin{bmatrix}\mathbf{I}_{\gamma}\otimes\mathbf{K}_{0\gamma} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0}\\ \mathbf{0} & \mathrm{A}\otimes\mathbf{K}_{0\alpha} & \mathbf{0} & \mathbf{0} & \mathbf{0}\\ \mathbf{0} & \mathbf{0} & \mathbf{I}_{\kappa}\otimes\mathbf{K}_{0\kappa} & \mathbf{0} & \mathbf{0}\\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{I}_{\lambda}\otimes\mathbf{K}_{0\lambda} & \mathbf{0}\\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \Sigma^{\oplus}\mathbf{R}_{0i}\end{bmatrix} \tag{6}$$

$$\mathbf{K}_{0\alpha} = \mathrm{var}\begin{bmatrix}\alpha_{\mathbf{k}0}\\ \alpha_{\mathbf{k}1}\\ \vdots\\ \vdots\\ \alpha_{\mathbf{k_A}-1}\end{bmatrix} = \begin{bmatrix}\sigma^2_{\alpha 0} & \sigma_{\alpha 0\alpha 1} & \cdots & \cdots & \sigma_{\alpha\mathbf{0}\alpha(\mathbf{k_A}-1)}\\ & \sigma^2_{\alpha 1} & \cdots & \cdots & \sigma_{\alpha 1\alpha(\mathbf{k_A}-1)}\\ & & \ddots & \ddots & \vdots\\ & & & \ddots & \vdots\\ & & & & \sigma^2_{\alpha\mathbf{k_A}-1}\end{bmatrix} \tag{7}$$

(Co)variance components for random regression coefficients were estimated by REML (restricted maximum likelihood) using VCE statistical package (Version 5, 2012) (Kovač et al., 2002). (Co)variance matrices for random regression coefficients presented covariance functions for the observed milk traits. In addition, eigenfunctions with adherent eigenvalues for covariance functions were calculated with the SAS software (Statistical Analysis System, Version 8.2, 2001). To define a sufficient order of Legendre polynomial, eigenvalues were expressed in percentage of total variance caused by individual random effect. Modul SAS/IML was used for this calculation. Furthermore, estimation of (co)variance components for random environmental and genetic effects was done with the SAS statistical package.

RESULTS AND DISCUSSION

Eigenvalues were estimated to determine the order of Legendre polynomial, which would be sufficient for the (co)variance component estimation of random effects in the observed milk traits (Table 3). Eigenvalues of the additive genetic covariance functions for DMY (Table 3) showed that the constant (zero) term accounted for 76–87% of the total additive genetic variability, depending on the LG order. This means that approximately 13–24% of the additive genetic variability was explained by the individual lactation curve for each ewe. In FC, the constant term accounted for 78–87% of the total additive genetic variability. The percentage for PC made 83–87%. From 13 to 22% in FC and from 13 to 17% in PC of the additive

Table 2. Number of records (*N*), means, and standard deviations (SD) for milk traits on the selected days of lactation

Day of lactation	*N*	Daily milk yield (g)		Fat content (%)		Protein content (%)	
		mean	SD	mean	SD	mean	SD
24	1 465	2 073	1 017	4.53	1.35	4.71	0.49
51	5 632	1 755	756	5.37	1.03	4.69	0.51
79	7 248	1 290	581	5.99	1.06	4.90	0.54
108	7 619	941	443	6.57	1.18	5.28	0.65
138	7 226	714	356	7.15	1.35	5.84	0.90
167	5 660	564	304	7.69	1.54	6.40	1.18
196	2 855	497	288	7.86	1.60	6.57	1.19
226	1 278	492	273	7.95	1.70	6.64	1.10
Total	38 983	1 022	692	6.62	1.59	5.51	1.07

Table 3. Eigenvalues for random effects in milk traits as a percentage of total variance according to the power of Legendre polynomial (LG) from the first (LP1) to the fourth (LP4) power

