

Contents lists available at ScienceDirect

Small Ruminant Research



journal homepage: www.elsevier.com/locate/smallrumres

Estimation of genetic parameters for dairy traits in Pag sheep with single and multi – trait test–day models



M. Špehar^{a,*}, D. Mulc^a, Z. Barać^a, B. Mioč^b, A. Kasap^b

^a Croatian Agricultural Agency, Ilica 101, 10000, Zagreb, Croatia

^b University of Zagreb, Faculty of Agriculture, Department of Animal Science and Technology, Svetošimunska 25, 10000, Zagreb, Croatia

ARTICLEINFO

Keywords: Pag sheep Dairy traits Test–day records Multi– trait model Genetic parameters

ABSTRACT

The objective of the study was to estimate genetic parameters and other estimable sources of phenotypic variability for daily milk yield (DMY), fat content (FC), and protein content (PC) in the Pag sheep breed reared in predominantly outdoor breeding environment. A total of 79,937 phenotypic records from 7132 ewes were used in the analysis. After pruning of the pedigree, a total of 7870 animals were included in the additive relationship matrix. Single - trait (ST) and multi - trait (MT) approaches were applied in the statistical analysis using fixed regression repeatability test-day model. Parity, litter size, season of lambing, flock, stage of lactation, and age at lambing were fitted as fixed effects, while additive genetic, permanent environment, and flock-test-day as random effects. The estimates of heritabilities with MT model were 0.32, 0.19, and 0.40 for DMY, FC, and PC, respectively. Repeatabilities for DMY, FC, and PC were 0.46, 0.21, and 044, respectively. Negative genetic correlations were found evident between DMY and FC (-0.35), and DMY and PC (-0.36), while positive between FC and PC (0.66). The average reliabilities of breeding values (BVs) for DMY, FC, and PC for ewes were 0.771, 0.788, and 0.846, and for rams 0.675, 0.677, and 0.708, respectively. Estimates of genetic parameters and reliabilities of BVs with ST approach were very similar to MT approach as well as ranking of the animals based on BVs. Rank correlations of BVs between examined approaches (ST and MT) for DMY, FC, and PC were 0.995, 0.987, and 0.999 for ewes, and 0.991, 0.984, and 0.998 for rams, respectively. The use of the MT approach provided small gain in accuracy of genetic evaluation, but we encourage its usage wherever possible, particularly taking into account small size of dairy sheep populations and negligible extra computational costs.

1. Introduction

Sheep dairy products (milk, cheese, and curd) are important sources of income in Mediterranean homesteads. In Croatia, sheep milk is mainly produced in the southern Mediterranean part of the country. According to the Annual Report of Croatian Agricultural Agency (CAA, 2017), 7526 dairy ewes have been included in the national selection programme. This dairy sheep population consists of Pag, Istrian, and East Friesian breeds. The Pag sheep breed represents the major part of this population (5156) and is Croatian autochthonous breed primarily used for the milk production (Mioč et al., 2007). Milk is mainly used for cheese production either in small family dairies in a traditional manner or industrially in larger dairies. The Pag cheese is exceptionally priced on domestic and foreign market and therefore more attention has been paid to the quality of the milk (dry matter components) than to the yields. In accordance with the recommendations of the National Breeding and Selection Programme for sheep (Mioč et al., 2011), the total merit index is based on contents of fat (FC) and protein (PC).

The Pag sheep breed is reared in a traditional way which is typically extensive: ewes are fed on karst pastures during the whole year, while supplements, consisting of hay and concentrates (cereals) are occasionally available during winter period (Barać et al., 2008). Seasonal breeding activity of the ewes causes seasonality of milk production (Barać et al., 2008). Lambings start in late November and end in late March or early April while the most of the lambings occurs from December to February. Suckling period lasts around 40 days after lambing and milking period around 160 days (CAA, 2017). In Pag sheep, milking period lasts until May or June. Milk recording system follows the rules, standards, and guidelines of the International Committee for Animal Recording (ICAR, 2011). Test–day records are collected monthly in accordance with the regular alternate scheme (morning / evening system) based on ICAR rules.

The strategies of genetic improvement towards desired goals were defined with a new breeding programme for the sheep populations

* Corresponding author.

https://doi.org/10.1016/j.smallrumres.2019.106029

Received 15 June 2018; Received in revised form 22 November 2019; Accepted 25 November 2019 Available online 27 November 2019

0921-4488/ © 2019 Elsevier B.V. All rights reserved.

E-mail addresses: mspehar@hpa.hr (M. Špehar), dmulc@hpa.hr (D. Mulc), zbarac@hpa.hr (Z. Barać), bmioc@agr.hr (B. Mioč), akasap@agr.hr (A. Kasap).

established in 2011 (Mioč et al., 2011). In accordance with the breeding programme, genetic evaluation for dairy traits in the population of Pag sheep has been conducted based on the BLUP procedure (test-day repeatability animal model - TDM). This model, which considers records within lactations as repeated observations, has been used to estimate genetic parameters in various sheep populations such as French Lacune (Barillet and Boichard, 1994), Spanish Churra (Baro et al., 1994; El-Saied et al., 1998), Latxa and Manchega sheep (Serrano et al., 2001), Slovenian (Brežnik, 1999; Komprej et al., 2009.), Czech dairy breeds (Bauer et al., 2012), Slovakian Tsigai and Improved Walachian (Oravcova et al., 2005; Oravcova, 2014) and Lacune breed (Oravcova, 2007). It has been found that the multi - trait TDM has several advantages over the single - trait TDM: improved precision of the prediction due to reduced prediction error variance (Schaeffer, 1984); reduced selection bias (Pollak et al., 1984); usage of all available data in the prediction of breeding values by accounting for genetic correlations (Wiggans and Godard, 1997).

