

Heritability and repeatability of the number of lambs born and reared estimated using linear and threshold models

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Abstract

The research was conducted on 3 844 Polish Merino lamb dams born in 1991-2001, used in 15 flocks from the Pomerania and Kujawy region in Poland. The assessed parameters were the number of lambs born from a dam after lambing (LSB) (1, 2, 3) and the number of lambs reared (LSW) (0, 1, 2, 3). The genetic parameters LSB and LSW were estimated with the use of two methods: Average Information – REML (AI-REML) and Gibbs sampling (GS). For estimation of components by means of the AI-REML method the animal's linear model was used, and in the case of the GS method a threshold model was also used alongside the linear one. The LSB heritability estimated using the AI-REML and GS methods in combination with a linear model were similar and their values were respectively 0.025 and 0.029, with similar standard errors for variance components. Applying the GS method combined with a threshold model resulted in a two times higher heritability (0.054) compared to when linear models were used. A similar tendency was found to exist in respect of estimated repeatability. When using linear models, the obtained values were closely matched: 0.064 (AI-REML) and 0.065 (GS). The highest repeatability occurred when a threshold model was used (0.118). The LSW heritability was low and, depending on the model and method (0.016-0.020). Similar values LSW repeatability were obtained with the use of linear models (0.048 – REML and 0.049 – GS), and when a threshold model was used the result was higher – 0.070.

Keywords: sheep, linear model, threshold model, genetic parameters, litter size, Merino

Zusammenfassung

Bewertung der Heritabilität und Wiederholbarkeit der Anzahl von geborenen und aufgezogenen Lämmern mittels Linearen Modells und Schwellenmodells

Die Untersuchungen wurden an 3 844 Mutterschafen der Rasse Polnische Merino durchgeführt. Die Tiere stammten aus 15 Herden und wurden zwischen 1991 und 2001 in der Region Pommern und Kujawien in Polen geboren. Bewertet wurden die Anzahl der durch das Mutterschaf (LSB) geworfenen Lämmer (1, 2, 3) und die Anzahl der aufgezogenen Lämmer (LSW) (0, 1, 2, 3). Die genetischen Parameter von LSB und LSW wurden mit Hilfe von zwei Verfahren bewertet: Average Information-REML (AI-REML) sowie Gibbs-Sampling-Verfahren (GS). Bei der Komponentenbewertung mit AI-REML wurde das lineare Modell des Tieres angewendet, bei GS zusätzlich das Schwellenmodell. Die Werte der Heritabilitätskennziffern von LSB, die unter Einsatz des Verfahrens AI-REML und GS in Verbindung mit dem

linearen Modell bewertet wurden, waren angenähert und betrug: 0,025 und 0,029 - bei vergleichbaren Fehlerwerten in Bezug auf die standardmäßige Varianzkomponente. Die Anwendung des GS-Verfahrens mit dem Schwellenmodell ergab einen doppelt höheren Wert der Heritabilität (0,054) als beim linearen Modell.

Eine ähnliche Tendenz wurde im Bereich der Wiederholbarkeitskennziffern festgestellt. Angenäherte Werte wurden beim Einsatz des linearen Modells erreicht: 0,064 (AI-REML) und 0,065 (GS). Eine deutlich höhere Wiederholbarkeitskennziffer ergab sich bei der Anwendung des Schwellenmodells: 0,118. Die Heritabilität der Anzahl aufgezogener Lämmer war niedrig und schwankte abhängig von dem eingesetzten Modell und der angewendeten Methode zwischen 0,016 und 0,020.

Vergleichbare Werte der LSW-Wiederholbarkeit wurden bei Nutzung vom linearen Modell (0,048 – REML und 0,049 – GS) erreicht, ein deutlich höheres Ergebnis (0,07) wurde dagegen bei Verwendung des Schwellenmodells erreicht.