Effect	Eigenvalue	Daily milk yield				Fat content				Protein content			
		LP1	LP2	LP3	LP4	LP1	LP2	LP3	LP4	LP1	LP2	LP3	LP4
Additive genetic effect	0th	87.30	82.16	76.31	75.59	86.85	77.76	80.12	82.83	87.44	84.92	83.57	82.54
	1st	12.70	17.13	22.73	23.57	13.15	13.16	13.58	10.91	12.56	12.57	11.44	11.50
	2nd		0.71	0.96	0.62		9.08	6.30	6.27		2.51	3.90	3.56
	3rd			0.00	0.23			0.00	0.00			1.10	1.91
	4th				0.00				0.00				0.49
Common flock environment	0th	82.98	82.22	80.16	73.79	84.19	76.80	73.77	75.51	92.65	88.50	87.64	88.98
	1st	17.02	10.32	11.99	18.02	15.81	17.65	20.45	18.97	7.35	9.68	7.82	7.26
	2nd		7.46	5.75	5.19		5.55	3.12	3.79		1.81	3.58	2.28
	3rd			2.09	3.01			2.66	1.73			0.96	1.48
	4th				0.00				0.00				0.00
Permanent environment over lactations	0th	92.60	89.96	83.07	81.89	77.38	65.89	60.77	55.98	81.21	73.71	79.94	79.29
	1st	7.40	5.70	11.54	10.19	22.62	26.49	20.54	25.05	18.79	26.30	20.06	18.84
	2nd		4.33	4.46	5.25		7.61	13.56	14.30		0.00	0.00	1.87
	3rd			0.93	2.67			5.12	4.67			0.00	0.00
	4th				0.00				0.00				0.00
Permanent environment within lactation	0th	87.69	84.91	77.23	72.15	87.08	55.62	53.89	52.43	82.29	80.05	66.93	65.79
	1st	12.31	11.63	17.44	20.77	12.92	28.33	34.05	28.40	17.71	16.00	20.87	18.97
	2nd		3.46	4.44	5.35		16.05	12.06	17.83		3.95	6.85	7.62
	3rd			0.89	1.73			0.00	1.34			5.35	4.72
	4th				0.00				0.00				2.90

genetic variability was explained by the individual lactation curve for each ewe. Cubic LG (LG3) with four regression coefficients is sufficient to model the additive genetic variability in DMY, FC, and also PC. Large differences among individual courses of lactation curve indicate the possibility of selection in dairy sheep. In first lactation cows (Druet et al., 2005), the constant term accounted for 92% of the total additive genetic variability in DMY, 94% in FC, and 90% in PC. In this case, 8, 6, and 10% of the total additive genetic variability in DMY, FC, and PC, respectively, remained for higher terms, which represent the course of the lactation curves for individual animals. Kominakis et al. (2001) modelled test-day records in Sfakia sheep by random regression model where the first eigenvalue accounted for 88% of the total additive genetic variability in DMY in the first, 96% in the second, and 97% in the third lactation. Banos et al. (2005) estimated population parameters for DMY in the first three lactations of the Chios sheep, but without pedigree information. The first term of the eigenvalues explained between 80 and 84% of the total animal variability, depending on lactation number, and was by far the most important. The second, third, and fourth terms explained 11–15%, 4–5%, and about 1% of the animal variance, respectively, depending on lactation number. In Alpine goats (Breda et al., 2006), the first term of the eigenvalues explained 85% of the total additive genetic variability in DMY, the second term explained 8%, and the third term explained 7% of the variability.

For other random effects, common flock environment, permanent environment over lactations, and permanent environment within lactation, also LG3 is sufficient for modelling the variability in all three observed milk traits (Table 3). The constant term accounted for more than 73% variability of the total common flock environment, for more than 55% variability of the total permanent environment over lactations, and for more than 52% variability of the total permanent environment within lactation. Overall, up to 48% variability for individual environmental random effect was explained by the individual lactation curve for each ewe, depending on the observed milk trait.

The estimates of genetic and environmental variance ratios for DMY, FC, and PC, obtained by LG3, are shown in Figures 1–3, respectively. Heritability estimates for all three milk traits were relatively low. In DMY, the heritability was the highest in the middle of lactation (to 0.16) and lower during early (0.11) and late (0.08) lactation (Figure 1). Ligda et al. (2000) estimated higher heritabilities (0.28–0.14) in Chios sheep, which were decreasing during lactation. In the range of 0.05 to 0.32 were the estimates in Sfakia sheep studied by Kominakis et al. (2001). The heritabilities in East-Friesian sheep estimated by Horstick et al. (2002) made 0.03–0.70. In Alpine goats (Breda et al., 2006), the heritability estimates for DMY were slightly decreasing from the beginning toward the end of lactation (from 0.51 to 0.12). Heritabilities for DMY in Saanen goats obtained by Menezes et al. (2011) showed similar trend compared to our results, with an increasing phase from the beginning toward the middle of lactation (0.07–0.25) and a decreasing phase thereafter (0.15). Higher heritability estimates for DMY compared to our study were also obtained in dairy cows by Jamrozik and Schaeffer (1997), Olori et al. (1999), Kettunen et al. (2000), Cobuci et al. (2005), and Silvestre et al. (2005).

