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Multiple trait genetic evaluation of ewe traits in Icelandic sheep

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Abstract

The fertility of the ewes were defined as 4 traits measured as number of lambs born (litter size, LS) in age 1 to 4 years. The maternal ability related to the same age interval was measured by special ewe production indices (EPI) which have been developed previously. The genetic parameters for these traits were estimated by series of bivariate REML analyses using animal models. The material used for the genetic analysis contained 540,518 records on 193,213 ewes. The heritability for number of lamb born were $h^2 = 0.17, 0.13, 0.11, 0.10$ for the four respective age classes. Corresponding estimates for ewe production index were $h^2 = 0.16, 0.17, 0.17, 0.15$. The genetic correlations between lamb born at different ages were ranging from 0.63 to 0.98. For the ewe production index the corresponding range was 0.82 to 0.99. The genetic correlations between fertility and production index were generally low. Therefore it was concluded that the multiple trait genetic evaluations needed to include two sets of 4 correlated traits. The material used for estimating the breeding values by the MT-BLUP Animal Model consisted of 1,5 million individuals in the pedigree file. 815,782 ewes had records for number of lambs born and 763,491 ewes had production index (at least one year). The records were registered in years 1990-2006. All possible missing patterns were present in the data. In the iteration process expected values for missing traits were generated and solutions were obtained on canonical transformed scale.

Introduction

Ewe production traits are economically very important for Icelandic sheep farmers. So far, good genetic evaluations for these traits have been lacking. Application of a modern genetic evaluation procedure to assist effective selection for ewe production traits would enhance genetic improvement in these traits and would have important economical impact on Icelandic sheep breeding. The objective of this study was to estimate genetic parameters for fertility traits and maternal ability traits for Icelandic ewes and to develop programs for computing Multiple Trait – Animal Model – BLUP for these traits.

Material and methods

All data in this study were obtained from the Farmers Association of Iceland and were collected by the Icelandic Sheep Breeders' Association for use in the national sheep recording system. The study was directed to the following traits: a) ewe fertility measured as the number of lambs born (litter size, LS) in each parity in the age interval of one to four years; and b) the ewe production index for the same age interval. The ewe production index (EPI) for each parity is an adjusted phenotypic measure of weaning weights in lambs (Sverrisson, 1977).

Lambing of Icelandic ewes is, by tradition and climatic conditions, predominantly seasonal. The vast majority of lambing are in the spring (April/May). The weaning time and/or the slaughtering time of the lambs is in the autumn (September/October). Out of season breeding is unusual so parity in this study is strictly equal to age of the ewes in years.

First part of the study aimed at the estimation of genetic parameters. In the analyses the data was used from the following five counties: 04 (Snæfellsnes og Hnappadalssýsla), 09 (Strandasýsla), 14 (S-Þingeyjarsýsla), 15 (N-Þingeyjarsýsla) og 18 (A-Skaftafellssýsla). In addition the data from the state owned experimental farm “Hestur” was included in the statistical analyses. Due to the widespread use of AI - rams from “Hestur” good genetic connectedness between the different districts was established. The data used for estimation of genetic parameters for LS and EPI consisted of 540,518 records from years 1990-2003 on 193,213 ewes. The pedigrees of the ewes were traced five generations and the pedigree files contained 270,259 animals.

The variance components were estimated by the ASReml programs of Gilmour (2004). As it was not possible to include more than two traits simultaneously in the computations, bivariate analyses were repeated until all variance and covariance components pertaining to all the traits were estimated. The following linear animal model was used:

$$y_{ijkl} = \text{birth-year}_i + \text{county}_j + \text{herd}_{jk} + \text{animal}_{ijkl} + e_{ijkl}$$

where y_{ijkl} is the observation; birth-year, county and herd within county are fixed effects (i=1,...17; j=1,...,6; k=1,...,406) but the animal effects are random ~ND(0, $\mathbf{A}\sigma^2_A$), where **A** is the numerator relationship matrix. The residual effects e_{ijkl} are ~ IND(0,$\mathbf{I}\ \sigma^2_e$).