Schlüsselwörter: Schaf, Lineares Modell, Schwellenmodell, genetische Parameter, Wurfgröße, Merino

Introduction

The Polish Merino is the most commonly used sheep breed in Poland. It comes from the French Merino Precoz which was improved after World War II with the breeds of the German, Caucasian Merino. The breeding of the Polish Merino is centred in the regions of Wielkopolska, and Pomerania and Kujawy. Ewes of this breed in 2008 constituted approximately 14 % of female sheep being assessed in terms of their performance in Poland (Sheep and Goats Breeding in Poland in 2008, 2009).

Merino Sheep are much more common in countries to the west of Poland, for instance, in Germany. Based on the research conducted by Süß *et al.* (2004) it was established that the proportion of German Mutton Merino and Merinoland Sheep in the Saxon-Anhalt region is as high as 57.7 %. The used merinos are most frequently of the wool-meat type. The mean prolificacy of the breed in 2008 was relatively low and equalled 128.3 %. It is a clearly lower level than that presented by Strittmatter (2004) with respect to HB-German Mutton Merino – 146-168.8 %.

Variables like number of lambs born and reared take discrete values. These traits are considered threshold variables, that is traits which are discontinuous in their expression, usually representing a number of categorized phenotypic values, however, they are conditioned by polygenes (Dempster & Lerner 1950, Gianola 1982). Their characteristic property is the fact that exceeding the so-called threshold referring to the genes possessed results in a fundamental change of the phenotype.

The distribution of these variables is incompatible with a normal distribution. Therefore prior to estimation of the (co)variance components the said traits must undergo the Snell transformation (Naazie *et al.* 1991), or a probit transformation (Piwczyński 2004), then linear model calculations may be made using the REML method. Matos *et al.* (1997a), De Vries *et al.* (2005) and Olesen *et al.* (1994), estimating genetic parameters, applied, as one of the models which it is possible to use for estimation of prolificacy variance components, the Poisson

model. Results of numerous research studies (Altarriba *et al.* 1998, Matos *et al.* 1997a, 1997b, Olesen *et al.* 1994, Yazdi *et al.* 1999) show on the other hand that the genetic parameters of discreet reproduction traits should be estimated with the use of threshold models. Genetic parameters of reproduction traits may be estimated with the use of multitrait models (Hagger 2002, Vries *et al.* 1998) as well as repeatability models; results for these models are usually published in subject-related scientific literature (Dobek *et al.* 2004, Matos *et al.* 1997a, Noor *et al.* 2001, Olesen *et al.* 1994, Saboulard *et al.* 1995, Schmalwasser *et al.* 1991, Piwczyński 2009). It must be emphasised though that multitrait models have advantage over repeatability models as they take into account covariance between values of a trait obtained in subsequent measurements (Szyda 2001). Apart from establishing correct model selection, the researcher must choose between estimation methods. Usually, genetic parameters of the aforementioned reproduction traits are determined with the use of the Restricted Maximum Likelihood (REML), and Gibbs sampling.

Estimations of genetic parameters conducted so far indicate low influence of genetic assumptions on reproduction traits in Merino sheep (h^2 : fertility – 0.0720-0.203; number of lambs born from a mother that had lambed before – 0.060-0.260; number of lambs reared by a mated mother – 0.039-0.183 (Duguma *et al.* 2002, Lee *et al.* 2009, Mroczkowski *et al.* 1981, Olivier *et al.* 1998, 2001, Piwczyński 2009). Such significant differences in presented values of heritability indices may be caused, among other things, by the method or model used in statistical analysis.

The objective of the study was to compare the effects of heritability and repeatability estimates for lambs born and reared, obtained by means of the Average Information REML and Gibbs sampling using a linear and a threshold model.

Material and methods

The research was conducted on 3 844 dams of the Polish Merino breed, born in the years 1991-2001 and used in 15 flocks from Pomerania and Kujawy, Poland. Data on descent and performance of sheep came from the breeding documentation from the years 1990-2004, made available by the Local Sheep and Goat Breeders Association in Bydgoszcz. The animals which underwent reproduction performance assessments between 1993 and 2003 were at the age of 2 to 12. The assessed parameters were the number of lambs born from a dam after lambing (LSB) (1, 2, 3) and the number of lambs reared by a mated dam (LSW) (0, 1, 2, 3).