The heritability estimates in FC ranged from 0.08 at the beginning to 0.13 at the end of lactation (Figure 2). The ratio was slightly increasing throughout lactation. Horstick et al. (2002) ob-

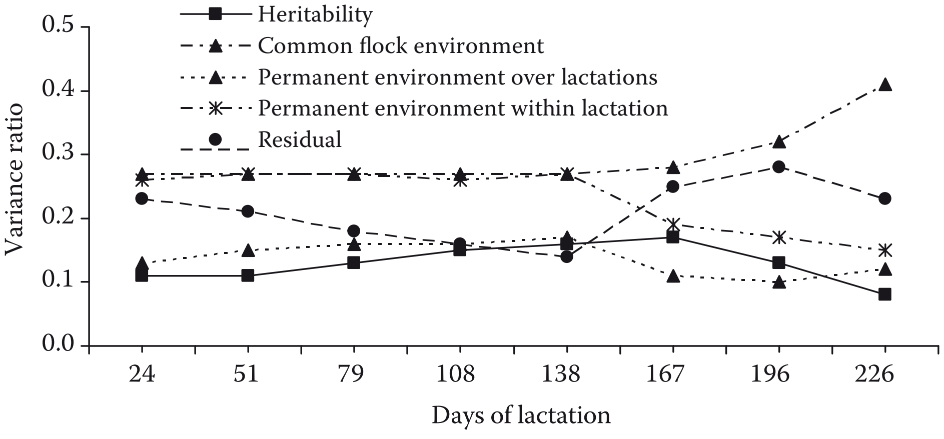

Figure 1. Variance ratios for random effects in daily milk yield

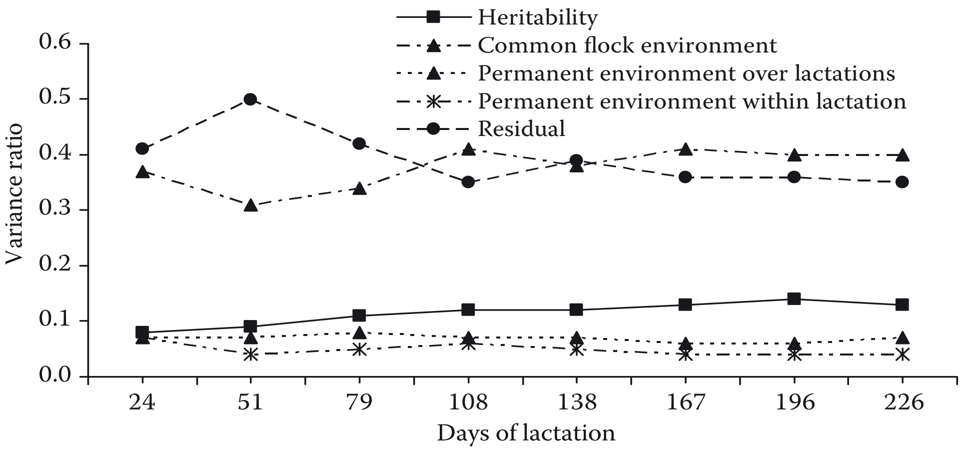

Figure 2. Variance ratios for random effects in fat content

tained quite higher values in East-Friesian sheep, which ranged 0.30–0.70. Also in dairy cows, Druet et al. (2005) estimated higher heritabilities during lactation (0.24–0.60), which were the highest in mid lactation.

In PC, the heritability estimate was 0.15–0.19 during early and mid-lactation, while it rapidly increased toward the end of lactation (to 0.28) (Figure 3). From 0.44 to 0.92 were the heritability estimates in East-Friesian sheep, obtained by Horstick et al. (2002), who treated only the additive genetic effect and permanent environment effect over lactations in the random part of the model. Druet et al. (2005) reported the highest values in dairy cows in the mid lactation (0.51) and the lowest in the early lactation (0.08).