The non-genetic factors affecting dairy traits in Pag sheep population were examined in some of the our previous studies (Barać et al., 2012a, b; Barać et al., 2013) but without tackling the estimation of the genetic parameters. The objectives of this study were: 1) to examine the effects of various non-genetic factors on dairy traits - daily milk yield (DMY), fat content (FC), and protein content (PC), 2) to estimate their genetic parameters and covariance components with single – trait (ST) and multi – trait (MT) repeatability TDM, and 3) to compare performances of ST and MT models.

2. Material and methods

2.1. Data collection and experimental animals

All phenotypic and pedigree data used in the statistical analyses were provided by the Croatian Agricultural Agency. Phenotypic records were collected in accordance with the ICAR guidelines (ICAR, 2011) using regular alternate AT4 scheme (morning / evening system). A total of 133,051 test–day records with information about stage of lactation, parity, age at lambing, litter size and assignment to a flock were available for the period from March 2003 to December 2016.

Prior to the final inferential statistical analysis, some of the original records were excluded or modified. The following were deleted: records collected after sixth parity, records collected in flocks with less than three animals at the same test-day, records collected before 5th and after 200th day of milking. In order to ensure reasonable age-parity relation, the following records were retained in the data set: lambings within 12-27 months for the first parity, 23-38 months for the second parity, 34-50 months for the third parity, 46-61 months for the fourth parity, 67-78 for the fifth, and from 79 to 90 months for the sixth parity. One may be confused about overlapping these intervals. However, the intention with this step was not to assign ewes to different parity classes based on their age, but to prune the real data set from the ewes (records) that were not a "true representatives" (outliers) of the Pag sheep breed. To be even more specific, it was a "pruning" filter to exclude the ewes from the analysis if their age for the particular parity was below or above acceptable age. Litters with multiple births (twins and triplets) were considered as one group which was hereinafter referred to as 2 + . Season of lambing was defined as month within year and a few seasons with less than 30 records were joined to the previous or next one to improve the frequency of the classes. After pruning of the original data set, a total of 79,937 records obtained from 7132 ewes were retained and used in the statistical genetic analysis.

All animals with records and their relatives tracing back for three generations were included in the pedigree file (Table 1). The total number of animals involved in the pedigree was 7870. Founders accounted for 40.2 % of a total number of animals in the pedigree. Among the non–base animals approximately 85 % of the animals had both parents known, 9 % only sire known and 6 % only dam known. The

Table 1 Pedigree structure.

Item	Ν
Animals with records	7132 4708
- both parents known	3982
- only sire known	446
- only dam known	280
Base animals	3162
Proportion of base animals (%)	40.2
Average number of progenies per sire	10.9
Average number of progenies per dam	1.6
Total number of animals	7870

average number of progeny per sire and dam was 10.9 and 1.6, respectively.

2.2. Statistical analysis

The GLM procedure in the statistical package SAS (SAS Inst. Inc, 2009) based on Least squares method was used to construct the fixed part of the model. In order to be included in the model, the effects had to be statistically significant (p < 0.05) while modelling of the selected variables was conducted by taking into account the proportion of explained variance (R^2). Test–day records for dairy traits ($y_{ijklmn0}$) were modelled using ST and MT repeatability animal models. A ST repeatability animal models for analysed traits are represented with Eq. 1 for DMY and Eq. 2 for FC and PC as follows:

$$y_{ijklmno} = \mu + P_i + L_j + S_k + \sum_{p=1}^{4} b_{ip}t_p + \sum_{p=1}^{4} b_{jp}t_p + b_{i9}(x_{ijklmno} - \bar{x}) + F_l + ftd_m + a_n + p_{in} + e_{ijklmno}$$
(1)

$$y_{ijklmno} = \mu + P_i + L_j + S_k + \sum_{p=1}^{4} b_{ip}t_p + F_l + ftd_m + a_{n+} + p_{in} + e_{ijklmno}$$
(2)

Overall mean (μ), parity (P_i ; i = 1, 2, 3, ..., 6), litter size (L_j ; j = 1, 2), season of lambing (S_k ; k = 1, 2, 3, ..., 56), and flock (F_l ; l = 1, 2, 3, ..., 71) were fitted as fixed class effects. Days in milk ($t_{ijklmno}$) and age at lambing ($x_{ijklmno}$) were fitted as covariates. The effect of days in milk was modelled using the Ali–Schaeffer lactation curve with four regression coefficients (Ali and Schaeffer, 1987). The curve was nested within parity and litter size for DMY and within parity for FC and PC. A transformation of the days in milk (Eq. 3) was done with the constant of 150 days representing the standardized length of the milking period under the Pag sheep production system.

$$t_{1} = t_{ijklmno}/150, t_{2} = (t_{ijklmno}/150)^{2}, t_{3} = \ln(150/t_{ijklmno}), t_{4}$$
$$= \left(\ln\left(\frac{150}{t_{ijklmno}}\right)\right)^{2}$$
(3)

Age at lambing was modelled as linear regression nested within parity in the model for DMY. For FC and PC the effect of age at lambing was not included in the model.

The random part of the model was the same for all studied traits and included flock–test–day (ftd_m ; m=1, 2, 3, ..., 2533), permanent environmental effect within lactations (p_{in} ; in=1, 2, 3, ..., 20,634), direct additive genetic effect (a_n ; n=1, 2, 3, ..., 7870), and residual ($e_{ijklmno}$). The same models were used in MT analysis.

