Estimation of genetic parameters and evaluation of test-day milk production in sheep

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ABSTRACT: Genetic parameters and breeding values were estimated based on 11 708 daily milk yields from 2255 lactations (1351 sheep, 19 different flocks) between the years 2004 and 2010. The pedigree covered 2334 individuals, including both the recorded animals and their known ancestors. The fixed effects were estimated by the least-squares method, while the genetic parameters were estimated by the REML method. The data were tested by 49 models, but on the basis of the coefficient-of-determination value and the significance of the effects, only 10 models were used for REML analysis. The most suitable model was chosen on the basis of the breeding values distribution and the heritability of daily milk production, which was estimated at 0.28. The fixed effects of the flock parity number, the flock test day, and the linear and quadratic coefficients of flock's days-in-milk in the chosen model were all highly significant ($P < 0.0001$) for the test-day milk yield. The breeding values had a normal distribution and a standard deviation of 0.46 kg.

Keywords: dairy; heritability; model selection; Lacaune; East Friesian; breeding values

Dairy sheep farming does not have a long tradition in the Czech Republic. However, in recent years, a distinct expansion of this specialized production has occurred and new, mainly large herds of dairy sheep have been established. The number of animals with recorded milk performance has increased from 157 ewes in 2005 (with only one herd with more than 50 ewes) to 1057 ewes in 2010 (with 73.8% kept in herds of over 50 animals). This situation encouraged the development of a more effective breeding program for dairy sheep in the Czech Republic, including an estimation of the genetic breeding values for milk production. The new breeding program involves, among other aspects, designing a suitable model of equations composed of the genetic and non-genetic factors affecting milk production and estimates of the genetic parameters implicated in milk production.

Milk production is usually expressed as test-day milk yield, the total milk yield or the transformed total milk yield to standard length of the lactation period (El Saied et al., 1998a; Oravcová et al., 2006), considering that the genetic correlation between the total and standardized lactation is quite high (0.99) (El Saied et al., 1998b).

Milk-yield breeding values for sheep are estimated using the test-day model (Othmane et al., 2002; Oravcová et al., 2006) rather than the older lactation model, because the test-day model is more accurate in accounting for the environmental variations associated with lactation.

The effects of days-in-milk, test day (possibly including the interactions with the flock effect), parturition number, age at parturition, litter size, and the number of weaned lambs are usually included in equations for evaluating milk production, in addition to the genetic and random environmental effects.

The test-day approach is characterized by a consideration for the effect of the lactation stage, accomplished by including days-in-milk in the equation

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model. Presently, it is common to evaluate milk yield and dry matter production in cows using a random regression model (Yazgan et al., 2010). This procedure has also been successfully applied to milk production in sheep (Horstick et al., 2002). However, the fixed regression model is more commonly used to reflect the effect of days-in-milk on milk yield in dairy sheep (Macciota et al., 1999; Hamann et al., 2004; Oravcová et al., 2005, 2006 and others). Because lambs are often allowed to suckle during the early phase of lactation, it can be difficult to correctly fit complete lactation trajectories (Schaeffer et al., 2004); thus, the only period usually taken into account is the milking period. Additionally, a strict lambing seasonality is characteristic for dairy sheep in the Czech Republic. The ewes recorded within one test day are usually at the same stage of lactation, and thus the variability connected with days-in-milk is explained by the effect of test day, as in the case of dairy goats in the Czech Republic (Ciappesoni et al., 2004).

The heritability of milk production in sheep is estimated to range from 0.13 (Gutierréz et al., 2007) to 0.35 (Baro et al., 1994), but most studies estimate the value of heritability of test-day milk production to fluctuate from 0.18 (e.g. El-Saied et al., 1998a) to 0.25 (e.g. Barillet and Boichard, 1994).

