

Breeding value evaluation in Polish fur animals: Estimates of (co)variances due to direct and litter effects for fur coat and reproduction traits

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ABSTRACT: 5 540 records of the arctic fox fur coat and reproductive traits collected in 1983–1999 were studied. The analyzed traits were: body size (BS), colour type (CT), colour purity (CP), coat density (CD), hair length (HL), general appearance (GA), total score (TS), skin length (SL), litter size at birth (LSB), litter size at weaning (LSW), number of dead pups (NPD), pup weight at weaning (PW), and pregnancy length (PL). (Co)variance components were estimated using a derivative-free algorithm of REML and a multi-trait animal model. Random effects were direct additive, common litter environment and residual. The genetic parameters for the fur coat traits (discrete characters) were estimated twice: using the original data set, and the data set in which the distribution of fur coat scores was normalised using a probit link function. Direct heritability estimates obtained from the original data set ranged from 0.108 for SL to 0.276 for HL, and were somewhat lower than those estimated using the transformed data set (they ranged from 0.109 for GA to 0.315 for CT). Reproductive traits were lowly heritable with direct heritabilities ranging from 0.060 for PW to 0.174 for LSB. Estimates of the portion of litter variation calculated from the original and transformed data set were comparable ranging from 0.045 for GA to 0.156 for CP, and from 0.059 for GA to 0.185 for TS, respectively. Genetic correlations between fur coat traits ranged from high favourable (0.948 between SL and BS, original data) to strong negative ones between CP and GA (–0.405, transformed data). High positive genetic correlations were found between LSB and LSW (0.954), and between LSB and NPD (0.783), whereas PL was negatively correlated with all other reproductive traits.

Keywords: arctic fox; fur coat traits; genetic parameters; normal probability scale transformation; reproductive traits

Breeding schemes in fur breeding mainly concentrate on skin size, skin quality traits and reproductive performance of animals. The skin size has gained great economic importance since an increasing skin length has a strong positive effect on the skin price (Filistowicz et al., 1999a; Hansen and Berg, 2004; Wierzbicki, 2005). In the last 15 years Polish fur breeders have aimed their efforts at genetic improvement of this trait. The skin size also became a priority in breeding programs in Finland (Peura et al., 2004b). The second trait that is among the characters of great economic importance is litter size. According to Lagerqvist (1997), an increased litter size substantially reduces production costs. However, the great improvement of skin size

was accompanied by deteriorated reproductive performance. It appeared that skin size was negatively correlated with litter size (Lagerqvist et al., 1994; Peura et al., 2003, 2004b). Although these two traits are main selection criteria, the skin quality traits are also taken into account when selecting animals. Therefore, it is necessary to estimate genetic correlations between selected traits to assess potential negative relations between them.

The paper presents estimates of genetic parameters for fur coat and reproductive traits of the arctic fox estimated by multivariate animal models. The study is another part of the project dealing with breeding value evaluation in Polish fur animals.

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MATERIAL AND METHODS

Data

5 540 records of the arctic fox fur coat and reproductive traits collected in 1983–1999 were studied. Information on fur coat traits: body size (BS), colour type (CT), colour purity (CP), coat density (CD), hair length (HL), general appearance (GA), total score (TS), and skin length (SL), and on reproductive performance: litter size at birth (LSB), litter size at weaning (LSW), number of dead pups (NPD), pup weight at weaning (PW), pregnancy length (PL) was recorded by farmers and collected in computer data bases. The trait definitions, descriptions and full statistical analyses of the data were given by Wierzbicki et al. (2004) in the first part of the study, whereas the structure of the data sets and pedigrees was presented in the second part of the study (Wierzbicki, 2004).

Analysis

(Co)variance components were estimated using a derivative-free algorithm of REML (Restricted Maximum Likelihood) methodology (Graser et al., 1987) and the DFREML computer package (Meyer, 1998), which provides approximations of standard errors for heritabilities and genetic correlations.

