The algorithm of Bayesian estimation of maternal genetic and permanent maternal environmental variances in a two-trait binary threshold model

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ABSTRACT: The paper presents an algorithm for the estimation and prediction of parameters in a two-trait binary threshold model. The model includes fixed effects and the following random effects: genetic direct additive, genetic maternal additive and permanent maternal environmental effects. The Gibbs sampling procedure was used to estimate the parameters. The algorithm was illustrated with a numerical example showing appropriateness of the proposed method.

Keywords: binary traits; genetic effects; Gibbs sampling; threshold model; maternal effects

In recent years significant reconstructions have been done in the programs of genetic improvement of farm animals. Although long-term selection for the improvement of production traits has reached the assumed objectives, it has also contributed to the degradation of the so-called functional traits (Hansen, 2000). Most production traits are genetically and phenotypically continuous. For this reason linear models could be successfully used for their analysis. However, even though determined by the number of loci, some functional traits are discontinuous variables. They are called threshold traits. Many of them, for instance fertility, hatchability or resistance to certain diseases are binary traits.

In order to take into consideration the specific character of threshold traits, threshold models are used for their analysis (Gianola and Foulley, 1983; Harville and Mee, 1984). In these models it is assumed that the phenotypic categorized variability of a trait is determined by the values of a certain unobserved random continuous variable, called liability. This variable is linked with the limits of categories (thresholds), i.e. the observation is classified on the basis of the phenotype to a given category if the value of the unobserved variable exceeds the threshold of this category (also unobserved). In the hidden scale standard deviation of the unobserved variable is used as the unit of measurement (Falconer, 1989). In the case of two categories it is assumed, without the loss of generality, that the threshold between these categories lies at point 0 (Gianola and Foulley, 1983; Misztal *et al.*, 1989).

Threshold models are an effective alternative to data transformation. It was shown that the adoption of such models gives more accurate estimates of genetic parameters (Matos *et al.*, 1997; Abdel-Azim and Berger, 1999; Dobek *et al.*, 2003).

Some of the threshold traits have a complex genetic background. They may be determined to a large extent by indirect maternal effects, both genetic and environmental ones (Sewalem, 1989). In this paper we extend a previously described model (Moliński *et al.*, 2003) by the genetic maternal and permanent environmental effects. We present an algorithm for the estimation of genetic parameters in a two-trait

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The study was conducted within the research project of the Committee for Scientific Research (Grant No. 5 P06 D 02019).

model when the interesting traits are threshold traits with two categories (binary traits).

MODEL

Let us consider the vector of observations $\mathbf{y}$. The components of $\mathbf{y}$ are taking values 0 or 1. The value of $\mathbf{y}$ is conditioned by an unobservable vector $\mathbf{w}$ (liabilities). When w is positive, the phenotypic expression y is 1, otherwise it is 0. For the vector $\mathbf{w}$ we are assuming the following model:

$$\mathbf{w} = (\mathbf{I}_2 \otimes \mathbf{X})\boldsymbol{\beta} + (\mathbf{I}_2 \otimes \mathbf{Z}_1)\mathbf{a} + (\mathbf{I}_2 \otimes \mathbf{Z}_2)\mathbf{m} + (\mathbf{I}_2 \otimes \mathbf{Z}_3)\mathbf{c} + \mathbf{e}$$

where:

$$\mathbf{w} = \begin{bmatrix} \mathbf{w}^{(1)} \\ \mathbf{w}^{(2)} \end{bmatrix},\ \boldsymbol{\beta} = \begin{bmatrix} \boldsymbol{\beta}^{(1)} \\ \boldsymbol{\beta}^{(2)} \end{bmatrix},\ \mathbf{a} = \begin{bmatrix} \mathbf{a}^{(1)} \\ \mathbf{a}^{(2)} \end{bmatrix},\ \mathbf{m} = \begin{bmatrix} \mathbf{m}^{(1)} \\ \mathbf{m}^{(2)} \end{bmatrix},\ \mathbf{c} = \begin{bmatrix} \mathbf{c}^{(1)} \\ \mathbf{c}^{(2)} \end{bmatrix},\ \mathbf{e} = \begin{bmatrix} \mathbf{e}^{(1)} \\ \mathbf{e}^{(2)} \end{bmatrix}$$