Table 1
Descriptive characteristic of number of lambs born (LSB) and reared (LSW)

Trait	n	Mean	Standard deviation
LSB	15 938	1.318	0.481
LSW	15 938	1.250	0.518

The pedigree information of the studied animal population was, if possible, completed up to 3rd generation. In total the pedigree database comprised 9 297 animals. In order to calculate the inbreeding index in the studied population, the INBREED procedure from the SAS package (SAS 2008) was used. Twenty inbred animals were found with the mean inbreeding of 14.76 % (SD=10.04 %).

Table 2
Distribution of number of lambs born (LSB) and reared (LSW)

Trait	Level	n	%
LSB	1	10 991	68.96
	2	4 830	30.3
	3	117	0.73
LSW	0	554	3.48
	1	10 942	68.65
	2	4 351	27.3
	3	91	0.57

As part of the statistical determination, the basic measures of location and variability of controlled traits were calculated. An explorative analysis of LSB and LSW was carried out using multiple logistic regression (SAS 2008). In the course of the analysis, using the selection method of the forward type regression model, the following variables, associated with the above traits, were selected: flock, year of birth, ewe's age and birth type, and flock×year of birth interaction. The significance of parameters, i.e. the selected variables, was evaluated by means of the Wald statistics (SAS 2008). The statistical analysis was conducted with the use of the SAS computer package, applying the LOGISTIC procedure (SAS 2008).

The LSB and LSW genetic parameters were estimated by means of two methods: Average Information – Restricted Maximum Likelihood (AI-REML) and Gibbs sampling (GS). Estimating components by means of the AI-REML method the animal's linear model (LM) was applied, and in the case of the GS method, a threshold model was used alongside a linear one (TM).

The GIBBS1F90 software (Misztal 2007) was used to estimate the LSB and LSW genetic parameters according to a linear model, and the THRGIBBS1F90 (Tsuruta & Misztal 2006) according to a threshold model.

Estimating variance components by means of the Gibbs sampling method, 100 000 samples were generated, 40 000 of which were considered as so-called »burn-in« samples. Due to occurrence of autocorrelation of results obtained from adjacent samples, genetic parameters were determined based on values obtained from every 100th sample. Variance components as well as heritability and repeatability indices were therefore determined based on results of 600 samples. The POSTGIBBS1F90 computer software (Tsuruta & Misztal 2006) was used to determine the number of samples initially rejected.

Below is the linear model applied to estimate variance components.

$$y = X_{fy} \beta_{fy} + X_w \beta_w + X_t \beta_t + Z_a a + Z_{pe} pe + e \quad (1)$$

where y is the 15 938×1 observation vector, β_{fy} , β_w , β_t are the fixed effects vectors: flock-year of birth (146×1), dam's age (6×1); dam's birth type (2×1), a is the 9 297×1 random genetic additive effects vector, pe is the 9 297×1 random permanent environment effects vector, X_{fy} , X_w , X_t are the incidence matrices for permanent effects: flock-year of birth (15 938×146), dam's age (15 938×6); dam's birth type (15 938×2), Z_a is the 15 938×9 297 incidence matrix for random direct additive genetic effects, Z_{pe} is the 15 938×9 297 incidence matrix for random permanent environment effects and e is the 15 938×1 random errors vector.

