VARIANCE COMPONENTS AND GENETIC PARAMETERS ESTIMATED FOR DAILY MILK YIELD IN INDIVIDUAL MONTHS OF LACTATION: THE CASE OF TSIGAI SHEEP

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Abstract. The objective of this study was to assess variance components and genetic parameters for daily milk yield of Tsigai sheep based on test day records. First, heritability estimates and genetic correlations were estimated using multivariate animal models in which milk yield in individual months of lactation was treated as a different trait. For comparison purposes, univariate animal models with milk yield treated as repeated measures of the same trait were employed. In both analyses, test day records between the second and the seventh month of lactation were considered. The fixed effects were lactation number, litter size and days in milk. All these effects were modelled as linear regressions. The random effects were animal genetic effect and permanent environmental effect of ewe. The effect of flock-year-month of test day measurement was fitted either as a fixed (FYM) or random (*fym*) effect. The number of test day records in the second, third, fourth, fifth, sixth and the seventh month of lactation was 9,943, 40,422, 43,982, 41,687, 32,158 and 3,878, respectively. In total, 172,070 test day records were included. Milk yield heritabilities in individual months of lactation were estimated between 0.11 and 0.14 when FYM was fitted and between 0.08 and 0.12 when *fym* was fitted. Variance ratios of permanent environmental effect of ewe were estimated between 0.17 and 0.22 when FYM was fitted and between 0.10 and 0.14 when *fym* was fitted. The proportion of phenotypic variance explained by *fym* fitted as a random effect ranged from 0.25 to 0.35. Genetic correlations between test day records of daily milk yield ranged from 0.58 to 0.98 and were higher between adjacent months of lactation. Daily milk yield heritabilities estimated with univariate animal models roughly corresponded with heritability estimates from multivariate models: 0.13 when FYM was fitted and 0.09 when *fym* was fitted. As a general pattern, phenotypic variances were slightly higher with a random effect of flock-year-month.

Keywords: sheep milk, test day, heritability, genetic correlations, variance ratios

Introduction. Milk yield is a trait which can be used as one of the measures of milking ability of ewes (Rovai et al., 1999, Tančin et al., 2011). Milk performance testing of ewes in Slovakia has been performed since 1995. Test day records are collected monthly following the AC method (alternate morning/evening system) of ICAR rules (ICAR, 2011). The data stored is thus an important source of information. Genetic evaluation of dairy sheep has been in place since 2006 (Oravcová et al., 2005). It is done on a routine basis, once a year. A repeatability three-trait animal model enabling joint evaluation of milk yield, fat and protein content is applied. Repeatability test day models are quite common in sheep and were studied by Serrano et al. (2001), Komprej et al. (2009) and Bauer et al. (2012). The main advantage of these models lies in a better possibility to account for sources of variation affecting each test day (Swalve, 1998) since test day records are analysed directly (Visscher and Goddard, 1995). According to Serrano et al. (2001), further advantages may be seen in fact that test day models not only allow the removal of abnormal measures without elimination of the whole lactation, but there is also no need to project lactation when information is missing. Repeatability test day models are based on assumption that milk yield is genetically the same trait across the whole lactation (Komprej et al., 2011).

A further strategy of using test day measurements is the analysis of single test day records separately with a multivariate animal model treating daily milk yield in individual months of lactation as a different trait. Such modeling is known from studies with dairy cows (Meyer et al., 1989, Rekaya et al., 1995, Swalve, 1995) as well as dairy sheep (Serrano et al., 2001, Kominakis et al., 2002, Komprej et al., 2011). In addition to heritability estimates, this approach enables to estimate genetic correlations between daily milk yields which tend to be higher between adjacent months of lactation (Ali and Schaeffer, 1987, Komprej et al., 2011). According to Swalve (1998), relationships among test days in the middle of lactation usually are the highest and close to unity. This may suggest that it is not very useful to consider all individual test days jointly in a multi-trait evaluation with its obvious advantages but also inherent problems of large (co)variance matrices. Nevertheless, the animal model considering daily milk yield in individual months of lactation as a different trait has not been applied in Slovak sheep until now.