and

$\mathbf{w}^{(k)}$ = the N-vector of the values of the unobserved random variable (liability)
$\boldsymbol{\beta}^{(k)}$ = the p-vector of fixed effects
$\mathbf{a}^{(k)}$ = the q-vector of random genetic direct additive effects
$\mathbf{m}^{(k)}$ = the q-vector of random genetic maternal additive effects
$\mathbf{c}^{(k)}$ = the v-vector of random permanent maternal environmental effects
$\mathbf{e}^{(k)}$ = the N-vector of effects of residuals for the k-th trait, $k = 1, 2$
$\mathbf{I}$ = the identity matrix of a given dimension
$\mathbf{X}$, $\mathbf{Z}_1$, $\mathbf{Z}_2$, $\mathbf{Z}_3$ = known matrices of corresponding dimensions with elements equal to 0 or 1

Further:
n = the number of observed animals
$N = \sum_{i=1}^{n} n_i$, while n_i is the number of observations (equal for two traits) for the i-th animal
q = the number of all the investigated animals
v = the number of dams

For the model parameters the following assumptions are adopted:

$$\mathbf{a}^{(k)} \sim N_q(\mathbf{0}, \mathbf{A}\sigma^2_{a_k}),\quad \mathbf{m}^{(k)} \sim N_q(\mathbf{0}, \mathbf{A}\sigma^2_{m_k}),\ \mathbf{c}^{(k)} \sim N_v(\mathbf{0}, \mathbf{I}_v\sigma^2_{c_k}),\ \mathbf{e}^{(k)} \sim N_N(\mathbf{0}, \mathbf{I}_N)$$

Moreover:

$$Var(\mathbf{u}) = Var\begin{pmatrix} \mathbf{a}^{(1)} \\ \mathbf{m}^{(1)} \\ \mathbf{a}^{(2)} \\ \mathbf{m}^{(2)} \end{pmatrix} = \begin{bmatrix} \sigma^2_{a_1} & \sigma_{a_1 m_1} & \sigma_{a_1 a_2} & \sigma_{a_1 m_2} \\ \sigma_{a_1 m_1} & \sigma^2_{m_1} & \sigma_{a_2 m_1} & \sigma_{m_1 m_2} \\ \sigma_{a_1 a_2} & \sigma_{a_2 m_1} & \sigma^2_{a_2} & \sigma_{a_2 m_2} \\ \sigma_{a_1 m_2} & \sigma_{m_1 m_2} & \sigma_{a_2 m_2} & \sigma^2_{m_2} \end{bmatrix} \otimes \mathbf{A} = \mathbf{V_u} \otimes \mathbf{A}$$

$$Var(\mathbf{c}) = Var\begin{pmatrix} \mathbf{c}^{(1)} \\ \mathbf{c}^{(2)} \end{pmatrix} = \begin{bmatrix} \sigma^2_{c_1} & 0 \\ 0 & \sigma^2_{c_2} \end{bmatrix} \otimes \mathbf{I}_v = \mathbf{V_c} \otimes \mathbf{I}_v$$

$$Cov(\mathbf{a}; \mathbf{c}) = \mathbf{0},\quad Cov(\mathbf{m}; \mathbf{c}) = \mathbf{0}$$

where: $\mathbf{A}$ = the q x q additive relationship matrix (Quaas, 1976)
$\sigma^2_{a_k}$ = the genetic direct additive variance for k-th trait
$\sigma^2_{m_k}$ = the genetic maternal additive variance for k-th trait
$\sigma_{a_k a_{k'}}$ = the covariance between direct additive effects for k-th and k'-th traits
$\sigma_{a_k m_{k'}}$ = the covariance between direct and maternal additive effects for k-th and k'-th traits
$\sigma_{m_k m_{k'}}$ = the covariance between maternal additive effects for k-th and k'-th traits
$\sigma^2_{c_k}$ = the permanent maternal environmental variance
k = 1, 2, k' = 1, 2