The pedigree file used for computing the genetic evaluations contained almost 1,5 million animals. Thereof 815,782 ewes with records for LS in at least one parity and 763,491 ewes with EPI at least one year. The data used for the genetic evaluations refer to production years 1990-2006. All data was used after edition which meant elimination of individuals with registered birth-years < 1900 or > 2006. Additionally records on few individuals with non-existing county numbers were eliminated.

Two quadrivariate analyses for genetic evaluations for fertility and maternal ability, respectively, were performed according to a multiple trait BLUP animal model (Henderson & Quaas, 1976). The basic linear mixed model for both analyses was as follows in matrix notation:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Za} + \mathbf{e},$$

where **y** is a vector of observations, **b** is a vector of unknown fixed systematic environmental effects of birth-year/county/herd classes, **a** is a random vector of breeding values for the set of four traits included in each run and **e** is a random vector of residual effects. **X** and **Z** denotes design matrices which assign fixed effects and animals, respectively, to the observed values. The standard assumptions are that $E(\mathbf{y}) = \mathbf{Xb}$, $E(\mathbf{a}) = E(\mathbf{e}) = \mathbf{0}$, $\mathrm{Var}(\mathbf{a}) = \mathbf{G} \otimes \mathbf{A}$, $\mathrm{Var}(\mathbf{e}) = \mathbf{R} \otimes \mathbf{I}$ and $\mathrm{Cov}(\mathbf{a}, \mathbf{e}') = \mathbf{0}$, where **G** is the additive genetic (co)variance matrix of the four variables included in each run and **A** is the numerator relationship matrix. **R** represents the residual (co)variance matrix of the four variables, **I** is an identity matrix and ⊗ denotes the Kronecker product.

The general mixed model equations of Henderson (1950) are:

$$\begin{bmatrix} \mathbf{X}'(\mathbf{R}^{-1} \otimes \mathbf{I})\mathbf{X} & \mathbf{X}'(\mathbf{R}^{-1} \otimes \mathbf{I})\mathbf{Z} \\ \mathbf{Z}'(\mathbf{R}^{-1} \otimes \mathbf{I})\mathbf{X} & \mathbf{Z}'(\mathbf{R}^{-1} \otimes \mathbf{I})\mathbf{Z} + (\mathbf{G}^{-1} \otimes \mathbf{A}^{-1}) \end{bmatrix} \begin{bmatrix} \mathbf{b} \\ \mathbf{a} \end{bmatrix} = \begin{bmatrix} \mathbf{X}'(\mathbf{R}^{-1} \otimes \mathbf{I})\mathbf{y} \\ \mathbf{Z}'(\mathbf{R}^{-1} \otimes \mathbf{I})\mathbf{y} \end{bmatrix}$$

The solution vector **b** is an estimable function of the fixed effects included in the model (BLUE, Best Linear Unbiased Estimate) and **a** is the vector containing BLUP estimates of the breeding values. These equations are only solvable with iterative methods and for large data and many correlated traits the task may require enormous computing power. In order to facilitate the simultaneous computation of breeding values for four correlated traits in such voluminous data it would be advantageous to apply canonical transformation of the correlated variables. Canonical transformation implies that the vector of variables for each animal is multiplied by certain transformation matrices. The canonical transformation makes the variables genetically and environmentally uncorrelated which results in drastic reduction in computing effort. (Thompson, 1977, Árnason, 1982, Mrode, 1996).

