

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

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Abstract: The methods of Henderson's method 3, maximum likelihood (ML), restricted maximum likelihood (REML) and minimum variance quadratic unbiased estimation (MIVQUE) 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 results were evaluated according to different criteria and discussed.

Key words: Variance components, Heritability, Growth traits, Morkaraman lambs

Introduction

In statistical genetics, estimating heritabilities and genetic correlations need to estimate variance components (Swallow and Monahan, 1984). Good estimates of genetic parameters (heritabilities and genetic correlation with the criteria of selection) are required to accurately predict responses to direct or indirect selection (Beaumont, 1991). Estimation of genetic parameters by full or half-sib correlations is based on partitioning variance into its causal components. Although procedures for estimating variance components differ in their degree of simplicity and their reliability, in general, the choice of a method for estimation of variance components is influenced more by simplicity than by reliability (Falconer, 1989; Kayaalp and Bek, 1994).

The use of variance components is an integral part of animal breeding theory and practice. Several methods have recently been developed for estimating variance components. These are Analysis of Variance (ANOVA), Maximum likelihood (ML) estimation, Restricted Maximum Likelihood (REML) estimation, Minimum Norm Quadratic Unbased Estimation (MINQUE), Symmetric Sums Approach (SSA) and Quadratic Least Squares (QLSE) methods. Two general classes of estimators have sparked considerable interest: maximum likelihood (ML) and restricted maximum likelihood (REML), and minimum norm quadratic unbiased estimation (MINQUE) and minimum variance quadratic unbiased estimation (MIVQUE).

The Henderson's Method 3 and MIVQUE for estimating variance components are based on equating the mean squares to their expectations. However, the problem with these methods is that they give negative estimates of variance components. This can be overcome by the use of likelihood-based methods (Fýrat, 1997).

In this study, Henderson's method 3, MIVQUE, ML and REML methods were compared to estimate variance components and genetic parameters in growth traits.

Materials and Methods

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

To estimate variance components for birth weight, weaning weight and daily weight gain until weaning in Morkaraman lambs, a mixed linear model describing the data 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 n th individual of the i th year, j th of age of dam, of k th type of birth, l th sex and of m th sire. The parameter μ is overall mean, a_i is the effect of i th year of birth ($i = 1, 2, \dots, 10$) from 1989 to 1999, b_j is the effect of j th age of dam ($j = 1, \dots, 7$), c_k is k th type of birth ($1 = \text{single}$; $2 = \text{twin}$), d_l is the effect of l th sex ($1 = \text{male}$, $2 = \text{female}$), S_m is the effect of m th sire ($m = 1, \dots, 26$), e_{ijklmn} is a random element assumed normally and independently distributed.

Because fixed effects are not assumed a source of variation, the essential source of the variation is based on 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 $N \times 1$ vector of observations; X is the $N \times p$ design matrix for fixed effects; Z is $N \times q$ design matrix for sires; and b is $p \times 1$ column vector of fixed effects, s is $q \times 1$ column vector of random effects, and e is $N \times 1$ random error vector. The normal equation for (2) is then expressed as

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

Henderson's Method 3: The ANOVA procedure used to estimate sire (σ_s^2) and error (σ_e^2) variance components 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 full model as follows (Searle, 1971):

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

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

where $R(s|b)$ is the additional sire sum of squares after fitting fixed effects 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. 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).

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

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

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

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 losing 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).

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

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

While 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 portion of the likelihood (Swallow and Monahan, 1984).

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 i th 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 in Morkaraman lambs were estimated using four different estimation methods and heritabilities were computed. The VARCOMP procedure in SAS[®] (1996) software was used for all computations in this study except heritabilities and standard errors. Estimated variance components were evaluated by using Bartlett homogeneity test (Yildiz and Bircan, 1991) and criterion of Swallow and Monahan (1984).