The following multivariate linear model was used for the estimation of (co)variance components of the fur coat traits:

$$y = X\beta + Za + Wc + e$$

$$\text{with } E \begin{bmatrix} \mathbf{a} \\ \mathbf{c} \\ \mathbf{e} \end{bmatrix} = \begin{bmatrix} 0 \\ 0 \\ 0 \end{bmatrix} \text{ and } \text{var} \begin{bmatrix} \mathbf{a} \\ \mathbf{c} \\ \mathbf{e} \end{bmatrix} = \begin{bmatrix} \mathbf{G}_0 \otimes \mathbf{A} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{C}_0 \otimes \mathbf{I} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{R}_0 \otimes \mathbf{I} \end{bmatrix}$$

where:

y, β, a, c, e = vectors of observations, fixed effects (year × birth season), additive genetic effects, common litter environment effects and residuals, respectively

X, Z, W = design matrices for fixed effects, additive genetic effects and common litter environment effects, respectively

A = the numerator relationship matrix

I = the identity matrix, while

G_0, C_0, R_0 = the covariance matrices of additive genetic effects, common litter environment effects and residual effects, respectively

For the reproductive traits the following model was fitted:

$$y = X_1\beta_1 + X_2\beta_2 + Za + e$$

$$\text{with } E \begin{bmatrix} \mathbf{a} \\ \mathbf{e} \end{bmatrix} = \begin{bmatrix} 0 \\ 0 \end{bmatrix} \text{ and } \text{var} \begin{bmatrix} \mathbf{a} \\ \mathbf{e} \end{bmatrix} = \begin{bmatrix} \mathbf{G}_0 \otimes \mathbf{A} & \mathbf{0} \\ \mathbf{0} & \mathbf{R}_0 \otimes \mathbf{I} \end{bmatrix}$$

where:

$y, \beta_1, \beta_2, a, e$ = vectors of observations, fixed effects of year × birth season, fixed effects of female age, additive genetic effects and residuals, respectively

X_1, X_2, Z = the design matrices for fixed effects of year × birth season, female age and additive genetic effects, respectively

A = the numerator relationship matrix

I = the identity matrix

G_0 = the additive genetic covariance matrix

R_0 = the covariance matrix for residuals

The genetic parameters for the fur coat traits (discrete characters) were estimated twice: from the original data set, and from the data set in which the distribution of the fur coat scores was normalised using a probit link function. The method of data transformation was described by Wierzbicki (2004). No data transformation was applied for the estimation of (co)variance components for the reproductive traits.

RESULTS AND DISCUSSION

Estimates of direct heritability (h^2) and portion of litter variation (c^2) for fur coat traits, estimated from the original and transformed data set are presented in Table 1. The direct heritabilities estimated from the original data were somewhat lower than those calculated with the use of the transformed data, and ranged from 0.108 for SL through 0.149 for GA to 0.276 for HL. Normal probability scale transformation of the data made the values of 6 out of the 7 traits higher (they ranged from 0.194 for CD to 0.315 for CT). Only heritability for GA lowered after the data transformation (0.109 vs. 0.149). In an earlier part of the study (Wierzbicki, 2004), the direct heritabilities for the fur coat traits were estimated by a single-trait animal model with or without the inbreeding coefficient included as linear covariable. The estimates of direct heritability were found within the ranges of those reported in the present study. However, the effect of

Table 1. Estimates of direct heritability (h^2), portion of litter variation (c^2) and their approximate standard errors (s.e.) of the arctic fox fur coat traits

