Single- and multi-trait animal model in the silver fox evaluation

Jedno- a víceznakový animal model pro hodnocení stříbrných lišek

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ABSTRACT: Data on 4 435 animals, collected on two fox farms in 1985–1999, were used in the estimation of genetic parameters and genetic trends for four traits evaluated according to Polish grading standard. The graded traits were: body size (BS), colour type (CT), purity of silvering and coat colour (PSCC), and coat quality (CQ). (Co)variance components were estimated by the restricted maximum likelihood method (REML) using the average information (AI) algorithm. A linear model that included herd, year of birth and birth season as fixed effects, and additive genetic as a random effect was used in both, single- and multi-trait analyses. The annual genetic trend of the studied traits was estimated as a regression of breeding value on time. Comparable estimates of heritability were derived using single- (ranging from 0.192 for CQ to 0.356 for CT) and multi-trait (ranging from 0.191 for CQ to 0.345 for CT) models. Quite high genetic correlations were found between CT and PSCC, and CT and CQ (0.47 and 0.43, respectively), whereas the correlations between other traits were low or moderate (ranging from 0.18). All phenotypic correlations were low ranging from –0.04 (between CQ and PSCC) to 0.15 (between CT and PSCC). The estimated genetic trends were positive for all the traits and ranged from 0.014 to 0.057 when single-trait analysis was used or they ranged from 0.017 to 0.057 when multi-trait analysis was applied.

Keywords: coat traits; genetic parameters; genetic trends; silver fox

ABSTRAKT: K odhadu genetických parametrů a genetických trendů u čtyř znaků, které byly hodnoceny podle polského klasifikačního standardu, jsme použili údaje o 4 435 zvířatech získané v letech 1985 až 1999 na dvou liščích farmách. Hodnocenými znaky byla velikost trupu (BS), typ zbarvení (CT), čistota stříbřitosti a zbarvení srsti (PSCC) a kvalita srsti (CQ). Odhad složek variance a kovariance jsem prováděli pomocí metody omezené maximální věrohodnosti (REML) s použitím průměrného informačního algoritmu (AI). Pro jedno- i víceznakové analýzy jsme použili lineární model, který jako pevné efekty obsahoval chov, ročník narození a sezónu narození a jako náhodný efekt aditivní genetiku. Odhad meziročního genetického trendu u sledovaných znaků vycházel z regrese plemenné hodnoty vzhledem k času. Pomocí jedno- (v rozpětí od 0,192 pro CQ do 0,356 pro CT) a víceznakového (v rozpětí od 0,191 pro CQ do 0,345 pro CT) modelu jsme odvodili srovnatelné odhady dědivosti. Zjistili jsme relativně vysoké genetické korelace mezi CT a PSCC a mezi CT a CQ (0,47 resp. 0,43), zatímco korelace mezi ostatními znaky byly nízké nebo střední (od 0,03 do 0,18). Všechny fenotypové korelace dosahovaly nízkých hodnot od –0,04 (mezi CQ a PSCC) do 0,15 (mezi CT a PSCC). Odhadnuté genetické trendy byly pro všechny znaky kladné; při použití jednoznakové analýzy se pohybovaly od 0,014 do 0,057 a při použití víceznakové analýzy od 0,017 do 0,057.

Klíčová slova: znaky srsti; genetické parametry; genetické trendy; stříbrná liška

The breeding value evaluation is the most important part of the multi-stage process aimed at improvement of the genetic merit of a population. The best method of breeding value evaluation that has widely been used in practice is the Best Linear Unbiased Prediction (BLUP) with the use of an animal model (AM) (Engel *et al.*, 1999). The BLUP AM incorporates all sources of genetic information into the prediction of genetic merit, improving the accuracy of breeding value predictors (Meyer, 1989).