The aim of the present study was to choose the most appropriate model equation for milk yield in dairy sheep in the Czech Republic by comparing different models either of our own design or based on literature, and to estimate the breeding values and genetic parameters for milk production in dairy sheep by the REML method. This is the first study to analyze milk yield by examining test-day records in dairy sheep in the Czech Republic.

MATERIAL AND METHODS

Observations were provided by the Association of Sheep and Goat Breeders of the Czech Republic (SCHOK, 2012).

To estimate variance components, the outlying observations and observations with insufficient numbers of records for the different classes were removed (i.e. records of milk yield over 7.5 kg, days-in-milk lesser than 14, ewes older than 3990 days, fewer than 10 observations within the flock or fewer than 7 ewes within the flock).

After these adjustments, the data were reduced to 11 708 observations and contained milk yields from 2255 lactations of 1351 sheep from 19 flocks between the years 2004 and 2010. Milk yield was measured using the AT method (ICAR, 2010). Measurements were performed at monthly intervals. According to the rules for milk performance recording (SCHOK, 2012), the first records within the milking period were carried out within 95 days (74 days on average) after lambing and 4 to 52 days after weaning.

The basic characteristics of observations prepared for analysis are shown in Table 1. The ewes were of various breeds, including East Friesian, Lacaune, Sumavska, and crossbreeds, mainly of the described breeds. For the ewe numbers, lactations and observations by breed see Table 2. The breed composition of the individual flocks is shown in Figure 1. Along with the pedigree (four generations of ancestors) the database contained 2334 individuals. The average relationship between animals in the whole relationship matrix was 0.0000638. Ewes with records were sired by 125 rams and had 685 dams in total.

The data were analyzed by the least-squares method (GLM) of SAS (Statistical Analysis System, Version 9.1, 2005), and a total of 49 fixed effects models were evaluated by the coefficient of determination and significance of the effects. Nine models with the highest coefficient of determination (above 0.76) were selected from the models with all effects significant in the GLM analysis and they are shown in Table 3. A mark of "P" denotes production models, while "R" denotes models with reproduction traits. The labels of the other models are based on the relationship to the P and R models (i.e. with a missing regression of age, the phrase 0AGE is included in the name or added effects are described, e.g. P-LDIM). Other models reported in the literature (e.g. El-Saied et al., 1998b; Hamann et al., 2004; Oravcová et al., 2006) and applied to our data are presented in Table 4 and are labelled according to the first author and year of publishing of the individual study.

The nine models reported in Table 3, in addition to one model from the literature (Oravcová et al., 2006), were further analyzed with the REML method, using the REMLF90 software (Misztal et al., 2002). An estimation of variance components, heritability, and distribution of breeding values (BV) were evaluated. The one literature model was chosen based on the highest coefficient of determination and the highest ratio of significant effects from Table 4. In the REML analysis, two random effects were added to all the models – a permanent environmental effect and an additive genetic effect. Unlike the GLM analysis, the effect of genotype (breed) was not treated as a fixed effect but it was included in the pedigree as phantom groups in the oldest (fifth) generation of ancestors or when ancestors were not known. For all the analyzed models, the convergence criterion was set to 1e-17, and the maximal number of rounds was set to 10 000.

The general linear model for REML analyses, including random effects in matrix notation, was as follows:

$$y = \mathbf{X}b + \mathbf{Z}u + e$$

where

y = vector of observations for daily milk yield (kg)

$\mathbf{X}$, $\mathbf{Z}$ = matrices of the order of fixed ($\mathbf{X}$) and random ($\mathbf{Z}$) effects

b = vector of fixed effects

u = vector of random effects

e = vector of random residual effects

The effects used in the models are listed as follows:

AGE = fixed regression of parturition age

br = fixed effect of genotype (22 types); used in the least squares-method only, in the REML the genotypes were defined as phantom groups

DIM = fixed regression of days-in-milk (days 14–291)

F = fixed effect of flock (19 levels)

F × TD = fixed effect of test day (as year × month × flock at 332 levels)

L = fixed effect of the parturition number (4 levels: 1, 2, 3–4, > 4)

O = fixed effect of the lambs weaned (3 levels: 0–1 (5851 observations), 2 (5112 observations), > 2 (745 observations))

PM = month of parturition (12 levels)

S = fixed effect of the litter size (3 levels: 0–1 (4589 observations), 2 (6083 observations), > 2 (1036 observations))

TY = fixed effect of the test year (as a year at 7 levels; years 2003 and 2004 were grouped together) and random additive genetic and random permanent environmental effects for the REML analysis only.

