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HERITABILITY AND BREEDING VALUE OF SHEEP FERTILITY ESTIMATED BY MEANS OF THE GIBBS SAMPLING METHOD USING THE LINEAR AND THRESHOLD MODELS

ODZIEDZICZALNOŚĆ I WARTOŚĆ HODOWLANA PŁODNOŚCI OWIEC OSZACOWANA METODĄ PRÓBKOWANIA GIBBSA Z WYKORZYSTANIEM MODELI LINIOWEGO I PROGOWEGO

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Abstract

The research was carried out on 4,030 Polish Merino ewes born in the years 1991-2001, kept in 15 flocks from the Pomorze and Kujawy region. Fertility of ewes in subsequent reproduction seasons was analysed with the use of multiple logistic regression. The research showed that there is a statistical influence of the flock, year of birth, age of dam, flock × year interaction of birth on the ewes' fertility. In order to estimate the genetic parameters, the Gibbs sampling method was applied, using the univariate animal models, both linear as well as threshold. Estimates of fertility depending on the model equalled 0.067 to 0.104, whereas the estimates of repeatability equalled respectively: 0.076 and 0.139. The obtained genetic parameters were then used to estimate the breeding values of the animals in terms of controlled trait (Best Linear Unbiased Prediction method) using linear and threshold models. The obtained animal breeding values rankings in respect of the same trait with the use of linear and threshold models were strongly correlated with each other ($r_s = 0.972$). Negative genetic trends of fertility (0.01-0.08% per year) were found.

Keywords: BLUP, fertility, heritability, Polish Merino, sheep, threshold model

Detailed Abstract

Badania przeprowadzono na 4 030 owcach rasy merynos polski utrzymywanych w 15 stadach zlokalizowanych na terenie Pomorza i Kujaw urodzonych w latach 1991-2001 a użytkowanych rozpłodowo w latach 1993-2003. Analizę eksploratywną płodności maciorek przeprowadzono za pomocą wielokrotnej regresji logistycznej. W ramach wykonywanej analizy za pomocą metody selekcji modelu regresji typu forward wybrano następujące zmienne istotnie związane z płodnością maciorek, tj.: stado, rok urodzenia matki, wiek matki oraz interakcję stado × rok urodzenia. Analizę eksploratywną przeprowadzono przy użyciu pakietu komputerowego SAS wykorzystując procedurę LOGISTIC. W celu oszacowania parametrów genetycznych płodności zastosowano metodę próbkowania Gibbsa posługując się jednocechowymi modelami zwierzęcia: liniowym (LM) i progowym (TM). Program komputerowy GIBBS1F90 wykorzystano do szacowania parametrów genetycznych płodności według modelu liniowego, zaś THRGIBBS1F90 progowego. Szacując komponenty wariancji za pomocą metody próbkowania Gibbsa generowano 100 000 próbek, z czego pierwsze 20 000 zostało uznane za tzw. próbki wstępne („burn in period"). Błędy standardowe komponentów wariancji i wyznaczonych na ich podstawie parametrów genetycznych obliczono jako odchylenia standardowe wartości tychże komponentów i wskaźników otrzymanych w 8 000 próbkach. Szacunki odziedziczalności płodności w zależności od modelu wyniosły odpowiednio: LM – 0,067 i TM – 0,104, zaś powtarzalności: LM – 0,076 i TM – 0,139. Stwierdzono, że parametry genetyczne wyznaczone za pomocą modelu progowego obarczone były nieznacznie większymi błędami standardowymi niż liniowego. Zaobserwowano również, że model progowy wyjaśnia większą część zmienności niż liniowy, z tego względu należy wnioskować, że oszacowania odziedziczalności tej cechy winny być realizowane za pomocą tego modelu pierwszego (TM). Oszacowane komponenty wariancji zostały wykorzystane do oszacowania wartości hodowlanych (BV) zwierząt w zakresie kontrolowanej cechy. Wartość te (BV) oszacowane za pomocą metody BLUP-Animal Model, posługując się modelem liniowym i progowym. Przy zastosowaniu współczynnika korelacji Spearmana ustalono zależność między uszeregowaniem zwierząt w zakresie wartości hodowlanych (BV) uzyskanej za pomocą modelu liniowego oraz progowego. Wykazano, że otrzymane rankingi BV zwierząt w zakresie płodności były ze sobą silnie skorelowane (r_s = 0,972), co pozwala wnioskować, że oszacowania wartości hodowlanych mogą być wykonywane za pomocą modeli liniowych i progowych. Trendy genetyczne doskonalonych cech wyznaczono jako współczynnik regresji liniowej średnich wartości hodowlanych na rok urodzenia zwierząt. Zarówno te wyznaczone na podstawie modelu liniowego (-0,01%), jak i progowego (-0,08%) świadczą o pogarszającej się wartości genetycznej badanej populacji w zakresie płodności.