The matrix notation of the model is as follows:

$$y = X\mathbf{b} + \mathbf{Z}_{c}\mathbf{c} + \mathbf{Z}_{p}\mathbf{p} + \mathbf{Z}_{a}\mathbf{a} + \mathbf{e}$$
(4)

where: **y** is a vector of the phenotypic observations for the examined dairy traits, **X** is an incidence matrix for the fixed effects; $\mathbf{Z}_{c}, \mathbf{Z}_{p}$, and \mathbf{Z}_{a} , are incidence matrices for the flock-test-day, permanent

environmental, and additive genetic effects, respectively; b is a vector of unknown fixed effects; c, p, and a, are vectors of unknown random effects; e is a vector of residuals. The variance structure of random effects is: $Var[c] = I_c \sigma_c^2$, $Var[p] = I_p \sigma_p^2$, $Var[e] = I_e \sigma_e^2$, where I is an identity matrix for individual random effects and residual. $Var[\mathbf{a}] = \mathbf{A}\sigma_a^2$, where **A** is an additive genetic relationship matrix, and $\operatorname{Var}[\mathbf{y}] = \mathbf{Z}_{\mathbf{a}} \mathbf{A} \mathbf{Z}'_{\mathbf{a}} \sigma_{\mathbf{a}}^{2} + \mathbf{Z}_{\mathbf{c}} \mathbf{Z}'_{\mathbf{c}} \sigma_{\mathbf{c}}^{2} + \mathbf{Z}_{\mathbf{p}} \mathbf{Z}'_{\mathbf{p}} \sigma_{\mathbf{p}}^{2} + \mathbf{I}_{\mathbf{e}} \sigma_{\mathbf{e}}^{2}.$ The assumption was that residuals, as well as trivial random effects were not correlated. Genetic covariances among animals were obtained in the numerator relationship matrix A.

The same models were used for estimation of covariance components in the MT analysis. Since there were no missing values for any of the traits examined, equal design matrices for all traits were used in the analysis. Covariance structure for the random effects is represented in the animal model as shown in Eq. 5. where covariances among traits were represented by matrices C₀, P₀ and G₀ for flock-test-day, permanent environmental, and additive genetic effects, respectively, \mathbf{R}_0 is a residual covariance matrix between traits of order three, I_c , I_n , and I_e , are identity matrices for individual random effects and residual, and A is a numerator relationship matrix. Symbol \otimes is a direct or Kronecker product.

$$Var \begin{bmatrix} c \\ p \\ a \\ e \end{bmatrix} = \begin{bmatrix} C & 0 & 0 & 0 \\ 0 & P & 0 & 0 \\ 0 & 0 & G & 0 \\ 0 & 0 & 0 & R \end{bmatrix} = \begin{bmatrix} I_c \otimes C_0 & 0 & 0 & 0 \\ 0 & I_p \otimes P_0 & 0 & 0 \\ 0 & 0 & A \otimes G_0 0 & 0 \\ 0 & 0 & 0 & I_e \otimes R_0 \end{bmatrix}$$
(5)

Covariance components were estimated by Residual Maximum Likelihood Method (REML) using analytical gradients in the VCE - 6 program package (Groeneveld et al., 2008). The estimated genetic parameters were used to predict breeding values (BVs) of the animals in the pedigree. The theoretical reliabilities of the estimated BVs were calculated from the inverse of the left hand side of the BLUP mixed model equation (a.k.a. coefficient matrix) as explained in detail for single - trait and multi - trait models by Mrode (2014). The formula used in ST analysis was $r^2 = 1 - (PEV/\sigma_a^2)$, where prediction error variance (PEV) represents the fraction of additive genetic variance not accounted for by the prediction. $PEV = var(a - \hat{a}) = C^{22}\sigma_{e}^{2}$, where C^{22} is lower right part of inverted coefficient matrix (generalised inverse). The reliability of animal *i* for trait $j(r_{ii}^2)$ in the MT analysis was calculated as $r_{ij}^2 = (g_{ij} - PEV_{ij})/g_{ji}$, where PEV_{ij} is the diagonal element of the coefficient matrix pertaining to animal *i* and trait *j*. Similarity of repeated measurements within lactation (repeatability - r) was calculated as $(\sigma_a^2 + \sigma_p^2)/(\sigma_a^2 + \sigma_p^2 + \sigma_c^2 + \sigma_e^2)$, with σ_a^2 , σ_p^2 , σ_c^2 , and σ_e^2 representing the additive genetic, permanent environmental, flock-test-day, and residual variances, respectively.

3. Results

Descriptive statistics for dairy traits is given in Table 2. The average values of DMY, FC, and PC were 0.799 kg, 7.39 %, and 5.95 %, respectively. Among the traits examined, FC was the most variable trait in the analysis.

The Least squares means estimated by the above discussed model are presented in Table 3. The estimated differences across the parities were negligible for all the traits examined which was also the case for the effect of the litter size. However, these differences were statistically

Table 2

Descriptive statistics for dairy traits.

Trait	Ν	Mean	SD	MIN	MAX
Daily milk yield (kg)	79,931	0.799	0.340	0.207	2.486
Fat content (%)	79,903	7.39	1.35	2.09	14.94
Protein content (%)	79,903	5.95	0.57	1.58	9.00

Table 3

least squares mean	(LSM)	and SE	(standard	error)	for	dairy	traits.	

Effect/Trait	Daily milk	yield (kg)	Fat con	Fat content (%)		content (%)
Parity	LSM	SE	LSM	SE	LSM	SE
1	0.785	0.009	7.37	0.02	5.94	0.01
2	0.849	0.009	7.37	0.02	5.97	0.01
3	0.796	0.008	7.44	0.02	6.01	0.01
4	0.790	0.009	7.52	0.02	6.04	0.01
5	0.817	0.009	7.56	0.02	6.06	0.01
6	0.868	0.009	7.63	0.02	6.08	0.01
Litter size						
1	0.797	0.005	7.48	0.01	5.99	0.01
2+	0.839	0.009	7.48	0.03	6.05	0.01

Table 4

Estimates of parameters (\pm standard errors) for dairy traits based on single trait and multi-trait analysis.