The following assumptions concerning the random effects variance model were adopted:

$$\text{var}(\mathbf{a}) = \mathbf{A}\sigma_a^2, \text{var}(\mathbf{pe}) = \mathbf{I}_q\sigma_{pe}^2, \text{var}(\mathbf{e}) = \mathbf{I}_n\sigma_e^2, \quad (2)$$

where \mathbf{A} is the $9\,297 \times 9\,297$ dimensional additive relationship matrix, \mathbf{I}_n and \mathbf{I}_q are the identity matrices, σ_a^2 is the direct additive genetic variance, σ_{pe}^2 is the random permanent environment effects variance, σ_e^2 is the error variance and σ_p^2 is the phenotypic variance ($\sigma_p^2 = \sigma_a^2 + \sigma_{pe}^2 + \sigma_e^2$).

While estimating variance components with the use of a threshold model, the same random and fixed effects were taken into account, the difference, however, was that with this model the modelled parameter was the so-called »unobserved tendency«.

Estimating genetic parameters with the AI-REML method, the same convergence index, equal to 10^{-10} , was adopted for all models. Errors of estimated (co)variances were approximated according to the method described by Klei & Tsuruta (2008). In the case of the GS method, standard variance components errors and genetic parameters, determined based thereon, were calculated as standard deviations for the values of these components, and indices obtained from the abovementioned 600 samples.

Heritability (h^2) and repeatability (r') were obtained applying the following formulas, respectively:

$$h^2 = \frac{\sigma_a^2}{\sigma_p^2} \quad r' = \frac{(\sigma_a^2 + \sigma_{pe}^2)}{\sigma_p^2} \quad (2)$$

Results

Table 1 shows basic measures of location and variability of the number of lambs born and reared. The share of multiple litters in the studied population was approximately 30 (Table 2).

Using the multiple regression method the following independent variables were selected, which were significantly associated with the number of lambs born and reared: flock, year of birth, age, and ewe's birth type, flock \times year of birth interaction. The selected variables were taken into account while estimating (co)variance components.

The values of LSB heritability indices estimated by means of the AI-REML and GS (linear model) methods were similar (Table 3). Also similar were the values of standard errors for variance components. Applying the GS method in combination with a threshold model resulted in obtaining nearly two times higher heritability compared to that obtained when using linear models. A similar tendency in terms of the influence of the model and method on obtained results was noted for estimated repeatability. Heritability of the number of lambs reared was basically similar regardless of estimation model and method, it fluctuated between 0.016 and 0.020. Influence of the model type was noted in terms of repeatability index, i.e. a significantly higher result was obtained using a threshold model.

Table 3

Estimates of (co)variances components, heritability and repeatability of number of born (LSB) and reared lambs (LSW)

	LSB			LSW		
	REML-LM	GS-LM	GS-TM	REML-LM	GS-LM	GS-TM
σ_a^2	0.0053	0.0061	0.0137	0.0039	0.0049	0.0032
SD σ_a^2	0.0019	0.0021	0.0049	0.0020	0.0021	0.0018
σ_{pe}^2	0.0084	0.0078	0.0162	0.0082	0.0074	0.0081
SD σ_{pe}^2	0.0021	0.0021	0.0053	0.0023	0.0022	0.0022
σ_e^2	0.1999	0.1998	0.2237	0.2385	0.2384	0.1498
SD σ_e^2	0.0025	0.0025	0.0079	0.0030	0.0030	0.0029
σ_p^2	0.2136	0.2137	0.2535	0.2506	0.2507	0.1610
h^2	0.025	0.029	0.054	0.016	0.019	0.020
SD h^2		0.010	0.019		0.008	0.011
r'	0.064	0.065	0.118	0.048	0.049	0.070
SD r'		0.006	0.012		0.006	0.010
σ_e^2 / σ_p^2	0.936	0.935	0.8824	0.952	0.951	0.930

LM: linear model, TM: threshold model

Discussion

Mean numbers of lambs born and reared, presented in Table 1, are typical of the Polish Merino bred in Poland (Sheep And Goats Breeding In Poland In 2008, 2009).