Introduction

The fertility of dams is the chief factor in the assessment of profitability of sheep farming. Unfortunately, genetic improvement in this area is very difficult relative to other production traits characterized with lower genetic conditioning (Matika, et al., 2001, Matos et al., 1997, Piwczyński, et al., 2004, Piwczyński and Mroczkowski, 2009, Sousa, et all, 2000). Moreover, discovering the genetic conditioning of fertility is more complicated than in the case of, for instance, body weight or milk yield. The reason for this is its binomial character, which, to make matters even more difficult, has abnormal distribution.

The results obtained in the research by Al-Shorepy and Notter (1997) indicate that improving sheep in terms of fertility one may expect a correlated selection effect on the number of lambs born in a litter. Also, findings by one of the authors (Piwczyński, et al., 2004) confirm favourable positive genetic dependencies between fertility and prolificacy (0.214) as well as the number of reared lambs from 1 mated ewe (0.334).

Various methods and models are used to estimate genetic parameter as well as the breeding value with regard to their binomial traits. Among other methods, those used for this purpose include the REML method (Lee et al., 2009, Matika et al., 2001, Piwczyński, et al., 2004, Sousa et al., 2000), the Gibbs sampling method (Piwczyński and Mroczkowski, 2009), and also the linear (Matos, et al., 1997, Olesen, et al., 1994, Piwczyński, et al., 2004, Sousa, et all, 2000, Varona, et al., 1999, Vatankhah et al., 2006) and the threshold model (Matos, et al., 1997, Olesen, et al., 1994, Piwczyński and Mroczkowski, 2009, Sousa et all, 2000, Varona, et al., 1999, Vatankhah, et al., 2006). Previous reports in the literature present studies in which probit or logit transformations were applied first (Matika, et al., 2001, Piwczyński, et al., 2004), before estimation of binomial trait heritability. Some papers describe estimates of parameters obtained in accordance with the mean value of several consecutive ewe performance values (for instance 2 or 3) (Piwczyński, et al., 2004) , or the life performance (Lee, et all, 2009).

The aim of the paper was to estimate heritability and breeding value as regards fertility of Polish Merino ewes, obtained in selected flocks in the Pomorze and Kujawy region by means of the Gibbs sampling method, using univariate linear (LM) and threshold (TM) animal models.

Material and Methods

The research was conducted on Polish Merino sheep maintained in 15 flocks located in the Pomorze and Kujawy region. Data concerning fertility of 4.030 ewes came from breeding documentation from the years 1991-2003, made available by the Regional Association of Sheep and Goat Breeders in Bydgoszcz. The assessed ewes were from the years 1991-2001, and they were used between 1993 and 2003.

Ewe fertility was analysed in subsequent reproduction seasons, gathering information on 17,934 lambings. The pedigree information of examined population of animals was completed as far as possible up to 3rd generation. In total, the pedigree base was constituted by 9,563 animals.

As part of the conducted statistical procedure, the basic descriptive measures of ewe fertility were calculated (Table 1). The explorative analysis of ewe fertility was carried out using multiple logistic regression (Piwczyński, 2009, SAS Inc., 2008). As part of the analysis, using the method of the forward selection type of regression model (Piwczyński and Mroczkowski, 2009, SAS Inc., 2008), the following significant variables connected with ewe fertility were selected: flock (X^2=339.2; P<0.0001), dam’s year of birth (X^2=54.3; P<0.0001), dam’s age (X^2=486.2; P<0.0001),, and the flock x year of birth interaction (X^2=28.8; P<0.0001). The assessment of significance of parameters, i.e. the selected variables, was carried out by means of the Wald statistics (SAS Inc., 2008). The statistical analysis was conducted by means of the SAS package, using the LOGISTIC procedure (SAS Inc., 2008).