Initially canonical transformation was only considered feasible when there were no missing traits and when the same model applied to all traits. Ducrocq and Besbes (1993) showed that canonical transformation was indeed possible even for cases with missing traits. They showed that when using iterative methods for solving the MME it is possible to create expected values for the missing traits with the EM algorithm. Furthermore Ducrocq and Chapuis (1997) have introduced what they call “generalized canonical transformation approach”, which in addition makes it possible to apply different models for the various correlated traits included in the computations. The generalized canonical transformation approach is now routinely used for the international genetic evaluations of the Icelandic horse (Árnason *et al.*, 2006). In the present study the same model applies to all traits. On the other hand every possible missing pattern is represented in the data, or $n^2 = 16$ for the four traits. Therefore the method of Ducrocq and Besbes (1993) was chosen to facilitate the computational process. A short description of the method follows: Data vector for each ewe_i with observations for all the four traits is denoted as $\mathbf{y}_i$. The canonical transformation matrix is then $\mathbf{Q}$ and its inverse $\mathbf{Q}^{-1}$. When one or more traits are missing one can reorder the traits such that observed values precede the missing ones, *i.e.*: $\mathbf{y'}_i = [\mathbf{y'}_{iv}\ \mathbf{y'}_{im}]$. Then corresponding rows and columns of $\mathbf{R}$ must be reordered and the transformation matrix and its inverse partioned accordingly: $\mathbf{Q} = [\mathbf{Q}_v\ \mathbf{Q}_m]$ and:

$$\mathbf{Q}^{-1} = \begin{bmatrix} \mathbf{Q}^v \\ \mathbf{Q}^m \end{bmatrix}$$

For each ewe with one or more missing trait two transformation matrices were created:

$$\mathbf{Q}_1 = \mathbf{Q}_v + \mathbf{Q}_m\mathbf{R}_{mv}\mathbf{R}^{-1}_{vv}$$

and

$$\mathbf{Q}_2 = \mathbf{Q}_m\mathbf{Q}^v - \mathbf{Q}_m\mathbf{R}_{mv}\,\mathbf{R}^{-1}_{vv}\mathbf{Q}^v$$

The transformed observations for each ewe_i with missing trait become:
$\mathbf{y}^*_i = \mathbf{Q}_1\,\mathbf{y}_{iv} + \mathbf{Q}_2[\,\mathbf{x'}_i\,\mathbf{b}^{*[k]} + \mathbf{a}^{*[k]}{}_i]$, where $\mathbf{b}^{*[k]}$ and $\mathbf{a}^{*[k]}$ are the solutions of the MME for fixed effects and breeding values, respectively, on the transformed scale. The transposed vector $\mathbf{x'}_i$ is the row of $\mathbf{X}$ which assigns ewe_i to the corresponding fixed effects.

Fifteen different pairs of $\mathbf{Q}_1$ og $\mathbf{Q}_2$ matrices were created, one pair for each missing pattern, and read by the BLUP program together with the original $\mathbf{Q}$ and $\mathbf{Q}^{-1}$ matrices. Solutions to the set of equations were then obtained by a methodology which is called “iteration on data” (Schaeffer og Kennedy, 1986; Mrode, 1996) which means that instead of storing all non-zero elements of the MME (many millions) the relevant elements were created for each individual in each round of iteration. Only information from the data together with the solution vectors were stored in memory. In the Gauss-Seidel iteration process both data and solutions were on the canonical transformation scale. When sufficient convergence was obtained the canonical transformed solutions were back transformed to the original scale by $\mathbf{b} = \mathbf{Q}^{-1}\mathbf{b}^*$ and $\mathbf{a} = \mathbf{Q}^{-1}\mathbf{a}^*$.

The index of genetic evaluations for each trait were scaled so that the mean value for ewes with at least one recorded year of production and born the last decade was equal 100. The distribution of index values were such that 10 units correspond to one additive genetic standard deviation for each trait. So far a total index is computed as a simple average of the genetic evaluations for the four traits included. The accuracy of index was computed with the approximate method of Meyer

(1989) which had been modified to accommodate inbreeding. Inbreeding was accounted for and the **A** diagonals were computed by the fast algorithm of Sigurdsson (Sigurdsson and Árnason, 1995).