RESULTS AND DISCUSSION

The data prepared for the analyses included 11 708 observations. The characteristics of the data are presented in Table 1.

Table 1. Characteristics of the observations prepared for analysis

	Min-max	Mean	Standard deviation
Month of parity	1–12	2.56	1.43
Litter size	1–3	1.70	0.62
Lambs weaned	1–3	1.57	0.61
Milk yield (kg)	0–5.0	1.26	0.78
Days-in-milk	14–291	132	53
Age at parity (days)	341–3694	1171	655

Fixed effects

There were no distinctive differences in the coefficients of determination between the P, P-LDIM, and P-0AGE-FTYDIM models or their analogues, with or without regression for age at parity. The age at parity effects were significant in all cases ($P < 0.0001$), but the regression coefficients had very small values.

The litter size, or the number of weaned lambs, was not significant when applied in models separately but it was significant ($P < 0.0001$) when combined in the models with reproduction traits (R models). In the R models, the litter size had a negative effect on milk yield. This result was unexpected because Oravcová et al. (2006) and others (e.g. Gonzalo et al., 1994 or El-Saied et al., 1998a) have reported the opposite relationship (i.e. more lambs implies a higher milk production). Nevertheless, in our study, the data supported a high correlation between these effects (0.75), resulting in the compensatory effects between the estimations. The models containing both of these reproduction effects could therefore be used for milk data adjustments, but a separate interpretation of these effects is impossible because of the previously mentioned compensatory effects. The effect of litter size is connected with prenatal influence on the udder development, consisting of the number of foetuses and the amount of placental hormones produced. The effects of stimulation and emptying of the mammary gland by suckling are connected with the number of lambs weaned because the majority of lamb losses occurs in the perinatal period. Because of this connectedness, both effects were tested, despite of their confounding nature.

The models of Serrano et al. (2001) and Othmane et al. (2002) were identical in their application to our data. The coefficients of determination of the validated models ranged from 0.7600 (P-LDIM) to 0.7999 (P-FLTY). Among the literature models applied to our data, the highest (0.7460) coefficient of determination found was for the model by Oravcová (2006).

The flock test-day effect accounted for 70% of the variability across the observations. Lambings in the Czech Republic are seasonal. Thus, most changes in the milk yield during lactation are linked to the flock test-day effect, as the majority of ewes on test days are in a similar phase of lactation. The decreasing tendency of the lactation curve was due to the absence of the observations at the maximum of the lactation curve, which corresponds to the period when milk is suckled by lambs. The interaction between the days-in-milk and the flock effect was more highly significant than the interaction between the days-in-milk and the parity effect.

More precise information about genotypes resulted in a better explanation of the variation in the recorded data. The crossbred individuals refined the results, providing more data for predicting the systematic and additive genetic effects.

Genetic parameters and breeding values

The variance of additive genetic, permanent environmental and residual effects, and heritability estimates from the REML models are shown in Table 5. The P-FLTY, R-0AGE-FLTY, and R-FTYDIM models had a heritability lower than 0.17 (data not shown).

The P-FLTY, P-0AGE-FLTY, P-0AGE-FTYDIM, R-0AGE-FLTY, and R-FTYDIM models had high coefficients of determination using the least–squares method, but the heritability determined with the REML models was low. This low heritability can result from insufficient connectedness of the data due to the grouping of the observations by three factors (flock and test-year, with either lactation or days-in-milk) in overparametrized models. Breeding values were calculated as the difference between the value of an individual and the mean of the population. The correlations between the calculated BV from the different models were 0.9 on average, except for the P-0AGE-FLTY model and the model by Oravcová (2006), which had an average correlation of 0.76 with the other models and 0.65 between them.