The estimators of the variance components were estimated by means of the Gibbs sampling method, using univariate animal models: linear and threshold (in the case of this model, the so-called “unobservable tendency” (l) was modelled). The analysis model looked as follows:

$$\mathbf{y}\ (\mathbf{l}) = \mathbf{X}_{fr}\boldsymbol{\beta}_{fr} + \mathbf{X}_{s}\boldsymbol{\beta}_{s} + \mathbf{Z}_{a}\mathbf{a} + \mathbf{Z}_{pe}\mathbf{pe} + \mathbf{e},$$

where: $\mathbf{y}$ – 17934 × 1 observation vector; ($\mathbf{l}$) – vector of the 17,934 underlying values; $\boldsymbol{\beta}_{fr}$, $\boldsymbol{\beta}_{s}$ – fixed effects vectors: flock-year of birth (146 × 1), age of dam (6 × 1); $\mathbf{a}$ – 9563 × 1 vector of random genetic additive effects; $\mathbf{pe}$ – 9,563 × 1 vector of random permanent influences of the animal’s specific environment; $\mathbf{X}_{fr}$, $\mathbf{X}_{s}$, – incidence matrices for fixed effects: flock-year of birth (17,934 x 146) and age of the dam

(17,934 x 6); $\mathbf{Z}_a$ – 17,934 × 9,563 incidence matrix for random direct additive genetic effects; $\mathbf{Z}_{pe}$ – 17,934 × 9,563 incidence matrix for random permanent influences of the animal's specific environment; **e** – 17,934 × 1 random error vector.

The following assumptions regarding variance of the random effects of the model were made: var(**a**) = $\mathbf{A}\sigma^2_a$, var(**pe**) = $\mathbf{I_q}\sigma^2_{pe}$, var(**e**) = $\mathbf{I_n}\sigma^2_e$,
where: **A** – 9563 × 9563 dimensional matrix of additive relationship among animals, $\mathbf{I_n}$, $\mathbf{I_q}$ – identity matrices; σ^2_a – genetic additive direct variance; σ^2_{pe} – variance of random permanent influences of the animal's specific environment; σ^2_e – error variance (in the case of the threshold model, variance equals 1); σ^2_p – phenotypic variance ($\sigma^2_p = \sigma^2_a + \sigma^2_{pe} + \sigma^2_e$).

Heritability and repeatability were obtained with the use of the following formulas, respectively: $h^2 = \sigma^2_a / \sigma^2_p$; $r' = (\sigma^2_a + \sigma^2_{pe}) / \sigma^2_p$.

When estimating variance components by means of the threshold model, the same random and fixed effects as in the linear model were taken into consideration.

The GIBBS1F90 software (Misztal, 2008) was used to estimate the genetic parameters of fertility in accordance with the linear model, whereas THRGIBBS1F90 (Tsuruta and Misztal, 2008) in accordance with the threshold model. While estimating variance components by means of the Gibbs sampling method, 100,000 samples were generated, the first 20,000 of which were declared as initial samples ("burn in period"). The POSTGIBBS1F90 software (Tsuruta and Misztal, 2008) was the tool used to determine the number of samples being initially rejected. Due to occurring autocorrelations between the results obtained from adjacent samples, genetic parameters were determined from values obtained from every tenth sample. Variance components as well as heritability and repeatability indexes were therefore determined based on the results of 8,000 samples.

Standard errors of variance components and the genetic parameters determined based upon them were calculated as standard deviations of the value of those components and indexes obtained in the said 8,000 samples.

The breeding value (BV) assessment of animals in terms of fertility was made by means of the BLUP-Animal Model, using the linear and threshold model. In the case of the former, the BLUPF90 computer software (Misztal, 2008) was used, and in the latter, CBLUP90THR (Misztal, 2008). One of the aspects of the conducted research was the determination of dependencies within the ranking of animals as regards breeding value (BV), obtained with the use of the linear and threshold model. In order to do that, the Spearman's rank correlation coefficient (SAS Institute Inc. 2008) was calculated. The changes in the mean breeding value of animals born in subsequent years were depicted in the graphs, for this purpose we used estimations resulting from the application of the threshold model. Genetic trends of fertility were determined as the linear regression coefficient of mean breeding values for the animal's year of birth.

