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Estimation of Variance Components and Heritabilities of Growth Characteristics in Morkaraman Lambs Using Different Statistical Methods

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Abstract

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Henderson's method 3, maximum likelihood (ML), restricted maximum likelihood (REML) and minimum variance quadratic unbiased estimation (MIVQUE) methods were used to estimate variance components and to predict heritabilities of birth weight, weaning weight and daily weight gain until weaning in Morkaraman lambs. The different variance components methods gave similar results. The moderately-high estimate of heritability for weaning weight, demonstrates an opportunity for improvement of this trait through genetic selection.

Key words: Variance components, heritability, growth traits, Morkaraman lambs.

Introduction

The use of variance components is an integral part of animal breeding theory and practice. Several methods viz. Analysis of Variance (ANOVA), Maximum likelihood (ML), Restricted Maximum Likelihood (REML), Minimum Norm Quadratic Unbiased Estimation (MINQUE), Symmetric Sums Approach (SSA) and Quadratic Least Squares (QLSE) methods have been developed for estimating variance components.

With balanced data (equal numbers of observations in corresponding subclasses), the Henderson's Method 3 estimators have many attractive properties: they are unbiased, minimum variance among all unbiased estimators that are quadratic functions of the observations, and, under normality, minimum variance among all unbiased estimators. However, when the data is unbalanced (unequal subclass frequencies), all of these properties are lost except unbiasedness (Swallow and Monahan, 1984). ML estimates the variance components by those values which maximize the full likelihood function over the parameter space, REML partitions the likelihood into two pieces, one of which is free of the fixed effects, and maximizes only that

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portion of the likelihood (Swallow and Monahan, 1984). MIVQUE(0) estimators are defined as those obtained from REML equations without iteration, using a priori values set at 0 and 1, for σ_s^2 and σ_e^2, respectively (Hartley and Rao, 1967).

Two general classes of estimators have sparked considerable interest: maximum likelihood (ML), restricted maximum likelihood (REML), minimum norm quadratic unbiased estimation (MINQUE) and minimum variance quadratic unbiased estimation (MIVQUE).

The Henderson's Method 3 and MIVQUE are based on equating the mean squares to their expectations. However, these methods give negative estimates of variance components, which can be overcome by the use of likelihood-based methods (Firat, 1997). The present investigation was undertaken to compare the estimate variance components and genetic parameters in growth traits by Henderson's method 3, MIVQUE, ML and REML.

Materials and Methods

Materials

The data recorded between 1989 and 1999 on 946 Morkaraman lambs of 26 sire-lines maintained at Ataturk University Agricultural Research Farm were used for this study. In this province Morkaraman is the predominant sheep breed. Lambing occurred in March and April. The lambs were identified and weight at birth was recorded. All the lambs were allowed to be with their dams until approximately 2.5 months of age. At weaning (at the beginning of grazing season, June) they were weighed and then subjected to a semi-intensive feeding management.

Methods

To estimate variance components for birth weight, weaning weight and daily weight gain until weaning in Morkaraman lambs, the following mixed linear model was used:

$$Y_{ijklmn} = \mu + a_i + b_j + c_k + d_l + S_m + e_{ijklmn} \quad [1]$$

where Y_{ijklmn} is weight of nth individual of the ith year, jth dam's age, kth type of birth, lth sex and mth sire. μ is overall mean, a_i is the effect of ith year of birth (i=1, 2, ..., 10) from 1989 to 1999, b_j is the effect of jth age of dam (j=1,..., 7>), c_k is kth type of birth (1=single; 2=twin), d_l is the effect of lth sex (1=male, 2=female), S_m is the effect of mth sire (m=1,...,26), e_{ijklmn} is a random error assumed normally and independently distributed.

The fixed effects are not assumed as a source of variation, whereas the essential source of variation is random effects. Random effects are independent and not correlated (Henderson, 1986). Using matrix algebra, equation [1], assuming all genetic variation is additive, can be expressed as

$$y = Xb + Zs + e \quad [2]$$

where **y** is a Nxl vector of observations; **X** is the Nx*p* design matrix for fixed effects; **Z** is Nx*q* design matrix for sires; and **b** is *p*x1 column vector of fixed effects, **s** is *q*x1 column vector of random effects, and **e** is Nx1 random error vector. The normal equation for [2] is then expressed as :

$$\begin{bmatrix} X'X & X'Z \\ Z'X & Z'Z \end{bmatrix} \times \begin{bmatrix} b \\ s \end{bmatrix} = \begin{bmatrix} X'y \\ Z'y \end{bmatrix}$$

Henderson's method 3

The ANOVA procedure used to estimate the sire ($\hat{\sigma}_s^2$) and error ($\hat{\sigma}_e^2$) components of variance was the fitting constants procedure of Henderson commonly referred to as method 3 (Henderson, 1953). The estimates of sire and error effects are obtained by equating observed and expected mean squares from an analysis of variance and solving the resulting equations under the following model (Searle, 1971):

$$\hat{\sigma}_e^2 = \frac{(y'y - \hat{b}X'y - \hat{s}Z'y)}{N - r(XZ)}$$

$$\hat{\sigma}_s^2 = \frac{\left[R(s \mid b) - \sigma_e^2 \{r(XZ) - r(X)\}\right]}{tr\left[Z'Z - Z'X(X'X)^{-1}X'Z\right]}$$

where R $(\boldsymbol{s} \mid \boldsymbol{b})$ is the additional sire sum of squares after fitting fixed effects $\boldsymbol{b}$; r is the number of linearly independent columns of X. tr is the sum of the diagonal elements of the matrix or trace operator and N is the total number of animals.