Although in all modern breeding programmes the best linear unbiased predictions (BLUPs) of the breeding value are used when selecting animals, this method has not been introduced into Polish fur farming yet. Instead of BLUPs Polish fur farmers use as selection criteria the total score (sum of scores given to an individual during conformation and coat grading) or a simplified form of selection index (calculated as a sum of scores given for four sources of information) (Wierzbicki and Filistowicz, 2001). These methods, however, are not reliable enough since the subjectivity of grading, and construction of selection index without using all available sources of information on animal genetic merit lead to the low accuracy of selection and, as a result, to unsatisfactory genetic progress (Wierzbicki et al., 2000). Disadvantages of selection schemes based on the total score as a selection criterion were reported by many authors (Reiten, 1977; Jeżewska and Maciejowski, 1983; Jeżewska et al., 1994; Lohi, 1995; Lohi et al., 1996; Rasmussen, 1996).

In Nordic countries (Finland, Norway, Denmark) the genetic merit of fur animal populations (mainly foxes and mink) is evaluated with the use of BLUP AM (Smëds, 1992; Johannessen *et al.*, 2000). As a consequence considerably higher accuracy of breeding value estimation is achieved, and the genetic gain is bigger (for example, reproduction results on Finnish farms applying BLUP AM have been 0.1–0.4 cubs/litter above the national average – www.stkl-fpf.fi).

BLUP AM was not introduced into fur animal breeding at the same time as in major species of livestock. In Finland and Norway this method was applied for the fox breeding value estimation in the 1990s (Smëds, 1992; Johannessen *et al.*, 2000). However, in both countries the systems of breeding value evaluation are different. In Finland the breeding value evaluation is carried out on farms using the SAMPO computer software distributed by the Finnish Fur Breeders' Association. Breeding value of traits of economic importance (evaluated traits are selected by a breeder) is estimated using data collected on a farm (grading scores), data coming from skin auctions, or both sources of information are combined (Smëds, 1992; www.stkl-fpf.fi). In Norway, in contrast, the data are recorded on farms, and they are sent to the central data bank for processing. After the statistical analyses breeding values are estimated, combined selection index is calculated, and the results are sent back to the farmers (Johannessen *et al.*, 2000).

Although clear differences are seen in the methods and schemes used for breeding value estimation in Poland and Nordic countries (BLUP AM vs. phenotypic selection, centralised vs. non-centralised system), in all the countries the selection of foxes has always been oriented towards the improvement of conformation and coat traits as well as reproductive performance.

This paper presents the genetic parameters and genetic trends estimated in a population of silver fox (*Vulpes vulpes*) kept on Polish farms using the single- and multi-trait BLUP AM.

MATERIAL AND METHODS

Data on 4 435 silver foxes, collected in 1985 to 1999 on two farms were used in the estimation of genetic parameters and genetic trends for four traits evaluated according to Polish grading standard (CSHZ, 1997). The graded traits were: body size (BS), colour type (CT), purity of silvering and coat colour (PSCC), and coat quality (CQ). After grading the scores were summed up giving the total score that was the main selection criterion. The selection pressure put on each trait was different hence each trait had its own scale of scores. The animals were evaluated by a classifier when the fur coat was fully developed (in November each year). The data were collected in the database of the LISY computer system (Chudoba et al., 1988). Description of the scale of scores and statistical information on the data set are given in Table 1.

Pedigrees were traced back up to two generations giving the pedigree file of 4 435 animals (3 582 with records). The pedigree structure is presented in Table 2.

The estimation of (co)variance components was performed using the single- and multi-trait animal models and the restricted maximum likelihood

Trait	Scale of scores	No. of records	Mean	Standard deviation
Body size	0–6	3 582	5.04	1.35
Colour type	0–3	3 582	2.54	0.72
Purity of silvering and coat colour	0–5	3 582	4.33	0.71
Coat quality	0–6	3 582	5.01	0.52

Table 1. Statistical description of the data set

Table 2. Pedigree structure

Number of base animals	849	Sires with progeny records	406
Animals with records	3 582	Dams with progeny records	663
with unknown sire	77	Grand sires with progeny records	257
with unknown dam	125	Grand dams with progeny records	330

(REML) method. The DMU 6.4 package (Madsen and Jensen, 2000) and the average information (AI) algorithm were used in the estimation. The following mixed model was applied in both, single- and multi-trait analyses: with the above animal model. The genetic trends for the studied traits were estimated as a regression of EBVs on time.