Results

The fertility of controlled ewes was at a high level, generally exceeding corresponding indexes provided by the Polish Sheep Breeders Association [3] for the Polish Merino population in the years 2001-2008 (91.3-95.5%) (Table 1).

Using logistic regression analysis we selected the following traits associated with the fertility of the dam sheep: flock, ewe's year of birth, age of dams, flock x year of birth interaction). These traits were also indicated by other authors as a potential source of variability in ewe fertility (Piwczyński, 2009, Piwczyński, et al., 2004, Piwczyński and Mroczkowski, 2009). The fertility of dams, depending on their age, was between 92.0% and 95.0%. The most favourable results were observed within the group of animals aged 5 and 6 years. This is confirmed by percentage values presented in Table 1 as well as high values of the odds ratio, seen in Table 2.

Table 1. Descriptive characteristic of fertility

Level of the factor	N	Mean	SD
Age of dam			
2	5,165	92.0	27.2
3	3,312	92.2	26.8
4	2,797	93.6	24.4
5	2,265	94.9	22.0
6	1,816	95.0	21.8
7	2,579	94.1	23.5
Type of dams birth			
1	6,973	92.6	26.2
2	10,961	93.7	24.3
Flock			
A	1,483	88.9	31.4
B	2,999	88.2	32.3
C	1,053	96.6	18.2
D	935	93.0	25.4
E	622	96.3	18.9
F	695	95.1	21.6
G	2,446	96.0	19.5
H	1,143	95.5	20.7
I	1,108	90.2	29.8
J	861	92.6	26.2
K	419	92.4	26.6
L	833	95.3	21.1
M	1,463	92.7	26.0
N	752	98.0	14.0
O	1,122	98.5	12.2
Year of birth			
1991	637	92.5	26.4
1992	2,698	92.8	25.9
1993	2,463	92.0	27.1
1994	2,374	93.8	24.2
1995	2,292	95.3	21.1
1996	1,622	94.5	22.9
1997	2,146	95.2	21.4
1998	1,327	89.3	30.9
1999	1,092	94.0	23.7
2000	686	92.1	26.9
2001	597	89.9	30.1
Total	17,934	93.3	25.1

The odds ratios related to dams aged 5 and 6 mean that the odds of giving birth to offspring in these age groups is respectively 1.601 and 1.514 times higher than among dams lambing for the first time. We have not found any statistical proofs of the influence of the dam’s birth type on its fertility. However, we did observe that the relevant index was by 1.1 percent higher among twins as compared to sheep from single births (Table 1). There was a high diversity in terms of fertility indices depending on the flock (88.2-98.5%) and the dam's year of birth (89.3-95.2%).

Table 2. Odds ratios (OR) and 95% confidence limits (CL) in respect of dam's age (AgeDam)

Effect	OR	CL
AgeDam 3 vs 2	1.010	0.848-1.202
AgeDam 4 vs 2	1.216	1.000-1.479
AgeDam 5 vs 2	1.601	1.277-2.007
AgeDam 6 vs 2	1.514	1.183-1.938
AgeDam 7 vs 2	1.354	1.096-1.675

Table 3 shows heritability and repeatability estimated based on individual performance of ewes from subsequent reproduction seasons. The heritability of fertility obtained by means of the threshold model (TM) was 0.037 higher compared to that obtained by means of the linear model (LM). Whereas the repeatability index obtained using the threshold model was nearly twice as high as the linear one. It must be concluded that the obtained heritability and repeatability values indicate that the influence of genetic assumptions on ewe fertility is low.