| Trait | Original data set | | Transformed data set | |
|-------|-----------------------|-----------------------|-----------------------|-----------------------|
| | $h^2 \pm \text{s.e.}$ | $c^2 \pm \text{s.e.}$ | $h^2 \pm \text{s.e.}$ | $c^2 \pm \text{s.e.}$ |
| SL | 0.108 \pm 0.027 | 0.082 \pm 0.014 | n.e. | n.e. |
| BS | 0.232 \pm 0.031 | 0.101 \pm 0.015 | 0.272 \pm 0.034 | 0.095 \pm 0.015 |
| CT | 0.255 \pm 0.032 | 0.095 \pm 0.016 | 0.315 \pm 0.036 | 0.099 \pm 0.016 |
| CP | 0.166 \pm 0.029 | 0.156 \pm 0.017 | 0.197 \pm 0.033 | 0.145 \pm 0.017 |
| CD | 0.171 \pm 0.029 | 0.084 \pm 0.014 | 0.194 \pm 0.031 | 0.074 \pm 0.014 |
| HL | 0.276 \pm 0.033 | 0.138 \pm 0.017 | 0.289 \pm 0.035 | 0.122 \pm 0.017 |
| GA | 0.149 \pm 0.026 | 0.045 \pm 0.012 | 0.109 \pm 0.024 | 0.059 \pm 0.012 |
| TS | 0.151 \pm 0.028 | 0.187 \pm 0.017 | 0.231 \pm 0.037 | 0.185 \pm 0.018 |

n.e. – not estimated because SL was measured on a metric scale and its scores had normal distribution

data transformation was more pronounced when variance components were estimated by a model with the inbreeding coefficient as linear covariable (estimates of direct heritability were higher). In contrast, Wierzbicki (2000) using a single-trait animal model without common litter environment as a second random effect, found that the probit transformation of data resulted in lower heritabilities of fur coat traits in arctic foxes and slightly smaller standard errors of estimates.

Filistowicz et al. (1999b), who carried out the study in silver fox (*Vulpes vulpes*), reported higher estimates of heritability for fur coat traits estimated from probit-transformed data. They ranged from 0.168 for CP to 0.346 for HL and 0.374 for TS. Only heritability for BS was markedly lower (0.081) than that presented in this study. Contrary to these results, Peura et al. (2004b) reported higher estimates of direct heritability for BS and comparable to those presented in this study. Depending on the model applied (single- or multi-trait one), they found heritability for BS 0.24 or 0.25, respectively. High estimates of heritability for body weight and pelt quality were found in mink (Berg, 1993a, b). The heritabilities for body weight (in mink body weight is measured instead of body size) and pelt quality were 0.50 and 0.35, respectively.

Estimates of the portion of litter variation (c^2) calculated using the original and transformed data set were comparable and always lower (except for TS, original data) than estimates of direct heritability (Table 1). They explained from 4.5% (GA) to 18.7% (TS) of the variation in fur coat traits.

The estimates of common litter environment effect (nongenetic components of uterine nutrition, uterus capacity, nutrition during the suckling period, and partly nonadditive genetic effects such as dominance – Kaufmann et al., 2000) on fur coat traits were highest for HL, CP and TS (in TS the estimate of litter variation (0.187) was higher than direct heritability (0.151) – original data). In an earlier part of the study (Wierzbicki, 2004) when the portion of litter variation was estimated by a single-trait animal model, the highest estimates were also derived for CP, HL and TS.

Heritabilities for reproductive traits are given in Table 5. Although LSB shows a relatively high additive genetic variation ($h^2 = 0.174$), other traits are lowly heritable (h^2 ranges from 0.060 for PW to 0.121 for NPD). The estimates of heritability for LSB and LSW reported here are lower than those presented in the earlier part of the study (Wierzbicki, 2004). The same data set used for a single-trait analysis gave heritabilities of 0.205 and 0.250 for LSB and LSW, respectively.

Peura et al. (2004b), who carried out the study in the Finnish blue fox population, reported lower estimates of heritability for litter size calculated 3 weeks after whelping. In the single-trait analysis they reported heritability of 0.08. In the multi-trait analysis they regarded the 1st, 2nd and 3rd litter size as separate traits, and reported heritabilities of 0.08, 0.08 and 0.07, respectively.