RESULTS AND DISCUSSION

 $\begin{aligned} X_{ijkl} &= \mu + h_i + y_j + s_k + a_{ijkl} + e_{ijkl} \\ \text{where: } X_{ijkl} &= \text{the observation} \\ h_i &= \text{fixed effect of herd } (i = 1, 2) \\ y_j &= \text{fixed effect of the year of birth } (j = 1 - 15) \\ s_k &= \text{fixed effect of birth season } (k = 1, 2, 3) \end{aligned}$

- $k_k = 1122$ and the effect of birth season (k = 1, 2, 5
- a_{ijkl} = additive genetic effect of the animal
- e_{ijkl} = residual effect

The effect of animal and residual effect were assumed random with E (a) = 0, E (e) = 0, var (a) = A^*G_0 and var (e) = I^*R_0 , where A is additive relationship matrix, G_0 is additive genetic (co)variance matrix, I is identity matrix and R_0 is (co)variance matrix for residuals. The estimate standard errors were derived from the AI information matrix. Coefficients of determination (R^2) for the analysed traits, indicating the total variation explained by fixed effects were as follows: BS – 0.26, CT – 0.23, PSCC – 0.21, and CQ – 0.15.

After estimation of the (co)variance components, estimated breeding values (EBVs) for BS, CT, PSCC and CQ were computed using the BLUP The linear model used in the analyses did not include the joint herd-year-season (HYS) effect because the data were collected within the period of 14 years, and many very small classes herd-yearseason were created (some of them were empty). Moreover, the data originated from 2 farms, but there were a few years when we had data from one (bigger) farm only.

Fixed effects fitted for the studied traits explained from 15% (CQ – $R^2 = 0.15$) to 26% (BS – $R^2 = 0.26$) of the total variation for these traits. Although the values of R^2 are quite low, they can be comparable to those reported by Hermesch *et al.* (2000), who studied genetic parameters in Australian pigs. The coefficient of determination calculated for 4 performance traits ranged from 0.17 to 0.39, and for 8 carcass traits it ranged from 0.15 to 0.37.

The linear model fitted for all analysed traits included only direct effect of the animal. In the case of BS a maternal effect might have been included. However, in this study, which is a part of wider research, we decided to test one model for all the

Trait	$\sigma^2_{_{a}}$	$\sigma_{_{e}}^{2}$	σ_p^2	h^2	ΔG (point/year)	ΔG (% of mean)
Single-trait animal model						
Body size	0.364	0.995	1.359	0.268 (s.e. 0.034)	0.057	1.13
Colour type	0.149	0.270	0.419	0.356 (s.e. 0.037)	0.038	1.49
Purity of silvering and coat colour	0.103	0.291	0.394	0.261 (s.e. 0.033)	0.014	0.32
Coat quality ¹	0.047	0.198	0.245	0.192 (s.e. 0.031)	0.019	0.38
Multi-trait animal m	odel					
Body size	0.358	1.000	1.358	0.264 (s.e. 0.034)	0.057	1.13
Colour type	0.144	0.274	0.418	0.345 (s.e. 0.036)	0.041	1.61
Purity of silvering and coat colour	0.103	0.291	0.394	0.262 (s.e. 0.033)	0.017	0.39
Coat quality	0.047	0.198	0.245	0.191 (s.e. 0.031)	0.021	0.42

Table 3. Estimates of variance components, heritability and annual genetic trends (ΔG) for studied traits derived by the single- and multi-trait animal model

Variance components: σ_a^2 additive genetic; σ_e^2 error variance; σ_p^2 phenotypic variance ($\sigma_a^2 + \sigma_e^2$) $b^2 = \sigma_a^2 / \sigma_b^2$

s.e. = standard error

traits. Furthermore, according to Meyer (1992) standard errors of heritability estimates can be 3 to 5 times larger with maternal effect model as compared with a model involving only direct effect.