The research results confirm low influence of genetic assumptions on the number of lambs born and reared. The values of heritability and repeatability indices of both the traits found in the research are basically very much the same as those found by many other authors (Altarriba *et al.* 1998, Bromley *et al.* 2000, Hanford *et al.* 2002, 2003, Matos *et al.* 1997a, Okut *et al.* 1999, Olivier *et al.* 2001, Piwczyński 2009, Sousa *et al.* 2000). Considerably higher values of heritability index for ewe prolificacy were found by De Vries *et al.* (2005), Mroczkowski *et al.* (1981) in German Merino and Blackhead research. His estimates were made using analysis of variance.

Bromley *et al.* (2000), Hanford *et al.* (2002, 2003), Matos *et al.* (1997a), Okut *et al.* (1999), Olivier *et al.* (2001), Piwczyński (2009), Sousa *et al.* (2000) estimated heritability of the number of lambs born and reared with the use of the REML method and a linear model obtaining value ranges as follows: LSB – 0.01-0.23, LSW – 0.00-0.17. Matos *et al.* (1997a) and Piwczyński (2009) also estimated repeatability of this traits, and it equalled respectively: LSB – 0.107-0.111, LSW – 0.074. On the other hand, research based on using a threshold model (Altarriba *et al.* 1998, Matos *et al.* 1997a, Piwczyński 2009) resulted in obtaining the following values of heritability indices: LSB – 0.077-0.250, LSW – 0.054. Exceptionally high values of LSB heritability index (0.34-0.43), rising in subsequent litters, and estimated with the use of a threshold model and the Gibbs sampling method, were obtained by Yazdi *et al.* (1999). Altarriba *et al.* (1998) and Piwczyński (2009) conducted research on determining LSB repeatability, and obtained values ranging as follows: LSB – 0.141-0.186, LSW – 0.102.

Based on conducted research it was found that heritability estimated in respect of the number of lambs born was higher than that relating to the number of lambs reared, which is compatible with findings of numerous other studies (Bromley *et al.* 2000, Hanford *et al.* 2002,

2003, Okut *et al.* 1999, Olivier *et al.* 2001, Piwczyński 2009, Sousa *et al.* 2000). It may suggest that selection on the number of lambs born (prolificacy) should be more efficient than on the number of lambs reared from a mated dam.

In this research it was established that higher differences between estimations made using linear and threshold models occurred in respect of the number of lambs born as compared to reared (Table 3). Probably it is a result of a smaller number of trait 3 categories (1, 2, 3) and not 4 (0, 1, 2, 3). Abdel-Azim & Berger (1999) proved that increase in the number of trait value categories improves estimation accuracy, and at the same time the difference between estimations made using linear and threshold models decreases.

Currently conducted researches, similarly to an earlier one (Piwczyński 2009), are proof that the AI-REML and GS estimation methods yields similar outcome when a linear model is applied.

A number of authors (Matos *et al.* 1997a, Olesen *et al.* 1994, Piwczyński 2009, Sousa *et al.* (2000) have dealt with comparisons of heritability estimates obtained by means of linear and threshold models based on the same numerical input. Results of their researches confirm results of research by authors hereof, namely higher values of estimated indices were obtained when applying a threshold model as opposed to a linear model – twice as high, for the most part. One may presume that considerably higher heritability and repeatability indices obtained using threshold models as compared to linear models likely stem from the fact that threshold models account for the majority of total variability (Matos *et al.* 1997a, Olesen *et al.* 1994, Piwczyński 2009, Sousa *et al.* 2000).

A decision on whether to choose a linear or threshold model in order to estimate variance components may be taken based on measures of model quality. Kadarmideen *et al.* (2000) established that estimates obtained with the use of a threshold model usually have a higher standard error. Also, Olesen *et al.* (1994) conducted a genetic analysis of the number of lambs born, using linear and threshold models. They proved that model quality measures (MSE as well as the index of correlation between actual and forecast values) and predictive ability were similar in the case of both the linear and the threshold model (sire component). Abdel-Azim & Berger (1999) and Matos *et al.* (1997b) on the other hand, comparing accuracy of estimates made with the use of two different models, by means of such measures as MSE and predictive ability, found that they were similar or slightly more favourable in the case of a threshold model. Taking into account error variance percentage (%) in the total phenotypic variance, one may conclude that a threshold model accounts slightly better for total variability than a linear one.