Results and discussion

Genetic parameters which were estimated by the ASReml programs are shown in table 1 for litter size (LS) and in table 2 for ewe production index (EPI). Due the large data standard errors of the estimates are negligible. The results in table 1 show that the heritability of LS is highest for the first parity (one year of age), or $h^2 = 0.17$, and drops with age and is $h^2 = 0.10$ at the age of four years. Genetic correlation between the fertility (LS) at the first and later parities is significantly different from one , or $r_A = 0.63 – 0.68$, clearly indicating that fertility of one year-old ewes is to a large extent governed by different genes than fertility later in life. The genetic correlation between LS in later parities is higher ($r_A = 0.78 – 0.98$), especially between consecutive production years. These results support the use of a multiple trait model for genetic evaluations of LS in Icelandic sheep, instead of the traditional repeatability model. Heritability of EPI stays more constant over the age interval, $h^2 = 0.15 – 0.17$. Genetic correlation between EPI between first and later parities was estimated as $r_A = 0.82 – 0.88$. Between later parities higher genetic correlations were found, or $r_A = 0.94$ between second and later parities, while $r_A = 0.99$ between third and fourth parity. The advantage of the multiple trait model over a repeatability model is less for EPI than it is for LS. However, it is clear that EPI for one year-old ewes is genetically different from EPI traits later in life. The heritability estimates found in this study are in good agreement with the results of comprehensive analyses of data on Icelandic ewe traits some three to four decades ago (Hallgrímsson, 1966, Jónmundsson, 1977, Jónmundsson *et al.*, 1977). However the heritability estimates of adjusted lamb weight was somewhat lower in the present study compared with the earlier results in the breed. Compared to literature estimates of heritability for litters size in other breeds the estimates of heritability of LS in this study are rather high. A range from 0.0 to 0.35 has been reported in literature but most heritability estimates are 0.1 or less (Turner, 1969, Bradford, 1985, Al-Shorepy and Notter, 1996, Nagy *et al.*, 1999). Comparison of the results from the genetic analysis of the ewe production index (EPI) with other studies on adjusted lamb weight analysed as a trait of the ewe may be difficult due to different conditions and adjustment procedures. However the heritability estimates of EPI in this study fall well in the middle of the range (0.01-0.48) of estimated maternal heritability for lamb weights up to weaning in other breeds. (Näsholm and Danell, 1996, Al-Shorepy and Notter, 1996, Nagy *et al.*, 1999, Vaninisetti *et al.*, 2007) .

Further studies should be directed towards developing maternal trait models for analysing lamb weights, which could compete with or replace the use of EPI for genetic evaluations of maternal ability. However, this is a real challenge since inclusion of direct effects of lambs in the model will mean manifold increase in number of animals involved in the MME and the computational procedure for additional random components in multiple trait context will not be easy. Possibly the use of repeated records for lamb weight in different parities and a reduced animal model with maternal effects as shown by Mrode (1996) would be a feasible alternative.

Genetic and environmental correlations between LS and EPI at the same age was generally low, although highest at one year of age or $r_A = 0.3$. Consequently it was considered unnecessary to include all eight traits simultaneously in a single multivariate analysis.

Table 1 Estimated genetic parameters for litter size (LS) in the four first parities. Heritability (h^2) on the diagonal, phenotypic correlation (r_P) above and genetic correlation (r_A) below the diagonal. Genetic standard deviation (σ_A) is shown in the last row.

Parity	1	2	3	4
1	0.17	0.13	0.11	0.10
2	0.68	0.14	0.20	0.16
3	0.64	0.95	0.11	0.19
4	0.63	0.78	0.98	0.10
σ_A	0.17	0.20	0.17	0.16

Table 2 Estimated genetic parameters for ewe production index (EPI) in the four first parities. Heritability (h^2) on the diagonal, phenotypic correlation (r_P) above and genetic correlation (r_A) below the diagonal. Genetic standard deviation (σ_A) is shown in the last row.