The variance components and heritabilities of the studied traits are presented in Table 3. Regardless of the type of analysis (single- or multi-trait) the additive and error variance components and the estimates of heritability were comparable or identical. Slightly different were the estimates of additive genetic variance for BS and CT ranging from 0.364 to 0.358 and from 0.149 to 0.144, respectively. When the single- or multi-trait animal model was applied, the respective estimated heritabilities for these traits were 0.268 and 0.264 for BS and 0.149 and 0.144 for CT. For the remaining traits (PSCC and CQ) the variance components estimated using the single- and multi-trait analysis were identical giving similar heritabilities (PSCC - 0.261 and 0.262 when the single- or multi-trait model was used, respectively; CQ - 0.192 and 0.191, respectively).

In the earlier research Wierzbicki (2000) studied the effect of data transformation on the additive genetic and error variance components in a population of arctic fox (Alopex lagopus). He found similar heritabilities to those presented here, for BS (0.288, s.e. 0.047) and CT (0.342, s.e. 0.049). However, the heritabilities were estimated after application of the probit transformation of the data set. The estimates of heritability derived using untransformed data were markedly higher ranging from 0.461 for BS to 0.445 for CT. In contrast, Filistowicz et al. (1999, 2000) carried out studies in populations of silver and golden fox, respectively, and reported significantly lower heritabilities for CT (ranging from 0.08 to 0.168) and for BS (0.081). However, the estimates of heritability had high standard errors (from 0.07 to 0.14).

Heritabilities of the conformation traits (scored by a classifier) reported for other domesticated species were usually low or moderate (Manfredi *et al.*, 2001; Serenius *et al.*, 2001; Schaeffer *et al.*, 2001). Although the same traits of body conformation are

evaluated in different species (for example body size and general appearance), the genetic parameters estimated for these traits cannot be compared easily since evaluation standards differ between species, and are changed in the course of time. While continuous revision of the standards is desirable from a breed improvement standpoint, the consequences are that it is impossible to genetically compare individuals classified many years apart (Schaeffer et al., 2001). According to Schaeffer et al. (2001) another aspect of subjectively evaluated traits is the fact that the animal cannot receive a higher score than the highest category allowed for the trait. The effect of this limit may shrink the genetic variability that is present in the population. This finding seems to be supported by the results of the present study (Table 1). Means of the traits are very close to maximal scores (upper limits) and their standard deviations (except BS) are small indicating that a narrow scale of scores is used when evaluating the traits.

The genetic and phenotypic correlations are presented in Table 4. Quite high genetic correlations were found between CT and PSCC (0.47), and between CT and CQ (0.43) indicating a strong association between the pools of genes that determine these two traits. The other genetic correlations were low (0.04 between BS and PSCC) or moderate (0.14 between BS and CT, and 0.18 between BS and CQ) and had high standard errors (from 0.092 to 0.107). Almost all phenotypic correlations were very low ranging from -0.02 between PSCC and BS to 0.10 between CQ and CT. The moderate phenotypic correlation was found only between PSCC and CT (0.15).