Other literature estimates of heritability for reproductive traits are rather lower than those presented in this study. Kenttämies (1996) studied arctic foxes

and reported estimates of heritability 0.03 and 0.05 for LSB and LSW, respectively. Jakubczak (2002), studying reproduction performance in Polish pastel foxes, found very low heritabilities for LSB and LSW (0.060 and 0.026, respectively). Also lowly heritable were LSB and LSW in the raccoon dog (*Nyctereutes procynoides*) population (Ślaska, 2002). The author reported heritabilities 0.068 and 0.080 for LSB and LSW, respectively. However, pregnancy length (PL) had higher heritability than that presented in this study (0.174 vs. 0.081). Only Socha (1996), who carried out the study in Polish blue foxes, reported estimates of heritability for LSB and LSW comparable to those presented in this study (h^2 values were 0.202 and 0.181 for LSB and LSW, respectively).

Genetic correlations between fur coat traits are presented in Table 2. The estimates of genetic correlations derived from the transformed data were somewhat higher than those estimated using the original data set. The highest positive genetic correlation was found between SL and BS (0.948, original data), and between TS and group of 5 pelt traits (SL,

BS, CT, CP, CD – r_g ranged from 0.372 to 0.523). This indicates that selection for TS will improve (correlated response) other skin traits effectively at the same time. Negative genetic correlations were mainly found between pelt quality traits (CP, CT, HL), and between SL and BS (economically very important traits) and CP and HL. It means that the selection pressure on SL and BS (common practice in fox breeding) deteriorates CP and HL.

Socha (1994) estimated genetic correlations in a population of blue fox, and reported a positive but lower estimate of genetic correlations between BS and TS (0.016). The author reported a higher genetic correlation between BS and GA (0.214). Like in the present study Socha (1994) found negative genetic correlations between BS and CP, CT and HL (ranging from –0.065 to –0.436). In a silver fox population (Filistowicz et al., 1999b) most of the genetic correlations between BS and other skin traits were negative ranging from –0.027 between BS and TS to –0.711 between BS and CP. On the other hand, TS was favourably correlated with other (except for BS) skin traits. In contrast, in another

Table 2. Estimates of genetic correlation and their approximate standard errors (in brackets) between the fur coat traits of the arctic fox, estimated using the original data (above diagonal) and the transformed data (below diagonal)

| Trait | SL | BS | CT | CP | CD | HL | GA | TS |
|-------|------|--------------------|-------------------|-------------------|-------------------|-------------------|-------------------|------------------|
| SL | – | 0.948 (0.051) | 0.186 (0.127) | –0.128 (0.151) | 0.619 (0.133) | –0.206 (0.129) | 0.156 (0.140) | 0.481 (0.123) |
| BS | n.e. | – | 0.156 (0.095) | –0.114 (0.112) | 0.471 (0.0950) | –0.257 (0.093) | 0.264 (0.109) | 0.449 (0.094) |
| CT | n.e. | 0.240 (0.088) | – | 0.279 (0.104) | –0.280 (0.104) | –0.268 (0.089) | –0.095 (0.108) | 0.511 (0.082) |
| CP | n.e. | –0.160 (0.1070) | 0.239 (0.100) | – | –0.028 (0.125) | –0.245 (0.102) | –0.313 (0.125) | 0.523 (0.094) |
| CD | n.e. | 0.466 (0.117) | –0.221 (0.101) | –0.041 (0.121) | – | 0.039 (0.106) | –0.094 (0.124) | 0.372 (0.106) |
| HL | n.e. | –0.309 (0.092) | –0.233 (0.088) | –0.140 (0.106) | 0.111 (0.103) | – | 0.109 (0.107) | 0.146 (0.108) |
| GA | n.e. | 0.334 (0.089) | –0.013 (0.122) | –0.405 (0.134) | –0.062 (0.138) | 0.151 (0.124) | – | 0.045 (0.128) |
| TS | n.e. | 0.446 (0.117) | 0.502 (0.075) | 0.614 (0.074) | 0.334 (0.095) | 0.263 (0.094) | 0.050 (0.133) | – |

n.e. – not estimated because SL measurements were not transformed

silver fox population Wierzbicki and Filistowicz (2002) estimated positive genetic correlations between BS and other fur coat traits. However, the authors estimated genetic parameters based on a new grading standard, whereas Filistowicz et al. (1999b) estimated genetic parameters using an old grading standard.