ESTIMATION OF PARAMETERS

Estimators and predictors of unknown model parameters may be obtained by Gibbs sampling (Sørensen *et al.*, 1995; Moliński *et al.*, 2003). In the Gibbs sampling method, the values of the parameter are generated from its *a posteriori* conditional distribution, assuming all the other parameters are known. The generated values may be treated as a sample from corresponding marginal distribution, when the condition of the stationarity of the process is satisfied. Let us adopt the following assumptions concerning the conditional distributions for the parameters (Sørensen *et al.*, 1995):

$w_{lj}^{(k)} \mid$ all the other parameters and $y_{lj}^{(k)} = 1$ ~

$N(\mathbf{x}_{lj}\boldsymbol{\beta}^{(k)} + \mathbf{z}_{1_{lj}}\mathbf{a}^{(k)} + \mathbf{z}_{2_{lj}}\mathbf{m}^{(k)} + \mathbf{z}_{3_{lj}}\mathbf{c}^{(k)}; 1)$ (left-truncated)

$w_{lj}^{(k)} \mid$ all the other parameters and $y_{lj}^{(k)} = 0$ ~

$N(\mathbf{x}_{lj}\boldsymbol{\beta}^{(k)} + \mathbf{z}_{1_{lj}}\mathbf{a}^{(k)} + \mathbf{z}_{2_{lj}}\mathbf{m}^{(k)} + \mathbf{z}_{3_{lj}}\mathbf{c}^{(k)}; 1)$ (right-truncated)

where: $y_{lj}^{(k)}$ = the j-th observation of the k-th trait for the l-th animal ($y_{lj}^{(k)} = 1$ or $y_{lj}^{(k)} = 0$)
$\mathbf{x}_{lj}$, $\mathbf{z}_{1_{lj}}$, $\mathbf{z}_{2_{lj}}$, $\mathbf{z}_{3_{lj}}$ = the lj-th row of corresponding matrices
$l = 1, 2, ..., n$
$j = 1, 2, ..., n_l$

Let the inverses of $\mathbf{V_u}$ and $\mathbf{V_c}$ be:

$$\mathbf{V_u}^{-1} = \begin{bmatrix} d_{11} & d_{12} & d_{13} & d_{14} \\ d_{12} & d_{22} & d_{23} & d_{24} \\ d_{13} & d_{23} & d_{33} & d_{34} \\ d_{14} & d_{24} & d_{34} & d_{44} \end{bmatrix},\quad \mathbf{V_c}^{-1} = \begin{bmatrix} d_{55} & 0 \\ 0 & d_{66} \end{bmatrix}$$

Elements of vectors $\boldsymbol{\beta}$, $\mathbf{a}$, $\mathbf{m}$, $\mathbf{c}$ are generated from normal distributions, the parameters of which are determined from the formulas given below:

i) fixed effects ($i = 1, ..., p; k = 1, 2$):

$$E(\boldsymbol{\beta}_i^{(k)}) = (\mathbf{x}_i'\mathbf{x}_i)^{-1}\mathbf{x}_i'(\mathbf{w}^{(k)} - \mathbf{Z}_1\mathbf{a}^{(k)} - \mathbf{Z}_2\mathbf{m}^{(k)} - \mathbf{Z}_3\mathbf{c}^{(k)})$$

$$Var(\boldsymbol{\beta}_i^{(k)}) = (\mathbf{x}_i'\mathbf{x}_i)^{-1}$$

ii) genetic direct additive effects ($i = 1, ..., q$):