The objective of this study was to assess variance components and genetic parameters for daily milk yield in individual months of lactation using a multivariate animal model. The obtained estimates of genetic parameters and variance ratios were discussed and compared with estimates from univariate animal models. The analyses were performed on test day data of Tsigai breed.

Material and methods. Data. Tsigai breed is the second most spread sheep breed in Slovakia. This is a multipurpose breed well adapted to local climate, mostly kept in areas from 500 to 800 m above sea level under the semi-extensive production system (Krupová et al., 2009). The income of breed is distributed between milk (cheese) production and production of offspring for slaughter as young animals; wool is of negligible importance. Most of lambs are sold to EU countries before Easter Eve each year. Production is of seasonal character, lambing occurs mostly in January and February (Oravcová et al., 2006) and weaning of lambs takes about 50 days on average. After weaning, ewes are mostly milked since April or May and are dried off in August or September (Oravcová and Peškovičová, 2008).

Data for analyses were test day records of 24,021 Tsigai ewes from 51 flocks collected between 1995 and 2010 by the State Breeding Services of the Slovak Republic. The AC method (alternate morning/evening system) of ICAR rules (ICAR, 2011) was applied. Only records with daily milk yield measured between the second and the seventh month of lactation were taken into account. Restriction was due to the fact that most of test day measurements were taken in these six months. Each ewe had at most one record with milk yield in each month (Komprej et al., 2011). Following this procedure, if it had more than one record in one month, only one was kept within this month and the other was moved to a different month. The second month of lactation consisted of records between days 40 and 69 after parturition, the third month of lactation consisted of records between days 67 and 99 after parturition, the fourth month of lactation consisted of records between days 88 and 130 after parturition, the fifth month of lactation consisted of records between days 102 and 159 after parturition, the sixth month of lactation consisted of records between days 133 and 189 after parturition and the seventh month of lactation consisted of records between days 181 and 210 after parturition. Only records with known lactation number and age of ewe, known litter size, days in milk and flock-year-month of measurement were included. At least 6 test day records per flock-year-month effect were required. The number of test day records in the second, third, fourth, fifth, sixth and the seventh month of lactation was 9,943, 40,422, 43,982, 41,687, 32,158 and 3,878, respectively. The number of test day records per lactation ranged from two to seven. In total, 172,070 test day records were considered.

Pedigree consisted of 34,942 animals. Of these, 1,857 were sires and 18,431 were dams. The number of base animals (animals with unknown sire and dam) was 6,535 and the number of non-base animals was 28,407. The number of animals with known sire and dam was 26,238. The number of animals with the only unknown sire and with the only unknown dam was 1,510 and 659, respectively.

Basic statistics (means and standard deviations) for days in milk and daily milk yield in individual months of lactation is given in Table 1. The overall means and standard deviations (regardless of month of lactation) are added.

Statistical analysis. Estimation of (co)variance components was done by restricted maximum likelihood method (REML) using VCE6 (Groeneveld et al., 2010). Alternative multivariate and univariate animal models fitting flock-year-month either as a fixed or random effect, accounting for further fixed and random effects were applied. These were based on actual investigations and previous studies of dairy sheep in Slovakia (Oravcová et al., 2005, Oravcová and Peškovičová, 2008). Preliminary statistical analyses were done in SAS (SAS, 2009). General linear model (GLM procedure) was employed.

Table 1. **Basic statistics for daily milk yield** (by month of lactation)

	Month of lactation	Means and standard deviations
Days in milk	2	59.2 ± 6.8
	3	84.3 ± 8.1
	4	113.6 ± 8.6
	5	144.3 ± 8.5
	6	172.8 ± 8.3
	7	196.6 ± 5.8
	Total	123.9 ± 37.1
Milk yield, kg	2	0.804 ± 0.350
	3	0.757 ± 0.319
	4	0.682 ± 0.293
	5	0.545 ± 0.245
	6	0.486 ± 0.229
	7	0.462 ± 0.212
	Total	0.632 ± 0.301

First, multivariate animal models in which milk yield in individual months of lactation was treated as a different trait were used. For comparison purposes, univariate animal models with milk yield treated as repeated measures of the same trait were employed.