Table 3. Estimates of variances components, heritability (h^2) and repeatability (r') of fertility, and correlation between rankings of breeding values of animals estimated using the linear and threshold models (r_s)

Estimates	Linear model	Threshold model
$\sigma^2_a \pm SD$	0.00413 ± 0.00053	0.12114 ± 0.03010
$\sigma^2_{pe} \pm SD$	0.00042 ± 0.00033	0.03989 ± 0.02578
$\sigma^2_e \pm SD$	0.05563 ± 0.00110	1.00275 ± 0.02163
$\sigma^2_p \pm SD$	0.06018 ± 0.00115	1.16377 ± 0.03748
h^2	0.067 ± 0.009	0.104 ± 0.024
r' ± SD	0.076 ± 0.008	0.139 ± 0.022
r_s	0.972***	

In Figure 1, we presented the genetic trend related to fertility, calculated using the linear and threshold models. In both cases, a negative, although small, tendency was observed in terms of the analysed trait. The conclusion with the threshold model is that the breeding value of the studied population decreased within the studied period by 0.0008, and with the linear model 0.0001. It needs to be emphasised that both regression indices proved insignificant. Such high differences as regards the calculated trend may arise from differences in estimated values of the genetic additive direct variance and heritability obtained with the use of the linear and threshold models (Table 3). It is worth noting the significant fluctuations of the genetic value of the examined population in subsequent years, particularly starting with the year 1996. A possible explanation for this could be the deteriorating conditions of sheep farming in Poland, including a dramatic drop in population (Polish Sheep Breeders Association). Fluctuations of the breeding value in terms of fertility at a similar level were observed in previous studies by Piwczyński and Mroczkowski (2009).

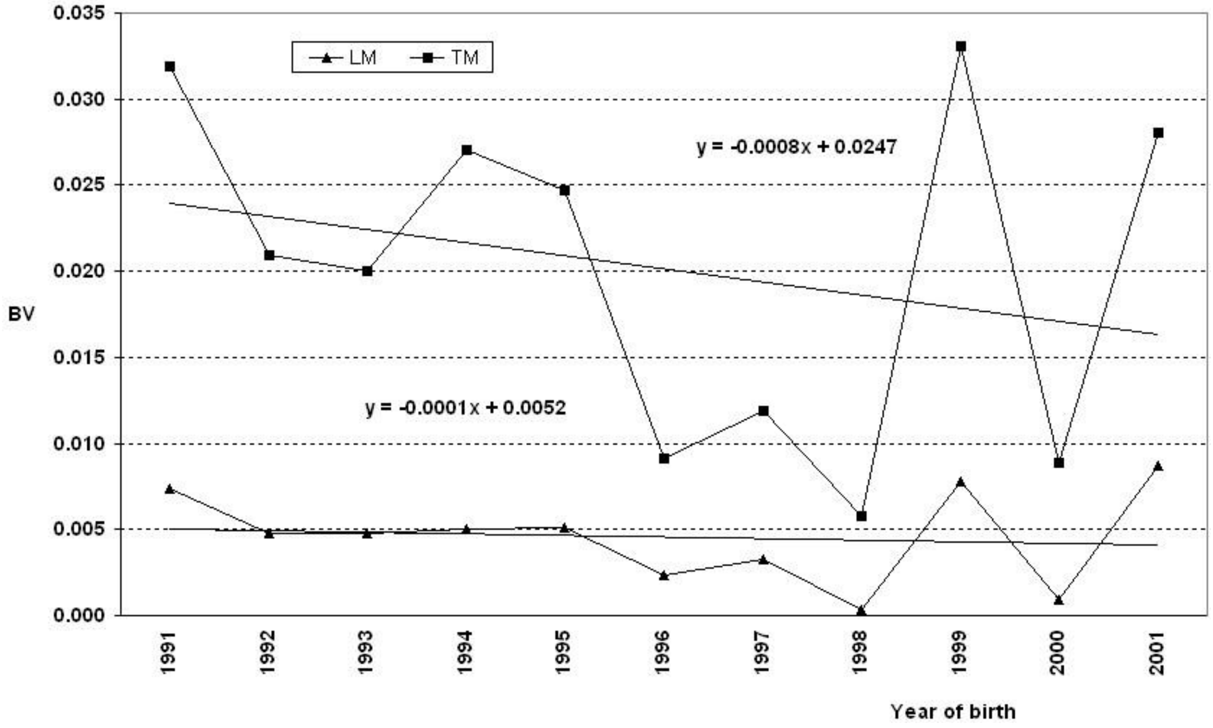

Figure 1. Genetic trends for the fertility of ewes

Discussion and Conclusions

The ranges of both the heritability index (0.01-0.39) and repeatability index (0.090-0.670) of fertility as seen in earlier works have been large: Lee, et all, 2009, Matika, et al., 2001, Matos et al., 1997, Olesen, et al., 1994,Olivier, et al., 1998, Piwczyński, et al., 2004, Piwczyński and Mroczkowski, 2009, Rosati, et al., 2002, Snyman, 1998, Sousa, et all, 2000, Vatankhah, et al., 2006). One may assume that, similarly as in the authors' own research, this is largely due to which method and the model of statistical analysis was used (Matos et al., 1997, Olesen, et al., 1994, Piwczyński and Mroczkowski, 2009, Sousa, et all, 2000, Vatankhah, et al., 2006).