Item	DMY	FC	PC
Single trait			
c^2	0.27 ± 0.01	0.44 ± 0.01	0.20 ± 0.01
p^2	0.14 ± 0.003	0.02 ± 0.002	0.05 ± 0.002
h^2	0.31 ± 0.01	0.19 ± 0.01	0.40 ± 0.01
e^2	0.28 ± 0.004	0.35 ± 0.01	0.36 ± 0.004
r	0.45	0.21	0.45
Multi-trait			
c ²	0.26 ± 0.01	0.43 ± 0.01	0.20 ± 0.004
p^2	0.14 ± 0.002	0.02 ± 0.001	0.04 ± 0.001
h^2	0.32 ± 0.003	0.19 ± 0.003	0.40 ± 0.004
e^2	0.27 ± 0.002	0.36 ± 0.004	0.36 ± 0.004
r	0.46	0.21	0.44

*DMY – daily milk yield; FC – fat content; PC – protein content; c^2 – ratio for flock-test-day; p^2 - ratio for permanent environmental effect; h^2 - heritability; e^2 – ratio for residual; r –repeatability.

significant due to large sample size and therefore were retained in the model used in the further analysis (estimation of genetic parameters and prediction of breeding values). Prior to inclusion of random effects in the model, the proportions of explained phenotypic variance were 26.4 %, 17.9 %, and 21.4 % for DMY, FC, and PC, respectively.

Results pertaining to the "random variability" obtained by ST test-day model are presented in the Table 4. In all traits examined, a large proportion of variability (above 0.20) was explained by the flock-test-day. Among the analysed traits, the FC was the most influenced by this effect (0.44). Permanent environmental effect was notably lower and accounted between 0.02 (FC) and 0.14 (DMY) of phenotypic variability. The estimates of heritability (additive genetic effect) were moderate as follows: 0.40 (PC), 0.31 (DMY), and 0.19 (FC). The larger repeatability was estimated for DMY (0.45) and PC (0.45), and lower for FC (0.21). The estimates of residual variance for DMY, FC, and PC were 0.28, 0.35, and 0.36, respectively. Low standard errors imply sufficient level of accuracy of the estimates.

Results obtained by MT analysis are presented in the Tables 4 and 5. Parameters obtained by MT negligibly differed from those obtained by ST analysis. The estimates of the flock-test-day effect were 0.26, 0.43, and 0.20 for DMY, FC, and PC, respectively. The estimates of the permanent environmental effect were 0.14, 0.02, and 0.04 for DMY, FC, and PC, respectively. The estimates of the additive genetic effects were 0.32, 0.19, and 0.40 for DMY, FC, and PC, respectively. The repeatability coefficients were moderate and ranged from 0.21 (FC) to 0.46 (DMY). The estimated correlations were positive between FC and PC and negative between DMY and FC, and DMY and PC for all the examined random effects. Moderate correlations among flock-test-day effect were obtained between FC and PC (0.25), and between DMY and PC (-0.17), and high between DMY and FC (-0.68). Moderate

Table 5

Genetic correlations for dairy traits.

Item	FC	PC
Flock-test-day DMY FC	-0.68 ± 0.01	-0.17 ± 0.01 0.25 ± 0.01
Permanent environmenta DMY FC	al effect - 0.25 ± 0.02	-0.21 ± 0.02 0.49 ± 0.02
Additive genetic effect DMY FC	-0.35 ± 0.01	-0.36 ± 0.01 0.66 ± 0.01
Residual DMY FC	-0.19 ± 0.004	-0.21 ± 0.004 0.33 ± 0.003

*DMY – daily milk yield; FC – fat content; PC – protein content.

correlations among permanent environmental effects were obtained between DMY and FC was (-0.25), and between DMY and PC (-0.21), while large between FC and PC (0.49). Additive genetic correlations between DMY and FC, and DMY and PC were -0.35 and -0.36, respectively. The estimated additive genetic correlation between FC and PC was 0.66.

3.1. Single and multiple trait comparison

Comparison of conducted ST and MT analysis was performed by taking into account reliabilities of predicted breeding values (BVs) and rank correlations of animals (Table 6). Two subsets (categories) of animals with different sources of information contributing to the BVs were considered: 1) 7132 phenotyped ewes with three available sources of information (parent average, yield deviation and progeny contribution), and 2) 399 rams with available parent average and progeny contribution.

The average reliabilities of ewes' BVs for DMY, FC, and PC with ST approach were 0.754, 0.770, and 0.834, and with the MT approach 0.771, 0.788, and 0.846, respectively. The average reliabilities of rams' BVs for DMY, FC, and PC with ST approach were 0.665, 0.669, and 0.703, and with the MT approach 0.675, 0.677, and 0.708, respectively. The reliabilities of estimated BVs were slightly higher with MT approach in all the investigated scenarios. Rank correlations of BVs between examined approaches (ST and MT) for DMY, FC, and PC were 0.995, 0.987, and 0.999 for ewes, and 0.991, 0.984, and 0.998 for rams, respectively.

4. Discussion

DMY (0.799 kg) of the Pag sheep breed (Table 2) was similar to the

Table 6

Comparison of reliability based on single and multi-trait approach in genetic evaluations of ewes (N = 7132) and rams (N = 399) and rank correlations of predicted breeding values.