Concluding, it must be said that estimated values for heritability of the number of lambs born in a litter point to low participation of genetic assumptions in shaping the phenotype of this trait regardless of the mathematical model used for estimation. The research showed low repeatability of the number of lambs born and reared. It was established that genetic parameters estimations made with the use of linear models as well as AI-REML and GS methods were similar. At the same time, approximately two times higher values were obtained using a threshold model. From the applied models, a threshold model was found to be the more adequate one, due to better accounting for total variability.

References

- Abdel-Azim GA, Berger PJ (1999) Properties of threshold model predictions. *J Anim Sci* 77, 582-590
- Altarriba J, Varona L, Garcia-Cortés LA, Moreno C (1998) Bayesian inference of variance components for litter size in rasa Aragonesa sheep. *J Anim Sci* 76, 23-28
- Bromley CM, Snowden GD, van Vleck LD (2000) Genetic parameters among weight, prolificacy and wool traits of Columbia, Polypay, Rambouillet and Targhee sheep. *J Anim Sci* 78, 846-858
- Dempster ER, Lerner IM (1950) Heritability of threshold characters *Genetics*. 35, 212-236
- De Vries F, Hamann H, Distl O (2005) Genetic parameter for reproduction traits in land sheep breeds. *Arch Tierz* 48, 76-85 [in German]
- Dobek A, Wójtowski J, Szwaczkowski T, Molinski K, Gut A (2004) Genetic variability for birth and fourth week weights in sheep. *Arch Tierz* 47, Special Issue, 64-72
- Duguma G, Schoeman SJ, Cloete SWP, Jordaan GF (2002) Genetic and environmental parameters for ewe productivity in Merinos. *S Afr J Anim Sci* 32, 154-159
- Gianola D (1982) Theory and analysis of threshold characters. *J Anim Sci* 54, 1079-1096
- Hagger C (2002) Multitrait and repeatability estimates of random effects on litter size in sheep. *Anim Sci* 74, 209-216
- Hanford KJ, van Vleck, LD, Snowden GD (2002) Estimates of genetic parameters and genetic change for reproduction, weight, and wool characteristics of Columbia sheep. *J Anim Sci* 80, 3086-3098
- Hanford KJ, van Vleck, LD, Snowden GD (2003) Estimates of genetic parameters and genetic change for reproduction, weight, and wool characteristics of Targhee sheep. *J Anim Sci* 81, 630-640
- Kadarmideen HN, Thompson R, Simm G (2000) Linear and threshold model genetic parameters for disease, fertility and milk production in dairy cattle. *Anim Sci* 71, 411-419
- Klei B, Tsuruta S (2008) Approximate variance for heritability estimates. http://nce.ads.uga.edu/html/projects/AI_SE.pdf [last accessed 23.02.2011]
- Lee GJ, Atkins KD, Sladek MA (2009) Genetic parameters for lifetime reproductive performance of merino ewes. *Proc Assoc Advmt Anim Breed Genet* 18, 382-385
- Matos CAP, Thomas DL, Gianola D, Tempelman RJ, Young LD (1997a) Genetic analysis of discrete reproductive traits in sheep using linear and nonlinear models: I Estimation of genetic parameters. *J Anim Sci* 75, 76-87
- Matos CAP, Thomas DL, Gianola D, Perez-Enciso M, Young LD (1997b) Genetic analysis of discrete reproductive traits in sheep using linear and nonlinear models: II Goodness of fit and predictive ability. *J Anim Sci* 75, 88-94
- Misztal I (2007) BLUPF90 family of programs. <http://nce.ads.uga.edu/~ignacy/newprograms.html> [last accessed 28.06.2011]
- Mroczkowski S, Schnarr W, Wassmuth R (1981) Heritability of fertility in Merino-sheep and black-face-meat sheep, *Züchtungskunde* 53, 71-77 [in German]
- Naazie A, Makarechian M, Berg RT (1991) Genetic, phenotypic, and environmental parameter estimates of calving difficulty, weight, and measures of pelvic size in beef heifers. *J Anim Sci* 69, 4793-4800
- Noor RR, Djajanegara A, Schüler L (2001) Selection to improve birth and weaning weight of Javanese Fat Tailed sheep. *Arch Tierz* 44, 649-659
- Okut H, Bromley CM, van Vleck LD, Snowden GD (1999) Genotypic expression at different ages: I Prolificacy traits of sheep. *J Anim Sci* 77, 2357-2365
- Olesen I, Perez-Enciso M, Gianola D, Thomas DL (1994) A comparison of normal and nonnormal mixed models for number of lambs born in Norwegian sheep. *J Anim Sci* 72, 1166-1173
- Olivier WJ, Snyman MA, van Wyk JB, Erasmus GJ (1998) Genetic parameter estimates for fitness traits in South African Merino sheep. *Livest Prod Sci* 56, 71-77
- Olivier WJ, Snyman MA, Olivier JJ, van Wyk JB, Erasmus GJ (2001) Direct and correlated responses to selection for total weight of lamb weaned in Merino sheep. *S Afr J Anim Sci* 31, 115-121