$$E(\mathbf{a}_i^{(1)}) = (\mathbf{z}_{1i}'\mathbf{z}_{1i} + d_{11}\mathbf{A}^{ii})^{-1}[\mathbf{z}_{1i}'(\mathbf{w}^{(1)} - \mathbf{X}\boldsymbol{\beta}^{(1)} - \mathbf{Z}_2\mathbf{m}^{(1)} - \mathbf{Z}_3\mathbf{c}^{(1)}) \\ - d_{11}\mathbf{A}^{i,-i}\mathbf{a}_{-i}^{(1)} - d_{12}\mathbf{A}^{i.}\mathbf{m}^{(1)} - d_{13}\mathbf{A}^{i.}\mathbf{a}^{(2)} - d_{14}\mathbf{A}^{i.}\mathbf{m}^{(2)}]$$

$$Var(\mathbf{a}_i^{(1)}) = (\mathbf{z}_{1i}'\mathbf{z}_{1i} + d_{11}\mathbf{A}^{ii})^{-1}$$

$$E(\mathbf{a}_i^{(2)}) = (\mathbf{z}_{1i}'\mathbf{z}_{1i} + d_{33}\mathbf{A}^{ii})^{-1}[\mathbf{z}_{1i}'(\mathbf{w}^{(2)} - \mathbf{X}\boldsymbol{\beta}^{(2)} - \mathbf{Z}_2\mathbf{m}^{(2)} - \mathbf{Z}_3\mathbf{c}^{(2)}) \\ - d_{33}\mathbf{A}^{i,-i}\mathbf{a}_{-i}^{(2)} - d_{34}\mathbf{A}^{i.}\mathbf{m}^{(2)} - d_{13}\mathbf{A}^{i.}\mathbf{a}^{(1)} - d_{23}\mathbf{A}^{i.}\mathbf{m}^{(1)}]$$

$$Var(\mathbf{a}_i^{(2)}) = (\mathbf{z}_{1i}'\mathbf{z}_{1i} + d_{33}\mathbf{A}^{ii})^{-1}$$

iii) genetic maternal additive effects ($i = 1, ..., q$):

$$E(\mathbf{m}_i^{(1)}) = (\mathbf{z}_{2i}'\mathbf{z}_{2i} + d_{22}\mathbf{A}^{ii})^{-1}[\mathbf{z}_{2i}'(\mathbf{w}^{(1)} - \mathbf{X}\boldsymbol{\beta}^{(1)} - \mathbf{Z}_1\mathbf{a}^{(1)} - \mathbf{Z}_3\mathbf{c}^{(1)}) \\ - d_{12}\mathbf{A}^{i.}\mathbf{a}^{(1)} - d_{22}\mathbf{A}^{i,-i}\mathbf{m}_{-i}^{(1)} - d_{23}\mathbf{A}^{i.}\mathbf{a}^{(2)} - d_{24}\mathbf{A}^{i.}\mathbf{m}^{(2)}]$$

$$Var(\mathbf{m}_i^{(1)}) = (\mathbf{z}_{2i}'\mathbf{z}_{2i} + d_{22}\mathbf{A}^{ii})^{-1}$$

$$E(\mathbf{m}_i^{(2)}) = (\mathbf{z}_{2i}'\mathbf{z}_{2i} + d_{44}\mathbf{A}^{ii})^{-1}[\mathbf{z}_{2i}'(\mathbf{w}^{(2)} - \mathbf{X}\boldsymbol{\beta}^{(2)} - \mathbf{Z}_1\mathbf{a}^{(2)} - \mathbf{Z}_3\mathbf{c}^{(2)}) \\ - d_{34}\mathbf{A}^{i.}\mathbf{a}^{(2)} - d_{44}\mathbf{A}^{i,-i}\mathbf{m}_{-i}^{(2)} - d_{14}\mathbf{A}^{i.}\mathbf{a}^{(1)} - d_{24}\mathbf{A}^{i.}\mathbf{m}^{(1)}]$$