The model by Oravcová (2006) had a lower heritability compared to the other models, a non-significant effect in the least-squares analysis (litter size), and a low correlation to the other models' BV. The parturition × days-in-milk interaction used in the P-LDIM model explained less variability than the flock × days-in-milk interaction in the comparable P model. The age at parity regression coefficients had very small values and the correlation between the P and the P-0AGE model was the highest (0.951). All the REML models had a normal distribution of BV. However, the BV in the P-0AGE model had the least number of outliers, represented mostly by animals without records in the oldest part of the pedigree (sheep born before the year 1990).

The heritability calculated with the chosen P-0AGE model (0.28) was higher than that determined by Hamann et al. (2004) and Serrano et al. (2001) (0.15 and 0.20, respectively) but lower than the value reported by Baro et al. (1994) (0.35).

The breeding values in the chosen P-0AGE model had a standard deviation of 0.46 kg of milk, and the regression of the days-in-milk in interaction with the flock effect, using the REML model, cor-

Table 2. Number of ewes, lactations, and observations on record by breed/crossbreed (data prepared for analysis)

Breed/crossbreed	Ewes	Lactations	Observations
East Friesian	732	1 320	6 606
Lacaune × Sumavska[1]	301	340	1 711
Lacaune	44	68	415
Lacaune × East Friesian[1]	154	350	2 022
East Friesian × Improved Wallachian[1]	54	88	580
Sumavska	34	40	179
Other	32	49	195
Total	1 351	2 255	11 708

[1] crossbreeds are shown together without consideration for the ratio of the breeds

Table 3. Fixed effects for the validated models (all of the effects were significant, $P < 0.0001$)

Fixed effects model	AGE	AGE^2	F × TD	br	F × DIM	F × DIM^2	F × L	L × DIM	L × DIM^2	F × L × TY	F × TY × DIM	F × TY × DIM^2	S	O	R^2
P	X	X	X	X	X	X	X								0.771
P-0AGE			X	X	X	X	X								0.768
P-LDIM	X	X	X	X			X	X	X						0.760
P-0AGE-FLTY			X	X	X	X	X			X					0.799
P-FLTY	X	X	X	X	X	X				X					0.800
P-0AGE-FTYDIM			X	X			X				X	X			0.795
R	X	X	X	X	X	X							X	X	0.771
R-0AGE-FLTY				X	X	X	X			X			X	X	0.801
R-FTYDIM	X	X	X	X			X				X	X	X	X	0.797
Number of levels	cov	cov	332	7	cov	cov	74	cov	cov	284	cov	cov	3	3	
Average No. of observations within levels			35.2	1672			158			41.2					

P = production model, R = model with reproduction traits, AGE = age of the ewe at parturition, F = flock, TD = test day, br = genotype (breed), DIM = days-in-milk, L = parturition number, TY = test year, S = litter size, O = number of weaned lambs, R^2 = coefficient of determination of the model using the least-square method, × = interaction in the combined effect, cov = covariable effect

Table 4. Fixed effects of the models used in the literature and applied to our data (significant effects ($P < 0.0001$) are in capitals and bold)

Fixed effects model	DIM	DIM^2	AGE	TD	F	F × TD	TY	br	L	S	AGE × DIM	L × AGE	PM	DIMx	L × TY × AGE	L × PM	R^2
Carta[a]						X			X		X						0.719
El-Saied[b]	*x*	**X**	**X**			X				x							0.733
El-Saied[c]				X					X	X							0.230
Fuertes[d]			X	X						X		X					0.143
Hamann[e]	*x*	*x*		X			X	X	X				**X**	*x*			0.516
Ligda[f]					X		X		**X**	*x*							0.497
Macciota[g]	**X**				X		X		**X**	*x*							0.588
Othmane[h], Serrano[i]	**X**		X			X				x							0.731
Oravcová[j]	**X**	**X**				X			**X**	*x*			X	X			0.746
Sanna[k]						X									**X**	**X**	0.745