Parity	1	2	3	4
1	0.16	0.25	0.24	0.21
2	0.88	0.17	0.32	0.28
3	0.84	0.94	0.17	0.34
4	0.82	0.94	0.99	0.15
σ_A	0.56	0.50	0.50	0.49

Diagrams revealing the distribution of estimated breeding values (EBV, average for the four parities) for LS and EPI are shown in figure 1 and figure 2, respectively. The distribution of the ewes´ index values for EPI is on the interval 68 to 136 and shows good fit to the normal distribution. The distribution of index values for LS has a more prominent upward tail and the ewes have index values ranging from 66 to 158. This is undoubtedly due to the effects of major genes causing abnormal prolificacy in ewes carrying such genes, *e. g.* the Thoka gene or the Loa gene (Jónmundsson and Adalsteinsson, 1985, Jónmundsson and Eythórsdóttir, 2003).

The trend in EBVs for EPI within the 21 counties is shown in figure 3. The largest genetic progress in the ewe production index (EPI) has apparently been obtained in Strandasýsla (9), A-Bardastrandasýsla (5), V-Bardastrandasýsla (6) and N-Múlasýsla (16). In general it can be concluded that genetic progress in LS and EPI has been rather low over the last decades, and there should be a scope for considerable more rapid improvement in fertility and maternal ability of

Icelandic ewes if breeders will make use of the new selection instrument provided by the MT-AM-BLUP procedure developed in this study. Economic weights for the different traits across parities have not been resolved and should probably be left to be the decision of the individual breeders.