Category	Item	DMY (kg)	FC (%)	PC (%)		
Ewes	Reliability (mean and standard deviation)					
	Single-trait	0.754 (0.105)	0.770 (0.108)	0.834 (0.085)		
	Multi-trait	0.771 (0.099)	0.788 (0.098)	0.846 (0.081)		
	Rank correlation	0.995	0.987	0.999		
Rams	Reliability (mean and standard deviation)					
	Single-trait	0.665 (0.141)	0.669 (0.140)	0.703 (0.134)		
	Multi-trait	0.675 (0.139)	0.677 (0.138)	0.708 (0.133)		
	Rank correlation	0.991	0.984	0.998		

*DMY - daily milk yield; FC - fat content; PC - protein content.

reported values for some dual purpose breeds and notably lower than for typical dairy breeds. For example, DMY of Tsigai and Improved Valachian were 0.63 kg and 0.62 kg, respectively (Oravcova et al., 2005). Slovenian Istrian Pramenka produced daily 0.73 kg of milk (Komprej et al., 2009), while Churra between 0.85 kg and 0.95 kg (Barro et al., 1994; Gonzalo et al., 1994; El-Saied et al., 1998). Slightly higher DMY was reported by Kasap et al. (2019) for Croatian Istrian breed (1.06 kg) and by Komprej et al. (2009) for local Bovec (1.09 kg) and Improved Bovec breed (1.10 kg). Considerably higher DMYs were reported for typical dairy breeds such as East Friesian (2.33 kg, Hamann et al., 2004), Assaf (1.93 kg, Pollot and Gootwine, 2004), and Lacaune (1.64 kg, Barillet et al., 2001). Pag sheep had higher FC (7.39 %) than Boyec (6.59 %), Improved Boyec (6.22 %), Istrian Pramenka (7.20 %), and Valle del Belice breed (6.80 %, Riggio et al., 2007). PC (5.95 %) was also higher than in previously reported studies. PC for Bovec, Improved Bovec, Istrian Pramenka, and Valle del Belice breed were 5.53 %, 5.33 %, 5.63 %, and 5.48 %, respectively. In addition to the so-called "dilution effect", which stands for a reduction in milk fat and protein when milk production increases (Nudda et al., 2004), lower FC and PC in their reports probably arose due to different dietary regime, and at least to some degree due to different genetic potential for synthesis of the fat and protein.

In the current study, random phenotypic variation was modelled by commonly used effects in the studies orientated towards estimation of genetic parameters for dairy traits (DMY, FC, and PC). The effect of flock-test-day was fitted in the random part of the model which was in accordance with statistical approach of some previous studies on this issue (Brežnik, 1999; Komprej et al., 2003; Oravcova et al., 2005; Oravcova, 2014). However, there were also some studies where the effect was included in the fixed part of the model (Baro et al., 1994; El-Saied et al., 1998; Serrano et al., 2001). The heritabilities estimated for DMY of 0.31 (ST) and 0.32 (MT) were close to those determined by Ligda et al. (2002) in Chios breed and Baro et al. (1994) in Churra breed (0.34). On the other side, they were considerably higher than those determined by El-Saied et al. (1998) in Churra (0.18), Horstick (2001) in East Friesian (0.17), Brežnik (1999) in Bovec (0.16), Barillet and Boichard (1994) in Lacaune (0.25), and Komprej et al. (2009) in joint analysis of three Slovenian dairy breeds (0.11). Estimated heritability for FC in various sheep breeds ranged from 0.06 in Improved Valachian and Churra breed (Oravcova et al., 2005; Othmane et al., 2002) to 0.24 in Lacune breed (Barillet and Boichard, 1994). The latter is in agreement with the results obtained in this study. Higher heritabilities for FC (from 0.32 to 0.52) were reported for Sfakia breed by Volanis et al. (2002) by test-day. The heritability estimate for PC (0.40) was within the range reported for dairy ewes. Heritability estimates for PC ranged from 0.07 (Oravcova et al., 2005) to 0.08 (Komprej et al., 2009) in Slovenian dairy breeds. Higher estimate (0.20) was reported for East Friesian ewes (Hamman et al., 2004) and Volanis et al. (2002) in Sfakia breed (to 0.44 to 0.55 by test-day). These inconsistences in heritability estimates between the studies arise primarily due to different structure of analysed data (e.g. genetic connectedness among contemporary groups) and different analytical approaches ("pruning" of the pedigrees, construction of statistical models, etc.). The repeatabilities for DMY (0.46) and PC (0.44) were within the range of estimates reported for different sheep populations (Carta et al., 1995; El-Saied et al., 1998; Othmane et al., 2002; Serrano et al., 2001; Riggio et al., 2007). The repeatability for FC was notably lower and in general agreement with those reported by Carta et al. (1995); Gonzalo et al. (1994), and Riggio et al. (2007). This is not surprising by taking into account the fact that FC is the most variable component of the milk and exceptionally prone to changes in diet.

One of the main advantages of MT over ST approach is higher accuracy of evaluations (Mrode, 2014). The measurements of correlated traits help to predict BVs with notably higher accuracy when records on some of the traits under consideration are missing, but also to some extent in the "full-balanced" data set. The gain in accuracy depends on the absolute difference between the genetic and residual correlations between the traits, the larger the difference, the greater the gain (Schaeffer, 1984). An additional benefit of MT BLUP model is that it allows BVs to be predicted even when records of some traits are missing. However, using information from associated traits is not as good as measuring the trait directly but on the whole it is beneficial (Simm, 1998).