Maximum Likelihood (ML) and Restricted Maximum Likelihood (REML)

Hartley and Rao (1967) presented an iterative ML estimation procedure to solve Henderson's mixed model. Under normality assumption, ML estimates of variance components are obtained as

$$\hat{\sigma}_e^2 = \frac{(y'y - \hat{b}'X'y - \sum_{i=1}^{q} s_i'Z_i'y)}{N}$$

$$\hat{\sigma}_s^2 = \frac{\left[s's + \hat{\sigma}_e^2 \, \mathrm{tr}\{(Z'Z + \hat{\sigma}_e^2/\hat{\sigma}_s^2)^{-1}\hat{\sigma}_s^2\}\right]}{n_s}$$

where n_s is the number of sires. Estimates of ML are sufficient, consistent, efficient and asymptotically normal. However, increasing number of fixed effects results in loosing unbiasedness of ML.

REML, like ML, is an iterative procedure. In contrast to ML, REML takes into account the loss in degrees of freedom associated with estimation of fixed effects. The main idea behind REML is that all the information used in estimating variance components is combined in any set of N-p linearly independent error contrasts, where p is the number of fixed effects and the error contrast is defined as a linear combination of observations whose expectation is zero (Scheffe, 1959).

$$\hat{\sigma}_e^2 = \frac{(y'y - \hat{b}'X'y - \sum_{i=1}^{q} s_i'Z_i'y)}{N - r(X)}$$

$$\hat{\sigma}_s^2 = \frac{\left[s's + \hat{\sigma}_e^2 \, \mathrm{tr}\{Z'(I - X(X'X)^{-1}X')\} + \hat{\sigma}_e^2/\hat{\sigma}_s^2\right]^{-1}}{n_s}$$

Minimum Variance Quadratic Unbiased Estimator (MIVQUE)

MIVQUE(0) estimators are defined as those obtained from REML equations without iteration, using a priori values set at 0 and 1, for σ_s^2 and σ_e^2, respectively (Hartley and Rao, 1967).

Estimates of Heritabilities were based on variance components using the method of paternal half-sibs. Heritabilities were estimated as:

$$h^2 = 4\sigma_s^2/(\sigma_s^2 + \sigma_e^2)$$

where: σ_s^2 is the sire component of variance; σ_e^2 is the environmental component of variance. Standard errors of heritability were computed using the formulae developed by Swinger *et al.* (1964)

$$S_h = 4\frac{(1-r)[1+(n-1)r]}{\sqrt{(1/2)n(n-1)(n_s-1)}}$$

where $r = \sigma_s^2/(\sigma_s^2 + \sigma_e^2)$,

$n = [\sum n_i - (\sum n_i^2 / \sum n_i)]/(n_s - 1)$, n_i is the number of ith subclass and n_s is the number of sires.

In the present study, variance components for birth weight, weaning weight and daily weight gain until weaning were estimated using four different methods and heritabilities were also computed in Morkaraman lambs. The VARCOMP procedure in SAS® (1996) software was used for all computations except heritabilities and standard errors. Estimated variance components were evaluated by using Bartlett homogeneity test and criterion of Swallow and Monahan (1984).

Results and Discussion

Sire and error components estimated from Henderson's method 3, ML, REML and MIVQUE were similar (Table 1). However, ML estimates of σ_s^2 and σ_e^2 were smaller than

estimates using other three procedures. The lower estimates from the ML procedure may arise due to its inherent bias under mixed models. On the other hand, the estimates from Henderson's method 3 were the highest for σ_s^2 and σ_e^2 variance components as compared with the other procedures. However, Bartlett homogeneity tests indicated that there were no significant differences ($p>0.05$) among four different estimates of σ_s^2 and σ_e^2 for all the traits. Whereas, σ_s^2/σ_e^2 were under 0.5 for all traits. Swallow and Monahan (1984) reported that the ML estimator of σ_s^2 has downward bias, which may be large when $\sigma_s^2/\sigma_e^2 > 0.5$. But when $\sigma_s^2/\sigma_e^2 < 0.5$, the ML estimator of σ_s^2 has small bias, low MSE and is the preferred estimator (Table 1, 2 and 3).