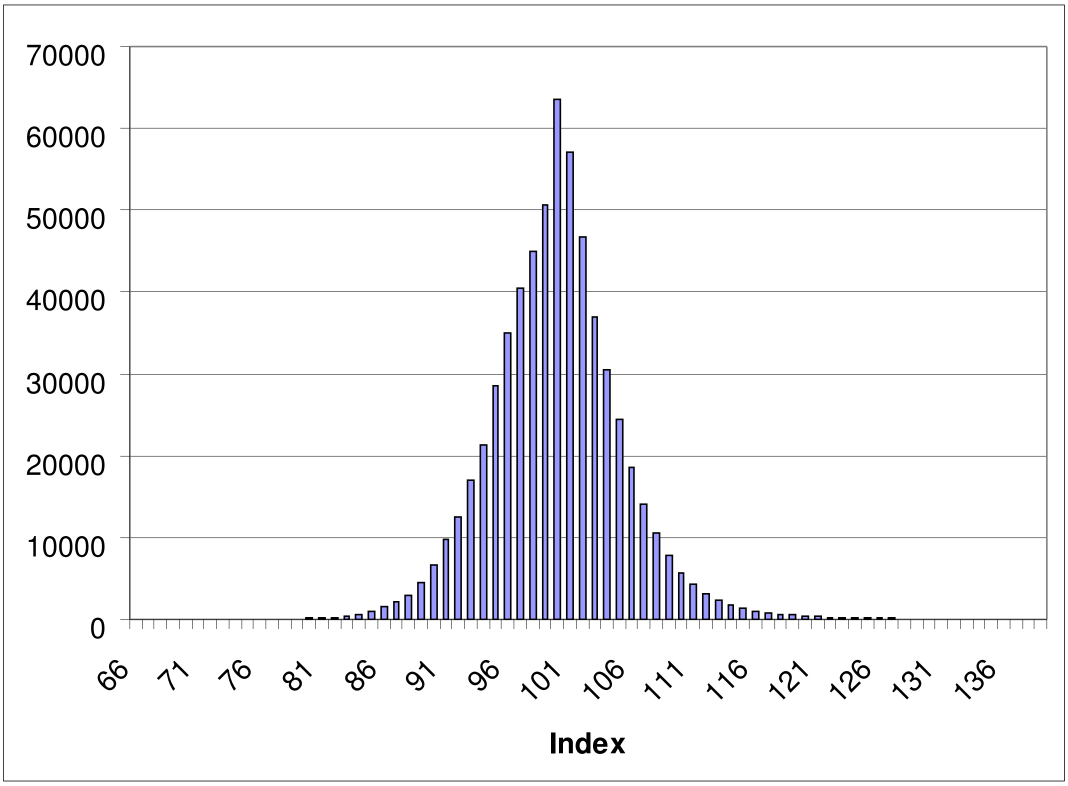

Figure 1. Distribution of EBVs for litter size. Ewes born 1990-2005.

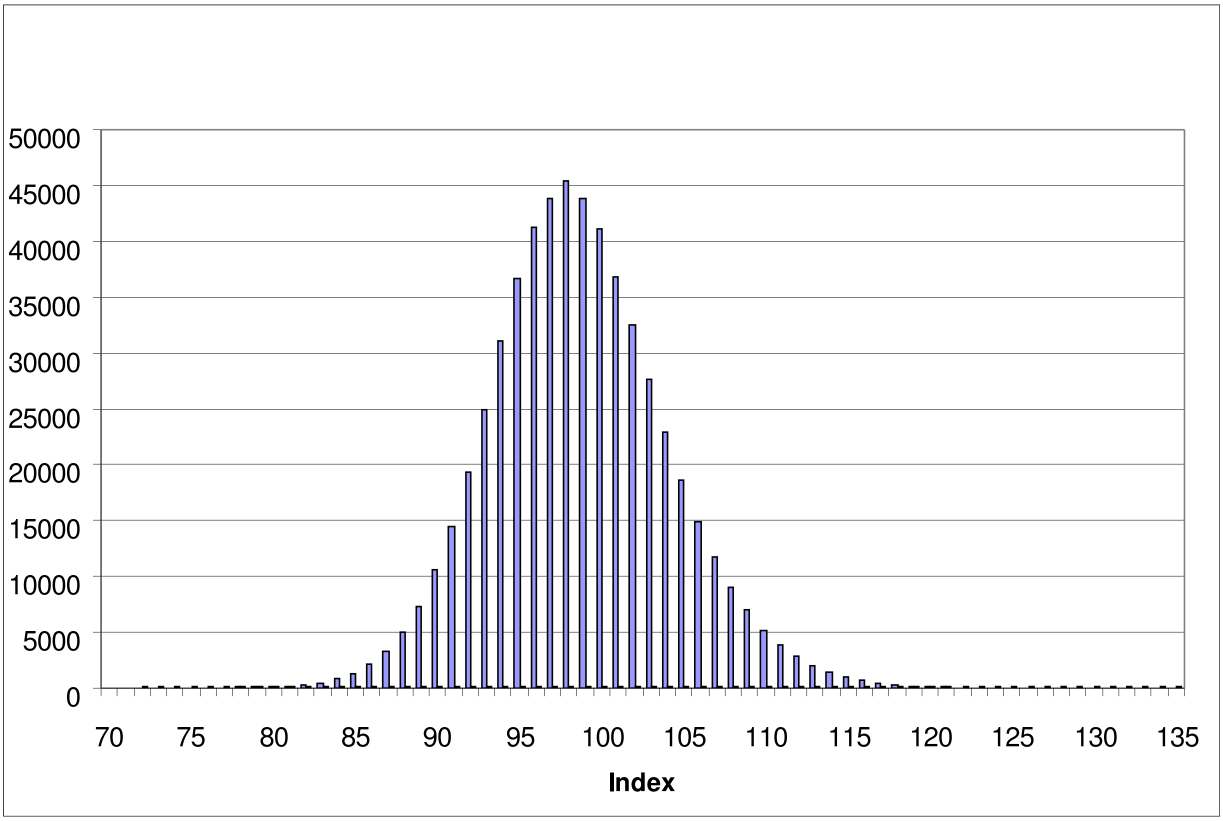

Figure 2   Distribution of EBVs for Ewe Production Index. Ewes born 1990-2005.