$$Var(\mathbf{m}_i^{(2)}) = (\mathbf{z}_{2i}'\mathbf{z}_{2i} + d_{44}\mathbf{A}^{ii})^{-1}$$

iv) permanent maternal environmental effects ($i = 1, ..., v$):

$$E(\mathbf{c}_i^{(1)}) = (\mathbf{z}_{3i}'\mathbf{z}_{3i} + d_{55})^{-1}[\mathbf{z}_{3i}'(\mathbf{w}^{(1)} - \mathbf{X}\boldsymbol{\beta}^{(1)} - \mathbf{Z}_1\mathbf{a}^{(1)} - \mathbf{Z}_2\mathbf{m}^{(1)})]$$

$$Var(\mathbf{c}_i^{(1)}) = (\mathbf{z}_{3i}'\mathbf{z}_{3i} + d_{55})^{-1}$$

$$E(\mathbf{c}_i^{(2)}) = (\mathbf{z}_{3i}'\mathbf{z}_{3i} + d_{66})^{-1}[\mathbf{z}_{3i}'(\mathbf{w}^{(2)} - \mathbf{X}\boldsymbol{\beta}^{(2)} - \mathbf{Z}_1\mathbf{a}^{(2)} - \mathbf{Z}_2\mathbf{m}^{(2)})]$$

$$Var(\mathbf{c}_i^{(2)}) = (\mathbf{z}_{3i}'\mathbf{z}_{3i} + d_{66})^{-1}$$

where: $\mathbf{A}^{ii}$ = the i-th diagonal element of $\mathbf{A}^{-1}$
$\mathbf{A}^{i.}$ = the i-th row vector of $\mathbf{A}^{-1}$
$\mathbf{A}^{i,-i}$ = the i-th row vector of $\mathbf{A}^{-1}$ with the i-th element skipped
$\mathbf{a}_{-i}^{(k)}$, $\mathbf{m}_{-i}^{(k)}$ = vectors $\mathbf{a}^{(k)}$ and $\mathbf{m}^{(k)}$ with i-th element removed
$\mathbf{x}_i$, $\mathbf{z}_{1i}$, $\mathbf{z}_{2i}$, $\mathbf{z}_{3i}$ = the i-th columns of corresponding matrices

The distributions for unknown components of variance and covariance are as follows:

$\mathbf{V_u} \mid$ all the other parameters ~ $IW_4[(\mathbf{U}^{1}\mathbf{A}^{-1}\mathbf{U})^{-1}, q]$

where: $\mathbf{U} = [\mathbf{a}^{(1)}, \mathbf{m}^{(1)}, \mathbf{a}^{(2)}, \mathbf{m}^{(2)}]$
$\sigma^2_{c_k} \mid$ all the other parameters ~ $(\mathbf{c}^{(k)'}\mathbf{c}^{(k)}) / \chi^2_v$
and *IW* denotes inverted Wishart distribution

SIMULATION STUDY

Data

The correctness of the proposed algorithm was checked through simulation studies. Therefore we simulated a female-limited trait for a real pedigree. The pedigree was taken from a layer flock and consisted of 9 generations, 6 476 birds, including 5 980 with known parents, out of which 5 353 were female. The distribution of the size of maternal groups is given in Figure 1. For each dam two binary traits were generated in 30 replications (corresponding to the average number of eggs destined for hatching). The simulation of data was conducted in two stages.