The fixed effects considered were lactation number (1, 2 and 3+), litter size (1, 2+) and days in milk. All these effects were modelled as linear regressions. The random effects were considered animal genetic effect and permanent environmental effect of ewe. Animal genetic effect (heritability) represents proportion of total variation of milk yield between individuals in a population due to genetic variation (genetic differences between animals). Permanent effect of ewe represents common environment within each ewe and indicates preparation of ewe for reproduction from its birth to the first lactation, affecting milk yield in all lactations (Komprej et al., 2011). The effect of flock-year-month was fitted either as a fixed (FYM, Models 1 and 3) or random (*fym*, Models 2 and 4) effect. This effect represents temporary conditions within flocks which can differ due to changes in farming system, management practice, feeding, weather etc. when individual daily milk yield is measured. Flock-year-month effect in multivariate analyses consisted of 297, 660, 752, 721, 476 and 121 levels, respectively. Flock-year-month effect in univariate analyses consisted of 1,510 levels. Permanent environmental effect of ewe consisted of 24,021 levels (regardless of model used).

The matrix notation of the models (either multivariate or univariate) is as follows:

$$y = X\beta + Z_a + Z_p + e \quad \text{(Model 1 and 3)}$$

$$y = X\beta + Z_a + Z_p + Z_f + e \quad \text{(Model 2 and 4)}$$

where y is a vector of observations of daily milk yield, matrix X is an incidence matrix and β is a vector of unknown parameters for fixed effects. Z_a, Z_p and Z_f are incidence matrices assigned for random effects: animal genetic (a), permanent environmental effect of ewe (p) and flock-year-month (f), e is a vector of residuals.

The expected values can be presented as follows:

$$E\begin{pmatrix} y \\ a \\ p \\ e \end{pmatrix} = \begin{bmatrix} X\beta \\ 0 \\ 0 \\ 0 \end{bmatrix} \quad \text{(Model 1 and 3)}$$

$$E\begin{pmatrix} y \\ f \\ a \\ p \\ e \end{pmatrix} = \begin{bmatrix} X\beta \\ 0 \\ 0 \\ 0 \\ 0 \end{bmatrix} \quad \text{(Model 2 and 4)}$$

The (co)variance matrices (V) which consist of variance components for random effects: additive genetic effect (G), permanent environmental effect of ewe (P), flock-year-month (F) and residual (R) can be written as follows:

$$V = Z_a G Z'_a + Z_p P Z'_p + R \quad \text{(Model 1 and 3)}$$

$$V = Z_a G Z'_a + Z_p P Z'_p + Z_f F Z'_f + R \quad \text{(Model 2 and 4)}$$

Results and discussion. The mean values of daily milk yield given in Table 1 showed the decreasing trend along with an increasing number of days in milk. Coefficients of variation of days in milk between the second and the seventh month of lactation ranged from 3 (seventh month) to 11% (second month). Coefficients of variation of daily milk yield ranged from 42 to 47%, being the highest in the sixth month of lactation. Milking ability of Tsigai sheep expressed by daily milk yield was lower than that reported for Slovenian breeds (Komprej et al., 2011), Spanish breeds (Serrano et al., 2001) and Greek Sfakia dairy sheep (Volanis et al., 2002), respectively. The exception was Greek Boutsico breed for which Kominakis et al. (2002) reported almost the same daily milk yield as it was found in Tsigai breed (between the second and the sixth month of lactation).