DIM = days-in-milk, AGE = age of the ewe at parturition, TD = test day, F = flock, TY = test year, br = genotype (breed), L = parturition number, S = litter size, PM = month of parturition, DIMx = modified version of the DIM effect, R^2 = coefficient of determination of the model in least-square method, × = interaction in the combined effect

[a]Carta et al. (2001), [b]El-Saied et al.(1998a), [c]El-Saied et al. (1998b),[d]Fuertes et al. (1998), [e]Hamann et al. (2004), [f]Ligda et al. (2003), [g]Macciota et al. (1999), [h]Othmane et al. (2002), [i]Serrano et al. (2001), [j]Oravcová et al. (2006), [k]Sanna et al. (1997)

The model by Hamann et al. (2004) uses the DIM, DIM^2, log10 DIM, and (log10 DIM)^2 effects, whereas the model by Oravcová et al. (2006) uses DIM, DIM^2, ln DIM, and ln^2 DIM

Table 5. Variances (in kg^2) of the additive genetic effects (σ^2_a), permanent environmental effects (σ^2_{pe}), residual (σ^2_e), and heritability (h^2) of daily milk yield for different models

Model	σ^2_a	σ^2_{pe}	σ^2_e	h^2
P	0.051	0.016	0.104	0.30
P-LDIM	0.051	0.017	0.109	0.29
P-0AGE	0.047	0.020	0.105	0.28
P-0AGE-FLTY	0.025	0.028	0.094	0.17
P-0AGE-FTYDIM	0.027	0.029	0.090	0.19
R	0.051	0.017	0.104	0.30
Oravcová[a]	0.043	0.019	0.113	0.26

P = production model, R = model with reproduction traits
[a]Oravcová et al. (2006)

responded well with the results determined by the least-squares method, showing a strong influence of the flock effect on lactation.

Potential models for a further development

Advancements in milk yield evaluations can be made with a multi-trait approach that includes parity numbers as different traits or by taking into account the heterosis advantage of cross-bred individuals. Relationships between the milk production and the fecundity traits (litter size, number of weaned lambs) should be further analyzed by including a multi-trait approach. The milk-component effects could be used to optimize BV for milk product yield, as the dry matter content and the milk yield are negatively correlated (Othmane et al., 2002; Komprej et al., 2009), and product yield depends on both the parameters. When more records are available and the data have better connectedness, which can be facilitated by broader production recording, the random regression of days-in-milk should be tested as well. The connectedness of data can be problematic because of the dominance of natural mating in the relatively closed flocks of the Czech Republic.

CONCLUSION

The results reported from this study indicate a moderate heritability for daily milk yield. The major source of variability is due to the flock test-day effect, which is associated with the effect of lactation phase due to seasonal lambing. Parturition number and days-in-milk, in combination with the flock effect, explain more variability than each particular effect alone.

From the total of 49 models of our own design or taken from the literature, the best model was chosen on the basis of the coefficient of determination, the significance of the effects, the coefficient of heritability, and the distribution of the breeding values. This model contained the fixed effect of flock test day, parity within a flock, and fixed linear and quadratic regression of the days-in-milk within the flock. Furthermore, it included random additive genetic, permanent environmental and residual effects.

Sufficient variability among the animals and a heritability of 0.28 gives a good perspective for breeding work in dairy sheep using breeding values that are estimated by BLUP methodology. Milk recording is in its infancy in the Czech Republic and the database of performance has so far been inextensive. With more performance data and possible changes in the organisation of breeding (e.g. seasonal lambing), modification of the BV estimation method will be needed.

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