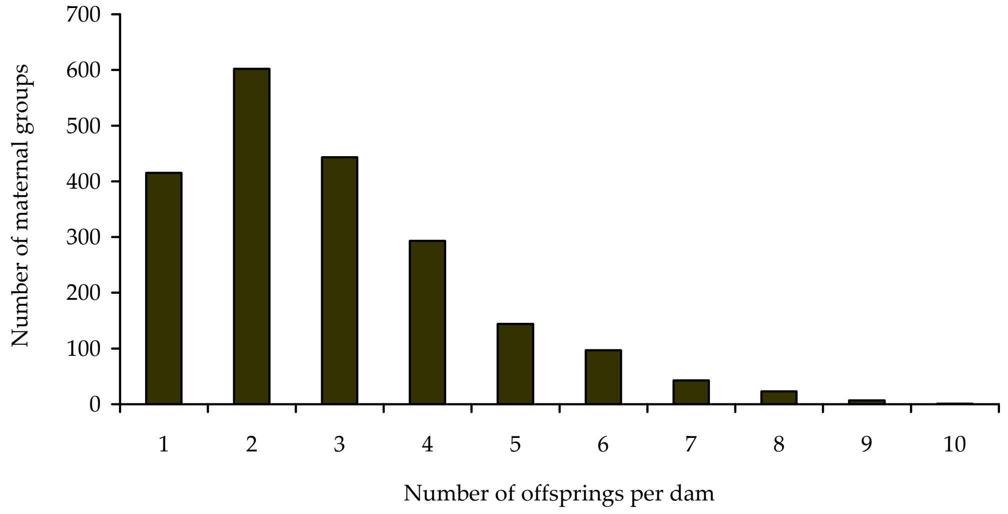

Figure 1. Empirical distribution of the number of offsprings per dam

Table 1. The results of simulation studies – estimators of fixed effects and variance and covariance components

Fixed effect/(co)variance component	True value	Starting value	Estimator (standard deviation)
$\beta_1^{(1)}$	0	0	0
$\beta_2^{(1)}$	1.0	0	1.0340 (0.0031)
$\beta_1^{(2)}$	0	0	0
$\beta_2^{(2)}$	0.5	0	0.5010 (0.0035)
$\sigma^2_{a_1}$	0.3	0.4	0.2999 (0.0089)
$\sigma^2_{m_1}$	0.03	0.1	0.0419 (0.0093)
$\sigma^2_{a_2}$	0.4	0.4	0.4262 (0.0122)
$\sigma^2_{m_2}$	0.04	0.1	0.0423 (0.0109)
$\sigma_{a_1a_2}$	0.104	0	0.1081 (0.0075)
$\sigma_{a_1m_1}$	–0.019	0	–0.0344 (0.0070)
$\sigma_{a_2m_2}$	–0.025	0	–0.0208 (0.009)
$\sigma_{a_1m_2}$	0	0	–0.0005 (0.0074)
$\sigma_{a_2m_1}$	0	0	–0.0018 (0.0077)
$\sigma_{m_1m_2}$	0.00692	0	0.0077 (0.0046)
$\sigma^2_{c_1}$	0.02	0.1	0.0211 (0.0058)
$\sigma^2_{c_2}$	0.03	0.1	0.0274 (0.007)

Note on symbols:

$\beta_1^{(k)}$ = the first level of the fixed effect for *k-th* trait, $\beta_2^{(k)}$ = the second level of the fixed effect for *k-th* trait, $\sigma^2_{a_k}$ = the genetic direct additive variance for *k*-th trait, $\sigma^2_{m_k}$ = the genetic maternal additive variance for *k*-th trait, $\sigma_{a_ka_{k'}}$ = the covariance between direct additive effects for *k*-th and *k'*-th traits, $\sigma_{a_km_{k'}}$ = the covariance between direct and maternal additive effects for *k*-th and *k'*-th traits, $\sigma_{m_km_{k'}}$ = the covariance between maternal additive effects for *k*-th and *k'*-th traits, $\sigma^2_{c_k}$ = the permanent maternal environmental variance, $k = 1, 2$, $k' = 1, 2$

In the first stage, elements of vector **w** were generated according to the studied model with one fixed effect. The assumed true values of the components of variance and covariance as well as the levels of fixed effect are presented in Table 1. In the second stage variables y_{lj} were determined based on the previously obtained vector **w**. The true values of the parameters used in simulation are given in Table 1.