Comparison of ST and MT analysis revealed that reliabilities of predicted BVs were slightly higher with MT approach in all the investigated scenarios (considering trait and category of the animals in the pedigree). According to the discrepancy detected for the reliabilities among the categories, ewes (BVs) were found to be more sensitive to the method of genetic evaluation than rams. Regarding the traits examined, the largest discrepancy within subpopulation of the ewes was determined for FC (0.018) which goes in line with theoretical expectations. To be more specific, the traits with lower heritabilities gain in their estimates when analysed in the multivariate analysis together with the traits having higher heritabilities. The gain in accuracy is dependent on the absolute difference between genetic and residual correlations between the traits, as stated by Thompson and Meyer (1986): the larger the differences, the greater the gain in accuracy. High rank correlations revealed great similarity in genetic evaluation of the animals based on BVs obtained with MT and ST approach. Regardless of the category, rank of the animals based on predicted breeding values changed only negligibly with different analytical approaches. However, the largest re-ranking of the animals was determined for FC in both categories (0.987 in ewes and 0.984 in rams), which is consistent with the previous explanation. Boosted computational power of modern devices has overcome the major obstacles for simultaneous solving of numerous equations, at least when confronted with relatively small scale data sets as predominantly present in many dairy sheep populations, so we hereby encourage usage of MT models.

Flock-test-day effect considers all environmental factors specific to each test-day as well as technologies of breeding and feeding within flock (Swalve, 1995). The flock-test-day effect explained the relatively large portion of the phenotypic variance (Table 3). The estimated values for DMY, FC, and PC were 0.26, 0.20, and 0.43, respectively. The estimates were considerably lower than those reported by (Oravcova et al., 2005) for Improved Valachian sheep for DMY (0.41) and FC (0.48) while quite similar for PC (0.46). On the other hand, in Tsigai breed, estimate for FC (0.39) was similar to that obtained in our study, while those for DMY (0.34) and PC (0.39) were notably higher. Komprej et al. (2009) reported practically the same value of variance ratio for DMY (0.27) and higher values for FC (0.43) and PC (0.57) in Slovenian dairy breeds using flock-month as contemporary effect.

It is believed that permanent environmental effect captures phenotypic variability due to animals' physical state within particular lactation (condition, health status, nutrition level). The results obtained (Table 3) are in agreement with those of Oravcova et al. (2005), especially those reported for the Improved Valachian breed. They published variance ratio for the permanent environmental effect of 0.14 and 0.11 for DMY, 0.02 and 0.04 for FC, and 0.04 and 0.04 for PC in the Improved Valachian and Tsigai breed, respectively. Variance ratios in this study were also similar to those obtained by Komprej et al. (2009) for DMY (0.13), FC (0.02), and PC (0.01).

Additive genetic correlations were negative between DMY and FC, and DMY and PC, but positive between FC and PC (Table 5) which implicates negative correlated response to selection for FC and PC if selection is directed exclusively on milk yield and vice versa. Carefully designed long-term breeding plan is required to maintain satisfactory quality of milk while increasing yield from generation to generation. The possibilities to achieve this goal are via tandem selection, independent culling level approach, and total merit index. In Croatia, the emphasis is given towards milk quality since practically all the milk is processed into cheese. The total merit index is constructed from the EBVs for FC and PC in ratio 1:2 as proposed by the national selection programme (Mioč et al., 2011). However, by taking into account previously discussed genetic correlations, one must be aware that such approach in long-term practice would probably lead to a decreased milk yield. In any breeding program, monitoring the genetic progress is important step of verifying if the breeding goals are achieved. The best way to achieve this goal is to analyze the genetic gains by visualizing the average breeding values of the traits by generation, or by the year (estimation of the genetic trends). Direction and speed of the genetic change in each trait should reveal success/failure of selected approach and provide scientifically based information for making selection decisions.

The additive genetic correlations in this study were in line with estimates between DMY and FC (-0.35) and FC and PC (0.56) reported by Ligda et al. (2002) for the Chios breed. However, they estimated lower genetic correlation between DMY and PC (-0.10). Additive genetic correlations between DMY and FC (-0.36), DMY and PC (-0.37), and between FC and PC (0.67) in the study of Komprej et al. (2009) in Slovenian dairy breeds were also quite similar to our results. In earlier research conducted on the same population of Slovenian dairy breeds (Brežnik et al., 1999), lower additive genetic correlations were reported between DMY and FC (-0.29), DMY and PC (-0.31), and FC and PC (0.63). Oravcova et al. (2005) also published lower additive genetic correlations between DMY and FC (-0.29 and -0.23), DMY and PC (-0.30 and -0.27), and FC and PC (0.57 to 0.58) for the Improved Walachian and Tsigai breeds, respectively. On the other hand, quite different additive genetic correlations were obtained between DMY and FC (0.08), DMY and PC (-0.13), and FC and PC (0.23) in the East Friesian sheep (Hamann et al., 2004).

The correlations for other random effects between dairy traits followed the pattern similar to the additive genetic correlations (Table 5). The correlations for flock-test-day between DMY and FC, DMY and PC, and FC and PC were –0.68, –0.17, and 0.25, respectively. Lower correlations for flock-test-day were estimated in the study of Oravcova et al. (2005) between DMY and FC for Improved Valachian and Tsigai breeds (–0.31 and –0.23). In their study, correlations between DMY and PC were close to zero (–0.01 and 0.05), while between FC and PC moderately positive (0.39 and 0.25). Komprej et al. (2009) also estimated lower correlations for flock-test-month effect between DMY and FC (–0.13) and between DMY and PC (–0.06) in Slovenian dairy breeds. They reported correlation between FC and PC (0.61) quite similar to correlation determined in this study.

The estimates for permanent environmental effect were similar to those estimated by Komprej et al. (2009) who reported correlation of -0.25 between DMY and FC, and DMY and PC, and 0.49 between FC and PC. In the study of Oravcova et al. (2005), notably lower correlations were found between DMY and FC (0.01 and 0.05) and DMY and PC (-0.08 and -0.13), and only slightly lower between FC and PC (0.45 and 0.36), respectively.