- Piwczyński D (2004) Heritability and repeatability of some reproductive traits of Polish Merino sheep. [in Polish] Zesz Nauk ATR in Bydgoszcz, Zootechnica 34, 29-33 [in Polish]
- Piwczyński D (2009) Improvement of performance traits in Polish Merino. postdoctoral dissertation 135, Appl Sci Rep of University of Technology and Life Sciences in Bydgoszcz, Poland [in Polish]
- Saboulard M, Russell WC, Riley M L (1995) Selection for lambing rate and clean fleece weight in sheep. J Anim Sci 73, 3195-3198
- SAS (2008) SAS/STAT User's guide 9.2. SAS Institute Inc., Cary, NC, USA
- Schmalwasser T, König KH, Al-Asli A (1991) Selection for fertility in Merino Mutton and Merino long wool sheep. I.: Heritability of fertility parameters and reliability of breeding values estimation for fertility. Arch Tierz 34, 69-75 [in German]
- Sheep And Goats Breeding In Poland In 2008 (2009) The Polish Sheep Breeders Association, Warsaw [in Polish]
- Sousa WH, Pereira CS, Bergmann JAG, da Silva FLR (2000) Estimates of components of variance and genetic parameters for reproductive traits by means of linear and threshold models. Rev Bras Zoot 29, s.2, 2237-2247 [in Portuguese]
- Strittmatter K (2004) The fine wool Mutton Merino in Germany – currently breed condition and problems. Arch Tierz 47, Special Issue, 25-35 [in German]
- Süß R, Siersleben K, Rösler H-J, Döring L. (2004) Analysis of the economic situation of sheep farms in Saxony-Anhalt. Arch Tierz 47, Special Issue, 135-141 [in German]
- Szyda J (2001) Application of the covariance function approach with an iterative two-stage algorithm to the estimation of parameters of a random regression test day model for dairy production traits. J App Genet 44, 177-191
- Tsuruta S, Misztal I (2006) THRGIBBS1F90 for estimation of variance components with threshold and linear models. J Dairy Sci 89, Suppl 1, 15
- Vries de MJ, van der Waaij EH, van Arendonk JAM (1998) Estimation of genetic parameters for litter size in sheep: A comparison of a repeatability and multivariate model. Anim Sci 66, 685-688
- Yazdi MH, Johansson K, Gates P, Näsholm A, Jorjani H, Liljedahl LE (1999) Bayesian analysis of birth weight and litter size in Baluchi sheep using gibbs sampling. J Anim Sci 77, 533-540

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