The variance ratios estimated for random effects by multivariate analyses are given in Table 2. The estimated heritabilities and variance ratios for permanent environmental effect of ewe were slightly higher when flock-year-month (FYM) was fitted as a fixed effect (Model 1). The heritability estimates increased from 0.11 (second month) to 0.14 (fourth and fifth month). Afterwards, the heritability estimates decreased to 0.13 (sixth month) and 0.12 (seventh month), respectively. The variance ratios estimated for permanent environmental effect of ewe ranged from 0.17 (second month) to 0.22 (seventh month). When *fym* was fitted as a random effect, a decrease of heritability estimates and variance ratios of permanent environmental effect of ewe was observed. The heritability estimates ranged from 0.08 (second month) to 0.12 (fourth and fifth month). The variance ratios of permanent environmental effect of ewe ranged from 0.10 (second month) to 0.14 (fourth month). With known random effects, the highest proportion of variance was explained by *fym* effect which ranged from 0.25 in the fourth month of lactation to 0.35 and 0.34 in the second and the seventh month of lactation, respectively. The total phenotypic variance increased by about one third when *fym* was fitted as a random effect. The residual variance ratios in Model 2 decreased by about one third since the higher proportion of phenotypic variance was explained by random effects included in the model. The residual variance ratios were slightly lower than 0.5 (Model 2). When Model 1 was applied, the residual variance ratios ranged between 0.65 and 0.72.

Table 2. **Variance ratios for random effects and total phenotypic variance for daily milk yield** (multivariate models)

	Month of lactation	Heritability	Permanent environmental	Flock-year-month	Residual	Phenotypic variance
Model 1	2	0.11	0.17	-	0.72	0.0717
	3	0.12	0.19	-	0.69	0.0668
	4	0.14	0.21	-	0.65	0.0593
	5	0.14	0.20	-	0.66	0.0405
	6	0.13	0.20	-	0.67	0.0341
	7	0.12	0.22	-	0.66	0.0301
Model 2	2	0.08	0.10	0.35	0.47	0.1111
	3	0.10	0.12	0.31	0.47	0.0975
	4	0.12	0.14	0.25	0.49	0.0796
	5	0.12	0.13	0.28	0.47	0.0574
	6	0.11	0.13	0.29	0.47	0.0490
	7	0.10	0.13	0.34	0.43	0.0460
Model 1: flock-year-month fitted as a fixed effect; Model 2: flock-year-month fitted as a random effect						

The comparison of results with literature values is not easy since models differ to a greater extent. The exceptions, in part, are studies of Komprej et al. (2011) who used a similar model as is Model 2 here (differences in fixed part of the model) and of Kominakis et al. (2002) who used a similar model as is Model 1 here (considering animal genetic and permanent environmental effect of ewe as random effects, however, instead of flock-year-month effect, these authors involved year of lambing and interaction of year of lambing by lactation). Thus, estimates from Model 1 are compared with findings of Kominakis et al. (2002) and estimates from Model 2 are compared with findings of Komprej at al. (2011). As an additional difference to our study, both Kominakis et al. (2002) and Komprej et al. (2011) analysed eight months of lactation. The heritabilities of daily milk yield estimated for Slovenian sheep (from the second to the sixth month of lactation) were about 40 to 50% higher than heritabilities estimated for Tsigai breed, though the trend was similar. The exception was the seventh month of lactation in which almost the same heritability was found for Slovenian and Tsigai sheep. The variance ratios estimated for permanent environmental effect of ewe in Slovenian sheep were similar and ranged from 0.09 (seventh month) to 0.15 (fourth month). Komprej et al. (2011) reported the variance ratios for *fym* by one tenth to one third lower than those found for Tsigai sheep. The trend was the same, with the lower variance ratios in the middle of lactation and the higher variance ratios in the beginning and the end of lactation. The lower variance ratios estimated for *fym* (Komprej et al., 2011) suggest that breeding conditions in Slovenian sheep are less variable than those in Tsigai sheep. Kominakis et al. (2002) reported by 30 to 50% higher heritabilities for Boutsico sheep than those estimated for Tsigai sheep. These authors estimated similar variance ratios for permanent environmental effect of ewe (lower by 15%), except for the third month of lactation. Serrano et al. (2001) who included only additive genetic effect as a random effect reported higher heritabilities for daily milk yield in Latxa and Manchega sheep in the first four months of lactation (between 0.18 and 0.33). Georgoudis et al. (1997) who considered only one fixed (month of lambing) and one random (animal genetic) effect reported heritabilities between 0.19 and 0.26 for Chios sheep (also in the first four months of lactation). The considerably higher heritabilities (between 0.41 and 0.47) were reported for Sfakia breed by Volanis et al. (2002).