Results

The stationarity of the process is illustrated by random values for direct additive genetic variance $\sigma^2_{a_1}$ (Figure 2). Similar stationarity of the random process was observed for other parameters as well. Point estimators and predictors of parameters of the model were calculated as averages from 20 000 random values coming from each 50-th iterative step. The starting values and estimates of parameters are presented in Table 1. The obtained results indicate the correctness of the method, the estimators of parameters are close to the true values.

PRACTICAL IMPLICATIONS

As it was already mentioned, the proposed algorithm exhibits good properties especially concerning the low values of the estimated parameters. Roughsedge *et al.* (2001) reported that the accuracy of the estimation of maternal variances was positively correlated with the actual value of this parameter.

It needs to be mentioned that the satisfactory results were obtained for the population whose size

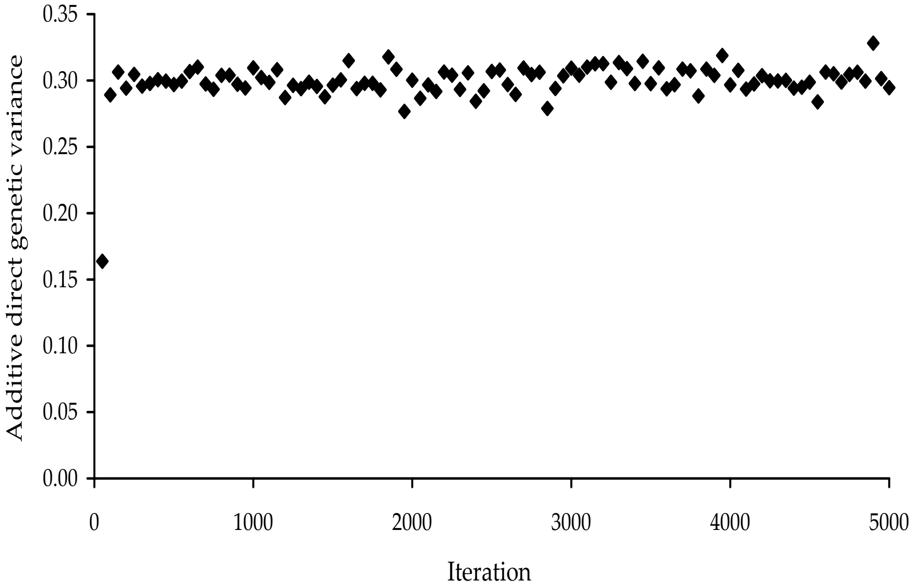

Figure 2. The Gibbs sampling process – the first 5 000 samples for the direct additive genetic variance

and structure were not very suitable for the estimation of maternal genetic environmental effects (Figure 1). It indicates considerable universality of the proposed method. On the other hand, further simulation studies are required. They should consider pedigrees of different size and structure.

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Received: 03–07–14
Accepted after corrections: 03–12–29

ABSTRAKT

Algoritmus Bayesovského odhadu maternálně genetických a permanentních maternálně genetických variancí ve dvouznakovém binárním prahovém modelu

V práci je předložen algoritmus pro odhad a předpověď parametrů ve dvouznakovém binárním prahovém modelu. Tento model obsahuje pevné efekty a následující náhodné efekty: genetické přímé aditivní, genetické mateřské aditivní a efekty trvalého mateřského prostředí. Pro odhad parametrů byl použit postup Gibbsova výběru. Algoritmus byl znázorněn na numerickém příkladě, který prokázal vhodnost navržené metody.

Klíčová slova: binární znaky; genetické efekty; Gibbsův výběr; prahový model; maternální efekty

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