Differences in the heritability estimates in comparison to the literature could be the result of different models used. Besides additive genetic effect, our model contained in its random part the common flock environment effect and two permanent environment effects. Other studies treat the common flock environment effect mainly in the fixed part of the model, while only the permanent environment effect over lactations and additive genetic effect were fitted random (Ligda et al., 2000; Kominakis et al., 2001; Horstick et al., 2002; Cadavez et al., 2011; Zavadilová et al., 2011). The permanent environment effect within lactation partly refers to the animal, thus, the heritability estimates in our study could be lower than in the literature. When the permanent environment effect within lactation is excluded, a part of this effect could be included into the additive genetic component, which is consequently overestimated.

In all three milk traits, common flock environment accounted for the highest variance ratio among genetic and environmental effects. Variance ratio in DMY for the common flock environment effect was about 0.27 during early and mid-lactation, while it rapidly increased thereafter to 0.41 (Figure 1). From 0.31 during early lactation to 0.40 during late lactation was ranging the variance ratio

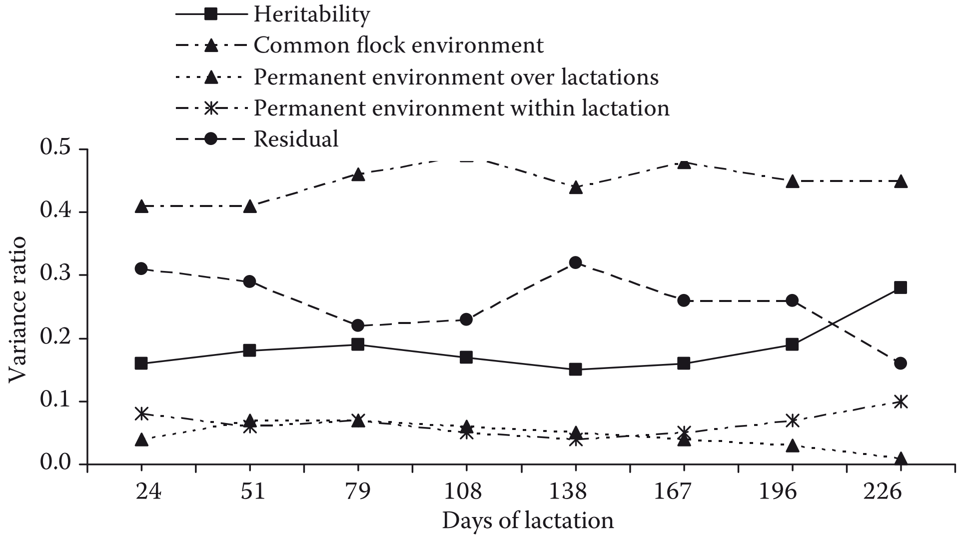

Figure 3. Variance ratios for random effects in protein content

Table 4. Additive genetic correlations between selected test-days for milk traits

	51	79	108	138	167	196	226
Daily milk yield							
24	0.94	0.75	0.55	0.53	0.32	0.27	0.18
51		0.94	0.80	0.79	0.60	0.54	0.48
79			0.96	0.96	0.82	0.77	0.74
108				1.00	0.94	0.90	0.89
138					0.94	0.90	0.90
167						0.99	0.99
196							0.99
Fat content							
24	0.73	0.35	0.18	0.17	0.18	0.23	0.30
51		0.88	0.72	0.70	0.50	0.49	0.60
79			0.95	0.94	0.72	0.69	0.77
108				1.00	0.89	0.85	0.90
138					0.90	0.87	0.91
167						1.00	0.99
196							0.99
Protein content							
24	0.89	0.76	0.62	0.61	0.41	0.37	0.35
51		0.95	0.81	0.79	0.48	0.39	0.34
79			0.94	0.93	0.66	0.55	0.46
108				1.00	0.87	0.98	0.96
138					0.87	0.78	0.65
167						0.98	0.89
196							0.96

for this effect in FC (Figure 2), while the ratio in PC was even higher (from 0.41 to 0.49) (Figure 3), and it was slightly increasing during lactation.