Matos et al. (1997) have found that heritability of fertility estimated by means of the animal's TM (0.10-0.17) was from three to four times higher than when the LM was used (0.03-0.04). On the other hand, the repeatability of a trait estimated with the use of sire's LM (0.10-0.13) and TM (0.10-0.17) was similar.

Olesen et al. (1994) compared estimated heritability values for the number of lambs born in a litter obtained with the use of linear and threshold sire models. A three times higher heritability of the trait was found with the use of the TM (0.12-0.20) then LM (0.26-0.39) model.

In earlier studies by Piwczyński and Mroczkowski (2009), the heritability of fertility obtained was 0.06 using the linear model, and 0.01 using the threshold model. Significant differences depending on the model were also established in the case of the repeatability index: LM – 0.23, TM – 0.09.

De Souse et al. (2000) found a four times higher heritability of fertility estimated with the use of the TM (0.12) compared to the LM (0.03). The authors (De Souse, et al., 2000) obtained higher heritability values when applying the threshold rather than the linear model in relation to the number of lambs born (TM – 0.13; LM – 0.09), and reared (TM – 0.05; LM – 0.01).

Whereas in the research by Vatankhah et al. (2006) the heritability index of conception rate was as much as eight times higher when estimated using the threshold model (0.08) than when using the linear one (0.01). In the case of repeatability the differences between estimates by means of the linear and threshold model were only slightly lower, equalling respectively 0.10 and 0.67.

Considerably higher indexes of heritability and repeatability obtained with the use of threshold models as opposed to the linear models probably stem from the fact that threshold models explain the majority of total variability (Matos et all., 1997, Piwczyński, 2009, Piwczyński and Mroczkowski, 2009).

Taking into consideration standard deviations for heritability indexes one may conclude that the estimates obtained with the use of the TM model were relatively (SD/h^2*100) more loaded than LM (23.1 vs. 13.4%). Standard deviations for repeatability indexes did not differ considerably between the models, respectively: LM – 10.52%; TM – 15.8%.

However, in previous studies by Piwczyński and Mroczkowski (2009), the relative errors in heritability and repeatability, estimated with the use of the linear and threshold models, were similar to each other but on average twice as high as in the present research.

The breeding value of the analysed animal population was estimated by means of two differing models – linear and threshold. Very high significant dependencies were found ($p < 0.001$) between rankings of animals' breeding values obtained using the two models (Table 3). The results obtained in this area correspond with earlier results in studies by Piwczyński and Mroczkowski (2009) as well as by Sousa et al. (2000), in which the correlation between the results for the order of breeding values obtained with the use of the linear and threshold models was close to unity. We may therefore suspect that it is possible to select animals in terms of their fertility by how the breeding value obtained using both the linear and threshold models is assessed.

Summing up the results of the research, one may conclude that the obtained fertility for the Polish Merino ewes from flocks in the Pomorze and Kujawy region was similar in comparison to the national average. Significant factors responsible for variability of ewe fertility were flock, age of dam, year of lamb birth, and flock × year of birth interaction. Heritability of ewe fertility, as well repeatability estimated with the use of the threshold model was higher than that obtained with the use of the linear model. The fact that the indexes of heritability and repeatability calculated using the threshold models are much higher as compared to those calculated using the linear models is likely due to threshold models accounting for the majority of total variability. Therefore, it may be concluded that the heritability of fertility should be estimated by means of the threshold model.

It was found that the ranking of breeding values of animals obtained using the BLUP method and the linear and threshold models were practically identical.

Negative genetic trends in terms of fertility were demonstrated, at the annual level of 0.01-0.08%, depending on the model.

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