Estimates of genetic correlations between reproductive traits are presented in Table 5. Strong positive genetic correlation was found between LSB and LSW (0.954), and between LSB and NPD (0.783). PL was the only trait negatively correlated with all other traits. The estimates of genetic correlation between PL and other reproductive traits ranged from -0.172 (between PL and LSB) to -0.970 (between PL and PW).

In populations of fur animals genetic correlations between reproductive traits are usually estimated between LSB and LSW. Filistowicz et al. (1999c) found a high positive genetic correlation between LSB and LSW (0.774) in a blue fox population. Jakubczak (2002) also reported a high positive (0.90) genetic correlation between LSB and LSW in a population of pastel fox. Different results were obtained by Jeżewska et al. (1996), who carried out the study in a population of blue fox. They reported a negative genetic correlation between LSB and LSW (-0.11). However, the authors estimated variance components using a linear model with random effects of sire and dam nested within sire.

Fur breeders mainly concentrate on genetic improvement of BS or SL and LSB or LSW because these traits are economically important. High positive genetic correlations between BS and SL (Table 2), and between LSB and LSW (Table 5)

indicate that selection for one trait improves the other one. However, it is also important to know the genetic relationship between animal size and litter size. In recent years animal size has substantially increased, while litter size has decreased (Peura et al., 2004b). This has given rise to studies on genetic relations between those two traits. It appeared that the genetic correlation between litter size and animal size or animal weight was negative.

Peura et al. (2004b) reported a negative genetic correlation between litter size calculated 3 weeks after whelping and animal size. The authors found genetic correlations -0.40 , -0.40 and -0.23 between the 1st, 2nd and 3rd litter size and animal size, respectively. In a mink population Lagerqvist et al. (1994) found a genetic correlation of -0.30 between body weight and litter size. Johannessen et al. (2000), who studied Norwegian silver foxes, also reported the negative effect of litter size on body weight. They estimated the negative effect of body length per kit at 3 weeks of age to amount to -0.08 to -0.09 cm.

The authors of the present study could not estimate genetic correlations between reproductive and skin traits because they had two different data sets: data on skin traits did not overlap data on reproductive performance. Thus, genetic parameters were estimated using each data set separately.

Estimates of correlations between common litter effects for fur coat traits, and residual effects between fur coat and reproductive traits are given in Table 3, Table 4 and Table 5, respectively. The highest positive common litter correlation was found between SL and BS (0.938). Furthermore, only favourable correlations were estimated between TS

Table 3. Estimates of correlation between common litter effects for the fur coat traits of the arctic fox from the original data (above diagonal) and the transformed data (below diagonal)

| Trait | SL | BS | CT | CP | CD | HL | GA | TS |
|-------|------|----------|----------|----------|----------|----------|----------|-------|
| SL | – | 0.938 | 0.215 | -0.198 | 0.205 | -0.376 | 0.498 | 0.155 |
| BS | n.e. | – | 0.255 | -0.231 | 0.285 | -0.356 | 0.311 | 0.184 |
| CT | n.e. | 0.282 | – | 0.316 | 0.421 | 0.047 | 0.169 | 0.686 |
| CP | n.e. | -0.192 | 0.287 | – | 0.231 | 0.318 | -0.224 | 0.756 |
| CD | n.e. | 0.324 | 0.404 | 0.237 | – | 0.057 | -0.120 | 0.603 |
| HL | n.e. | -0.266 | -0.065 | 0.282 | 0.145 | – | -0.011 | 0.496 |
| GA | n.e. | 0.292 | 0.068 | -0.224 | -0.106 | -0.152 | – | 0.055 |
| TS | n.e. | 0.188 | 0.584 | 0.754 | 0.684 | 0.425 | -0.029 | – |

n.e. – not estimated because SL measurements were not transformed

Table 4. Estimates of correlation between residual effects for the fur coat traits of the arctic fox from the original data (above diagonal) and the transformed data (below diagonal)