5. Conclusions

The study revealed magnitude of the parameters examined in semiintensive dairy orientated sheep facilities in closed insular environment. The generalization of estimates is always critical and "slippery" issue, especially in studies based on field and unbalanced data as usually presented in quantitative genetic studies. However, preciously performed statistical analysis on large amount of data makes us believe that our results approximately reflect "true" parameters in this population. The compliance of the results with previous reports on traits being examined suggests similarity in their genetic architecture and inheritance patterns between numerous dairy sheep populations (breeds). The results could be beneficial in breeding and business decisions, not only in this breed, but also in flocks of other breeds with similar genetic potential for milk production. The results suggest relatively small contribution of multi – trait approach in term of accuracy which was primarily due to completeness of the phenotypic data under consideration. However, an extra value of multi – trait approach can be reflected via unravelling genetic correlations among traits which is in turn beneficial for predicting correlated response to selection. By taking into account the fact that multi – trait models nowadays does not require serious computational extra costs, at least when considering relatively small populations as predominantly present in sheep breeding sector in Europe, we hereby encourage their usage in studies and routine BLUP based genetic evaluation systems.

Declaration of Competing Interest

None.

References

- Ali, T.E., Schaeffer, L.R., 1987. Accounting for covariances among test day milk yields in dairy cows. Can. J. Anim. Sci. 67, 637–644. https://doi.org/10.4141/cjas87-067.
- Barać, Z., Mioč, B., Havranek, J., Samaržija, D., 2008. Paška ovca-hrvatska izvorna pasmina. Matica Hrvatske Novalja i grad Novalja, Novalja.
- Barać, Z., Špehar, M., Mioč, B., 2012a. Utjecaj redosljeda i stadija laktacije, veličine legla, sezone janjenja i stada na neke odlike mliječnosti paške ovce. Stočarstvo 66, 3–19.
- Barać, Z., Mioč, B., Špehar, M., 2012b. The effect of breeding area, stage of lactation and herd on milk yield traits of Pag sheep. Mljekarstvo 62, 35–42.Barać, Z., Mioč, B., Špehar, M., 2013. The effect of lactation stage and parity, lambing
- season, and herd on fat and protein content in Pag sheep. Mljekarstvo 63, 81–90.
- Barillet, F., Boichard, D., 1994. Use of first lactation testday data for genetic evaluation of the Lacaune dairy sheep. In: Proceedings of the 5th World Congress on Genetics Applied to Livestock Production. Guelph, Canada, 18. pp. 111–114.
- Barillet, F., Marie, C., Jacquin, M., Lagriffoul, G., Astruc, J.M., 2001. The French Lacaune dairy sheep breed: use in France and abroad in the last 40 years. Livest. Prod. Sci. 71, 17–29. https://doi.org/10.1016/S0301-6226(01)00237-8.
- Baro, J.A., Carriedo, J.A., San Primitivo, F., 1994. Genetic parameters of test day measures for somatic cell count, milk yield, and protein percentage of milking ewes. J. Dairy Sci. 77, 2658–2662. https://doi.org/10.3168/ids.S0022-0302(94)77207-6.
- Bauer, J., Milerski, M., Přibyl, J., Vostry, L., 2012. Estimation of genetic parameters and evaluation of test-day milk production in sheep. Czech J. Anim. Sci. 57 (11), 522–528. https://doi.org/10.17221/6385-CJAS.
- Brežnik, S., 1999. Estimation of dispersion parameters of sheep milk traits. Master of Science Thesis. University of Ljubljana, Biotechnical Faculty, Zootechnical Department, Domžale, Slovenia, pp. 73.
- CAA (Croatian Agricultural Agency), 2017. Annual Report for 2016. Sheep and Goats. Croatian Agricultural Agency, Križevci.
- Carta, A., Sanna, S.R., Casu, S., 1995. Estimating lactation curves and seasonal effects for milk, fat and protein in Sarda dairy sheep with a test day model. Livest. Prod. Sci. 44, 37–44.
- El-Saied, U.M., Carriedo, J.A., Baro, J.A., De La Fuente, L.F., San Primitivo, F., 1998. Genetic and environmental estimations for test-day and standardized milk yield of dairy sheep. Small Rumin. Res. 27, 209–215. https://doi.org/10.1016/S0921-4488(97)00061-8.
- Gonzalo, C., Carriedo, J.A., Baro, J.A., San Primitivo, F., 1994. Factors influencing variation of test day milk yield, somatic cell count, fat and protein in dairy sheep. J. Dairy Sci. 77, 1537–1542. https://doi.org/10.3168/jds.S0022-0302(94)77094-6.
- Groeneveld, E., Kovač, M., Mielenz, N., 2008. VCE User's Guide and Reference Manual, Version 6.0.
- Hamann, H., Horstick, A., Wessels, A., Distl, O., 2004. Estimation of genetic parameters for test day milk production, somatic cell count and litter size at birth in East Friesian ewes. Livest. Prod. Sci. 87, 153–160. https://doi.org/10.1016/j.livprodsci.2003.09. 015.
- Horstick, A., 2001. Genetic analysis of milk performance and linear type traits in East Friesian and Black and Brown milk sheep. Dissertation. Tierärztlich Hochschule, Hannover.
- ICAR (International Committee for Animal Recording), 2011. Guidelines Approved by the

General Assembly Held in Riga, Latvia, on 31 May to 4 June 2010, Roma.