Markedly different genetic and phenotypic correlations between conformation and coat traits in silver and golden fox populations were found by Filistowicz et al. 1999, 2000). The authors estimated genetic parameters for seven (report from 2000) or eight (report from 1999) traits scored according to the old grading standard replaced by the new one in 1997. The wide ranges of genetic (from -0.97 to 0.87) and phenotypic (from -0.96 to 0.82) correlations were found between investigated traits. The pronounced differences between the results reported by Filistowicz et al. (1999; 2000) and the results presented in this study may have been caused by (i) subjectivity of this type of evaluation, (ii) different standards of evaluation (old and new ones) used in both studies, (iii) different methods of (co)variance components estimation (animal model vs. sire and dam model). Moreover, the number of animals used in this study was higher (4 435 individuals) as compared with the study by Filistowicz et al. (1999; 2000) (2 072 and 1 013 foxes, respectively).

The estimated genetic trends were positive for all analysed traits (Table 3). In both types of analyses (single- and multi-trait animal model) markedly higher genetic trends were estimated for BS and CT. When the single-trait model was applied, the genetic trends for BS and CT reached 0.057 and 0.038, respectively (expressed as percentages of the means the trends were 1.13% for BS and 1.49% for CT). In the case of the multi-trait analysis, when covariances between traits were taken into account,

Trait	BS	СТ	PSCC	CQ
BS	_	0.14 (s.e. 0.092)	0.04 (s.e. 0.098)	0.18 (s.e. 0.107)
СТ	0.03	_	0.47 (s.e. 0.081)	0.43 (s.e. 0.094)
PSCC	-0.02	0.15	_	0.03 (s.e. 0.108)
CQ	0.06	0.10	-0.04	-

Table 4. Estimates of genetic (above diagonal) and phenotypic (below diagonal) correlations between analysed traits

BS – body size, CT – colour type, PSCC – purity of silvering and coat colour, CQ – coat quality s.e. – standard error

the genetic trend estimated for BS did not differ from that estimated using the single-trait model, whereas the genetic trend for CT was higher and reached 0.041 (1.61%). In the remaining traits the genetic trends were lower when estimated using the single-trait model (0.014 and 0.019 for PSCC and CQ, respectively), whereas the estimation under the multi-trait model resulted in higher genetic trends (0.017 and 0.021 for PSCC and CQ, respectively).

The magnitude of genetic trends estimated for BS and CT was within the range (from 1% to 2% per year) comparable with that reported for other domesticated species (Falconer and Mackay, 1996). The lower genetic trends estimated for PSCC and CQ may have been brought about by measurement error introduced during scoring. Evaluation of these two traits is more subjective as compared with BS and CT, and causes more difficulties for classifiers. Low precision of this type of evaluation was indicated by Jeżewska and Maciejowski (1983), who found low repeatability of scores ranging from 0.25 to 0.66 in the populations of silver fox, arctic fox and mink. According to Jeżewska et al. (1994) only 21-54% of the total variation of scores was determined by animals, whereas up to 60% of the total variation was defined as an error variance.

Genetic trends in fur animals have not been estimated frequently. In populations of arctic fox the trends for conformation and coat traits were estimated by Socha (1996), Wierzbicki *et al.* (2000) and Wierzbicki and Filistowicz (2001). All these authors reported low or even negative genetic trends ranging from -0.0051 for body size to 0.073 for total score (Socha, 1996), or from -0.0004 for body size to 0.013 for colour purity (Wierzbicki and Filistowicz, 2001). However, these estimates cannot be considered as unbiased predictions of breeding values because of trait evaluation subjectivity (a completely objective conformation assessment system is difficult to find, or too costly to apply) (Schaeffer *et al.*, 2001).

CONCLUSIONS

Comparison of the single- and multi-trait animal model applied for genetic evaluation of silver foxes revealed small differences between the estimates derived by both methods. The estimates of heritability obtained by the single- and multi-trait analysis were comparable and had moderate values. Quite high genetic correlations were found between CT and PSCC, and CT and CQ, whereas the other ones were low or moderate. Low values of the phenotypic correlation indicated weak phenotypic associations between the studied traits. The genetic trends estimated by the multi-trait animal model, when covariances between traits were incorporated into prediction of breeding value, were slightly higher than those estimated with the use of the single-trait animal model.

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