| Trait | SL | BS | CT | CP | CD | HL | GA | TS |
|-------|------|--------|--------|--------|--------|--------|--------|-------|
| SL | – | 0.642 | 0.004 | –0.004 | 0.136 | –0.014 | –0.029 | 0.226 |
| BS | n.e. | – | 0.022 | 0.025 | 0.211 | 0.011 | –0.058 | 0.383 |
| CT | n.e. | –0.009 | – | 0.170 | 0.074 | –0.094 | –0.070 | 0.538 |
| CP | n.e. | 0.030 | 0.178 | – | –0.058 | –0.261 | –0.063 | 0.562 |
| CD | n.e. | 0.210 | 0.058 | –0.054 | – | 0.078 | 0.013 | 0.491 |
| HL | n.e. | 0.022 | –0.097 | –0.273 | 0.045 | – | 0.057 | 0.220 |
| GA | n.e. | –0.078 | –0.088 | –0.060 | 0.014 | 0.039 | – | 0.123 |
| TS | n.e. | 0.376 | 0.445 | 0.537 | 0.438 | 0.168 | 0.085 | – |

n.e. – not estimated because SL measurements were not transformed

Table 5. Estimates of heritability (bold), genetic (above diagonal) and residual (below diagonal) correlations and their approximate standard errors (in brackets) of the arctic fox reproduction traits

| Trait | LSB | NPD | LSW | PW | PL |
|-------|-------------------------|-------------------------|-------------------------|-------------------------|-------------------------|
| LSB | 0.174 (0.048) | 0.783 (0.195) | 0.954 (0.032) | 0.184 (0.443) | –0.172 (0.043) |
| NPD | 0.086 (0.040) | 0.121 (0.043) | 0.391 (0.285) | –0.297 (0.372) | –0.227 (0.315) |
| LSW | 0.923 (0.006) | –0.277 (0.038) | 0.112 (0.047) | 0.189 (0.422) | –0.276 (0.318) |
| PW | –0.386 (0.046) | 0.008 (0.051) | –0.363 (0.046) | 0.060 (0.061) | –0.970 (0.657) |
| PL | 0.014 (0.041) | 0.079 (0.038) | –0.013 (0.039) | 0.048 (0.049) | 0.081 (0.043) |

and other skin traits (ranging from low 0.055 to very high 0.756, original data). The remaining correlations, regardless of the data used for estimation (original or transformed), were rather moderate, both negative and positive.

Residual correlations between fur coat traits were rather low or very low, except the correlation between SL and BS (0.642), and between TS and other fur coat traits (Table 4). Once again TS was positively correlated with all other skin characteristics (the same was found in the case of genetic and common litter correlations), indicating that this trait could be treated as a good selection criterion.

Most of residual correlations between reproductive traits were low (Table 5), although a very

strong association was found between residual effects of LSB and LSW (0.923). Moderate negative correlations were also found between PW and LSB (–0.386), PW and LSW (–0.363), and LSW and NPD (–0.277).

CONCLUSIONS

Selection programs in fur breeding focus on genetic improvement of economically important traits. Litter size at birth or at weaning, and skin size (which is positively correlated with animal size) are the traits that reduce production costs (litter size) on the one hand, and on the other hand, they

mostly influence the pelt price (skin size). Genetic parameters reported in this study indicate that effective genetic improvement of these traits can be achieved (moderate h^2 for BS, favourable genetic correlations between BS and SL, TS; relatively high h^2 for LSB and LSW, high positive genetic correlation between these traits). However, reports of other researchers show that animal size is negatively correlated with litter size. This unfavourable genetic correlation has to be taken into account in planning breeding programs. If litter size gained higher economic weight in the total merit index than animal size, it could diminish the negative effect of the antagonistic genetic correlation between these traits. The second solution, which is considered in Finland (Peura et al., 2004a), could be to use the restricted selection index (Kempthorne and Nordskog, 1959).

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