Table 1
Sire (σ_s^2) and error (σ_e^2) variance components, $\hat{\sigma}_s^2/\hat{\sigma}_e^2$ and heritability (h^2) estimates for birth weight in Morkaraman lambs

Methods of estimation	Variance components			Heritability
	$\hat{\sigma}_s^2$	$\hat{\sigma}_e^2$	$\hat{\sigma}_s^2/\hat{\sigma}_e^2$	h^2±SE
Henderson's method 3	0.006760	0.65901	0.0103	0.028±0.041
MIVQUE	0.002394	0.66387	0.0036	0.014±0.036
ML	0.002369	0.65583	0.0036	0.014±0.036
REML	0.003992	0.66254	0.0060	0.024±0.038

Table 2
Sire (σ_s^2) and error (σ_e^2) variance components, $\hat{\sigma}_s^2/\hat{\sigma}_e^2$ and heritability (h^2) estimates for weaning weight in Morkaraman lambs

Methods of estimation	Variance components			Heritability
	$\hat{\sigma}_s^2$	$\hat{\sigma}_e^2$	$\hat{\sigma}_s^2/\hat{\sigma}_e^2$	h^2±SE
Henderson's method 3	3.2545	19.134	0.1701	0.581±0.185
MIVQUE	2.9944	19.941	0.1501	0.522±0.186
ML	2.7851	18.9351	0.1471	0.513±0.182
REML	3.1926	19.1474	0.1876	0.632±0.186

Table 3
Sire (σ_s^2) and error (σ_e^2) variance components, $\hat{\sigma}_s^2/\hat{\sigma}_e^2$ and heritability (h^2) estimates for daily weight gain until weaning in Morkaraman lambs

Methods of estimation	Variance components			Heritability
	$\hat{\sigma}_s^2$	$\hat{\sigma}_e^2$	$\hat{\sigma}_s^2/\hat{\sigma}_e^2$	h^2±SE
Henderson's method 3	0.000123	0.002583	0.0476	0.182±0.0810
MIVQUE	0.000121	0.002586	0.0468	0.177±0.0795
ML	0.000114	0.002556	0.0446	0.170±0.0778
REML	0.000123	0.002585	0.0476	0.182±0.0806

To obtain non negative and unbiased estimation of variance components is very important for analysis of data in animal breeding. Henderson's method 3 and MIVQUE have the disadvantage of producing negative estimates although it was not observed in this study. These negative variance components arise from either sampling error or lack of the model to explain total variance (Smith and Savage, 1992).

The heritability is an estimate rather than a solid figure. Less or more different estimates of the same trait can be presented by many authors (Duzgunes *et al.,* 1987; Bas, 1990; Kaymakci and Sonmez, 1996). This variation is based on genetic and environmental factors such as breed, herd, year, age, etc. The heritabilities predicted for birth weight, weaning weight and daily weight gain until weaning were reported as 0.10-0.30, 0.10-0.30 and 0.15-0.40, respectively (Duzgunes *et al.,* 1987; Bas, 1990; Kaymakci and Sonmez 1996). The heritability estimates using four different estimation methods in this study were lower for birth weight, higher for weaning weight and similar for daily weight gain until weaning as compared to those reported in the literature (Duzgunes *et al.,* 1987; Bas, 1990; Kaymakci and Sonmez 1996).

The heritabilities with the smallest standard error were estimated by ML procedure. In practice, errors in the estimation of genetic parameters (heritability or correlation) lead to under or over estimates of the genetic response and this bias is accumulated at each generation if it is not corrected. After several generations, this could lead to an unacceptable degree of the traits of economic importance. Similarly, such errors in estimates also hinder choosing the optimal selection method (Beaumont, 1991).

As the data used in this study were relatively balanced, the four different variance components methods gave similar results. The estimate of heritability for weaning weight, which was moderate-high, demonstrates an opportunity for improvement of this trait through genetic selection.

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ओ.सी.बिलगिन, एन.एसेनबुगा, एम.मैसित, एम.कराओग्लू। विभिन्न सांख्यकी विधियों के उपयोग से मोर्कारामान मेमनों में वर्धन लक्षणों के प्रसरण घटकों और वंशागतित्वता का आंकलन।

मोर्कारामान मेमनों के जन्म भार, बिलगाव पर शरीर भार और बिलगावन तक दैनिक शरीर भार वृद्धि में प्रसरण घटकों को ज्ञात करने और वंशागतित्वता के आंकलन के लिए हेन्डर्सन की तीसरी विधि, सर्वाधिक संभावना, नियंत्रित सर्वाधिक संभावना और न्यूनतम प्रसरण क्वार्डेटी निष्पक्ष आंकलन विधियों का उपयोग किया गया। प्रसरण घटकों की विभिन्न विधियों से समान परिणाम प्राप्त हुए। बिलगाव पर शरीर भार के वंशागतित्वता में सामान्य उच्च आंकलन से आनुवंशिक चयन द्वारा इस लक्षण में सुधार की संभावना दर्शाती है।