Genetic correlations estimated for daily milk yield (from the second to the seventh month of lactation) are presented in Table 3. The genetic correlations decreased from 0.98 to 0.58 (Model 2). They were higher between adjacent months of lactation and dropped for months which were apart. The genetic correlations were similar between Models 1 and 2 and did not differ more than 0.07. Similarly to studies of Kominakis et al. (2002) and Komprej et al. (2011), the trend in genetic correlations confirmed that daily milk yield in different months of lactation of Tsigai sheep is not genetically the same trait, being less than unity between distinct months of lactation. The estimates of genetic correlations obtained in this study are in accordance with findings of Komprej et al. (2011) who reported genetic correlations ranging from 0.99 to 0.62 between those months of lactation which correspond with our analyses. When interval between months of lactation increased (Komprej et al., 2011), genetic correlations decreased and the lowest genetic correlation was estimated between the first and the eighth month of lactation (0.37). Serrano et al. (2001) reported similar genetic correlations being between 0.87 and 0.90 for adjacent months of lactation and decreasing to 0.66 and 0.46 between the first and the fourth month of lactation in Latxa and Manchega breed, respectively. The genetic correlations reported by Kominakis et al. (2002) for Boutsico breed agreed with genetic correlations obtained in this study when relationships among the same months of lactation were compared.

Table 3. **Genetic correlations for daily milk yield between individual months of lactation** (Model 2)

Month of lactation	3	4	5	6	7
2	0.98	0.87	0.82	0.76	0.58
3		0.95	0.90	0.86	0.69
4			0.97	0.95	0.82
5				0.98	0.89
6					0.96

Genetic correlations for daily milk yield estimated with Model 1 were almost the same with maximum difference of 0.07

Daily milk yield heritabilities estimated with univariate animal models are presented in Table 4. The values (0.13 when FYM was fitted and 0.09 when *fym* was fitted) corresponded with estimates from multivariate models and were almost the same or slightly lower than in multivariate analyses. These findings partly contrast with results of Georgoudis et al. (1997) and Serrano et al. (2001) who reported clearly lower heritability estimates when univariate models treating daily milk yield as repeated measures of the same trait were applied. The lower phenotypic variance was found when FYM was fitted as a fixed effect, similarly as in multivariate approach. The heritability and the variance ratio for permanent environmental effect of ewe were higher (Model 3 vs. Model 4). The residual variance ratio was also affected and differed according to flock-year-month effect fitted as a fixed or random effect.

Table 4. **Variance ratios for random effects and total phenotypic variance for daily milk yield** (univariate models)

Source of variance	Model 3	Model 4
Heritability	0.13	0.09
Permanent environment	0.26	0.18
Flock-year-month	-	0.32
Residual	0.61	0.41
Phenotypic variance	0.0533	0.0785

Model 3: flock-year-month fitted as a fixed effect
Model 4: flock-year-month fitted as a random effect

Conclusion. The variance ratios and heritabilities of daily milk yield using multivariate models in which milk yield in individual months of lactation was treated as a different trait and univariate models in which daily milk yield was treated as repeated measures of the same trait were estimated. The highest impact on distribution of phenotypic variance was found due to flock-year-month effect which was fitted either as a fixed or random effect, in both multivariate and univariate models. The similarities found between multivariate and univariate models indicate that current genetic evaluation of Tsigai sheep based on a repeatability test day model seems to be a useful basis for genetic and environmental improvement of this breed.

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