- Kasap, A., Špehar, M., Držaić, V., Mulc, D., Barać, Z., Antunović, A., Mioč, B., 2019. Impact of parity and litter size on dairy traits in Istrian ewes. J. Cent. Eur. Agric. 20 (2), 556–562 DOI: /10.5513/JCEA01/20.2.2169.
- Komprej, A., Gorjanc, G., Kompan, D., Kovač, M., 2009. Covariance components by a repeatability model in Slovenian dairy sheep using test-day records. Czech J. Anim. Sci. 9, 426–434. https://doi.org/10.17221/1680-CJAS.
- Ligda, C., Mavrogenis, A., Georgoudis, A., 2002. Estimates of genetic parameters for test day somatic cell counts in chios dairy sheep. In: Proceedings of the Seventh World Congress on Genetics Appl. to Livest. Prod. Montpellier, France, CD-ROM Communication No. 09-21. INRA, Castanet-Tolosan.
- Mioč, B., Barać, Z., Pavić, V., Prpić, Z., Vnučec, I., 2007. Odlike vanjštine i proizvodnosti nekih hrvatskih izvornih pasmina ovaca. In: Conference on Native Breeds and Varieties as Part of Natural and Cultural Heritage. Šibenik, November 13th – 16th, 2007, State Institute for Nature Protection, Zagreb, Book of Abstracts. pp. 190–194.
- Mioč, B., Pavić, V., Barać, Z., Vnučec, I., Prpić, Z., Mulc, D., Špehar, M., 2011. Program uzgoja ovaca u Republici Hrvatskoj. (National Breeding and Selection Programme for Sheep). Hrvatski savez uzgajivača ovaca i koza, Zagreb.
- Mrode, R.A., 2014. Linear Models for the Prediction of Animal Breeding Values, third ed. CABI Oxfordshire, UK.
- Nudda, A., Battacone, G., Bencini, R., Pulina, G., 2004. Nutrition and milk quality. In: Pulina, G. (Ed.), Dairy Sheep Nutrition. CABI Publishing, Wallingford, Oxfordshire, UK, pp. 129–149. https://doi.org/10.1079/9780851996813.0129.
- Pollot, G.E., Gootwine, E., 2004. Reproductive performance and milk production of Assaf sheep in an intensive management system. J. Dairy Sci. 87, 3690–3703. https://doi. org/10.3168/jds.S0022-0302(04)73508-0.
- Riggio, V., Finocchiaro, R., Van Kaam, J.B.C.H.M., Portolano, B., Bovenhuis, H., 2007. Genetic parameters for milk somatic cell score and relationships with production traits in primiparous dairy sheep. J. Dairy Sci. 90, 1998–2003. https://doi.org/10. 3168/jds.2006-309.
- Oravcova, M., Groeneveld, E., Kovač, M., Peškovičova, D., Margetin, M., 2005. Estimation of genetic and environmental parameters of milk production traits in Slovak purebred sheep using test-day model. Small Rumin. Res. 56, 113–120. https://doi.org/10. 1016/j.smallrumres.2004.03.002.
- Oravcova, M., 2007. Genetic evaluation for milk production traits in Slovakian Lacaune sheep. Slovak J. Anim. Sci. 40 (4), 172–179.
- Oravcova, M., 2014. Variance components and genetic parameters estimated for daily milk yield in individual months of lactation: the case of Tsigai sheep. Vet. Med. Zoot. 68 (90), 55–59.
- Othmane, M.H., De La Fuente, L.F., Carriedo, J.A., San Primitivo, F., 2002. Heritability and genetic correlations of test day milk yield and composition, individual laboratory cheese yield, and somatic cell count for dairy ewes. J. Dairy Sci. 85, 2692–2698. https://doi.org/10.3168/ids.S0022-0302(02)74355-5.
- Pollak, E.J., Van der Werf, J., Quaas, R.L., 1984. Selection bias and multiple trait evaluation. J. Dairy Sci. 67, 1590–1595. https://doi.org/10.3168/jds.S0022-0302(84) 81481-2.
- SAS Inst. Inc, 2009. SAS/STAT® 9.2 User's Guide, Cary. SAS Institute Inc., NC.
- Schaeffer, L.R., 1984. Sire and cow evaluation under multiple trait models. J. Dairy Sci. 67, 1567–1580. https://doi.org/10.3168/jds.S0022-0302(84)81479-4.
- Serrano, M., Ugarte, E., Jurado, J.J., Perez-Guzman, M.D., Legara, A., 2001. Test day models and genetic parameters in Latxa and Manchega dairy ewes. Livest. Prod. Sci. 67, 253–264. https://doi.org/10.1016/S0301-6226(00)00203-7.
- Simm, G., 1998. Genetic Improvement of Cattle and Sheep. Farming Press First Published 1998, Reprinted with Amendments 2000 Ipswich, England (1998).
- Swalve, H.H., 1995. The effect of test day models on the estimation of genetic parameters and breeding values for dairy yield traits. J. Dairy Sci. 78, 929–938. https://doi.org/ 10.3168/jds.S0022-0302(95)76708-X.
- Volanis, M., Kominakis, A., Rogdakis, E., 2002. Genetic analysis of udder score and milk traits in test day records of Sfakia dairy ewes. Arch. Tierzucht 45 (1), 69–77. https:// doi.org/10.5194/aab-45-69-2002.
- Thompson, R., Meyer, K., 1986. A review of theoretical aspects in the estimation of breeding values for multi-trait selection. Livest. Prod. Sci. 15, 299–313. https://doi. org/10.1016/0301-6226(86)90071-0.
- Wiggans, G.R., Godard, M.E., 1997. A test day model for genetic evaluation of yield traits: possible benefits and an approach for implementation. J. Dairy Sci. 79 (1), 144.