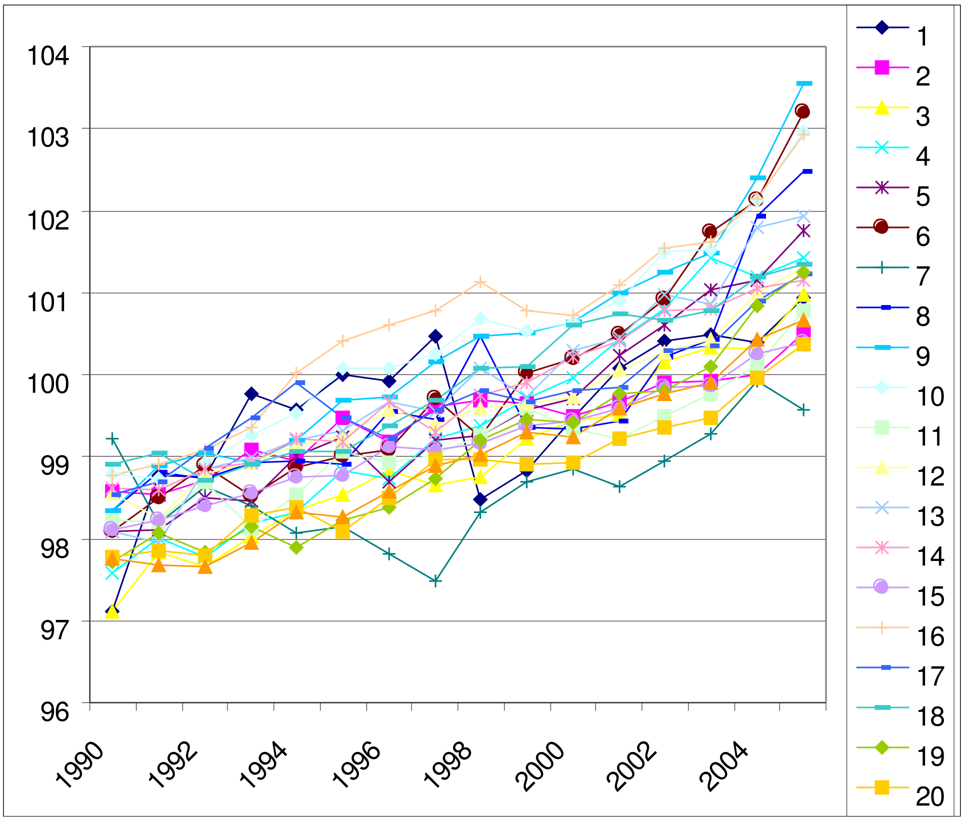

Figure 3. Genetic trend as mean EBV for ewe production index as the average for the four parities

within birth-years and counties.

Conclusions and implications

Heritability for litter size (LS) drops with increased age ($h^2 = 0.17 – 0.10$). The genetic correlations between first and later parities are $r_A = 0.68 – 0.63$. Heritability for ewe production index (EPI) is more constant across parities ($h^2 = 0.15 – 0.17$). The genetic correlations between first and later parities are $r_A = 0.88 – 0.82$. The advantage of using multiple trait model for genetic evaluations of LS and EPI in different parities is supported by the results of this study, especially for LS.

AM-MT-BLUP computational procedure using canonical transformation is feasible for genetic evaluation of ewe traits in the large Icelandic sheep population. Routine application of the procedure has already been realised.

The genetic progress has been limited in ewe traits in the Icelandic sheep population. There is a scope for larger genetic progress by more effective genetic evaluations and selection.

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