Variance ratio in DMY for the permanent environment effect over lactation was slightly increasing toward the middle of lactation (from 0.13 to 0.17), while it was decreasing thereafter (to 0.12) (Figure 1). A higher variance ratio reported Kominakis et al. (2001) in Sfakia sheep (from 0.34 to 0.76), and also Silvestre et al. (2005) in dairy cows (from 0.50 in the early to 0.60 in the late lactation). Ratio for the permanent environment effect in FC was relatively stable during lactation (0.06–0.08) (Figure 2), while in PC, it was decreasing throughout the entire lactation (from 0.07 to 0.01) (Figure 3).

Permanent environment effect within lactation explained about 26 to 27% of the variability in DMY from early to the mid lactation, but the percentage was decreasing to 15% toward the end of lactation (Figure 1). In FC, the percentage was slightly decreasing during lactation (from 7 to 4%) (Figure 2). An increase of the percentage was found in PC along lactation trajectory (from 4 to 10%) (Figure 3).

The unexplained variance ratio in DMY ranged from 0.14 in mid lactation to 0.28 in late lactation (Figure 1). The ratio in Sfakia sheep was found to be in the wider range (0.18–0.35) (Kominakis et al., 2001). Silvestre et al. (2005) reported higher variance ratio for residual in dairy cows in the early lactation (0.31), which was decreasing toward the end of lactation (0.19). Ratio for FC was decreasing from day 51 (0.50) to day 108 of lactation (0.35), and then it stayed almost the same toward the end of lactation (Figure 2). In PC, variance ratio for the residual was between 0.16 at the end of lactation and 0.32 on day 138 of lactation (Figure 3).

Additive genetic correlations during the selected days of lactation were the highest between the adjacent test-days shown in Table 4 for all three milk traits. Values were close to one. They tended to decrease at the extremes of the lactation trajectory. For DMY, the additive genetic correlations were decreasing faster (to 0.18) compared to FC (to 0.30) and PC (to 0.35). All three milk traits could be regarded as genetically different traits during lactation, since additive genetic correlations between distant test-day records were lower than one. Results confirm that the genetic variability exists and that the use of random regression model is justified. High additive genetic correlations for DMY between adjacent test-days and low between the extremes of the lactation trajectory were found also in Chios sheep by Ligda et al. (2000) and in Sfakia sheep by Kominakis et al. (2001). Banos et al. (2005) did not include pedigree information in their analysis in Chios sheep, but they also obtained similar animal correlation estimates, where daily yields on adjacent test-days were better correlated than yields on test-days further apart. Results in our study were in agreement also with the results in Alpine goats by Breda et al. (2006), Saanen goats by Menezes et al. (2011), and dairy cows by Olori et al. (1999), Kettunen et al. (2000), and Silvestre et al. (2005). Druet et al. (2003) estimated high additive genetic correlations for DMY in cows between adjacent test-days, but correlations between the extreme test-days were higher in comparison to our results on the corresponding interval. Higher additive genetic correlations between the extreme test-days compared to our study were also obtained by Cobuci et al. (2005).

CONCLUSION

Estimation of (co)variance components for DMY, FC, and PC in three dairy sheep breeds (B, IB, and IP) in Slovenia was performed using test-day random regression model. The analysis was done for all three breeds together due to small amount of data in IB and IP breeds. In all three milk traits, the third order of LG was sufficient for the (co)variance component estimation. The existence of 13 to 24% of additive genetic variability for the individual lactation curve depending on milk trait indicates that the use of random regression model is justified for selection on the level and shape of lactation curve in dairy sheep.

The heritability in DMY was the highest in mid lactation and lower during the early and late lactation. In FC, estimates were slightly increasing from the beginning toward the end of lactation. Values estimated in PC were relatively stable in the early and mid-lactation, while they rapidly increased toward the end of lactation. Heritability estimates for the observed milk traits were lower compared to the literature. Differences appeared due to different models used, which mainly include only the additive genetic effect and permanent environment effect over lactations in their random part. The common flock environment effect was treated as fixed in the literature, while the permanent environment effect within lactation was not found in the models. Additive genetic correlations during the selected test-days were close to one between the adjacent ones, and they were decreasing when the interval between test-days was increasing. Since additive genetic correlations between distant test-days were lower than one, DMY, FC, and PC could be regarded as genetically different traits during lactation.

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