Results and Discussion

In Tables 1, 2 and 3, sire (σ_s^2) and error (σ_e^2) variance components and heritability (h^2) estimates for birth weight, weaning weight and daily weight gain until weaning in Morkaraman lambs by Henderson's method 3, ML, REML and MIVQUE methods were presented. Sire and error component estimates from Henderson's method 3, ML, REML and MIVQUE were similar. However, ML estimates of σ_s^2 and σ_e^2 was smaller than estimates using Henderson's method 3, REML and MIVQUE procedures. The lower estimate from the ML procedure may arise due to its inherent bias under mixed models. In the other hand, the estimates from Henderson's method 3 as compared with the other procedures had a tendency to be the highest for σ_s^2 and σ_e^2 variance components. 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 traits.

For all traits, σ_s^2 / σ_e^2 were under 0.5. Swallow ve Monahan (1984) reports that the ML estimator of σ_s^2 has downward bias which may be large when $\sigma_s^2 / \sigma_e^2 \geq 0.5$. 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.

The results of Swallow and Monahan (1984), Beaumont (1991), Smith and Savage (1992), Firat (1997), Esenbuga and Dayıoglu (2002), Akbas *et al.* (2002) were similar those obtained in this study.

Table 1: Sire (σ_s^2) and error (σ_e^2) variance components, σ_s^2 / σ_e^2 and heritability (h^2) estimates for birth weight in Morkaraman lambs

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

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

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

To obtain nonnegative and unbiased estimation of variance components is very important for animal breeding. Although it was not observed in this study, Henderson's method 3 and MIVQUE have the disadvantage of producing negative estimates. 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 Fig. 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 variety 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 heritabilities predicted using four different estimation methods in this study as compared to those reported in the literature was lower for birth weight, higher for weaning weight and similar for daily weight gain until weaning.

The heritabilities with the smallest standard error were provided by ML procedure for our data. In practice, errors in estimates of genetic parameters (heritability or correlation) lead to under or overestimates of the genetic response. This bias will be accumulated at each generation if it was not corrected. After several generations, this could lead to an unacceptable degree of the trait considered. Such errors in estimates also hinder choosing the optimal selection method (Beaumont, 1991).

In conclusion, because the data used in this study were relatively balanced, the four different variance components methods gave similar results.

References

- Akbas, Y., Y. Unver, I. Oguz and O. Altan, 2002. Comparison of different variance component estimation methods for genetic parameters of clutch pattern in laying hens. Arch. Geflügelk, 66: 232-236.
- Bas, S., 1990. Merinos ve Morkaraman Kuzularının Verim Özelliklerine Etkili Çevre Faktörlerinin ve Bu Özelliklere Ait Genetik ve Fenotipik Parametrelerin Tahmininde Farklı Modellerin Değerlendirilmesi. (Doktora Tezi), Atatürk Üniv. Ziraat Fakültesi Zootekni Böl., Erzurum.
- Beaumont, C., 1991. Comparison of Henderson's Method 1 and Restricted Maximum Likelihood estimation of genetic parameters of reproductive traits. Poultry Sci., 70: 1462-1468.
- Duzgunes, O., A. Elicin and N. Akman, 1987. Hayvan Islahı. Ankara Üniv. Ziraat Fak. Yayınları:1003. Ders Notu:29, Ankara., 9-41.
- Esenbuga, N. and H. Dayiglu, 2002. Estimate of variance components with different methods for growth traits of lambs and reproductive characters of Awassi and Red Karaman ewes. Turk. J. Vet. Anim. Sci., 26: 161-169.
- Falconer, D. S., 1989. Introduction to quantitative genetics. 3rd ed. John Wiley and Sons, New York.
- Firat, M. Z., 1997. Hayvan islahında negatif varyans unsuru tahmini ve tahmin yöntemlerinin incelenmesi. Çukurova Üniv. Ziraat Fak. Derg., 12: 169-176.
- Hartley, H. O. and J. N. K. Rao, 1967. Maximum Likelihood Estimation for The Mixed Model Analysis of Variance Model. Biometrika., 54: 93-98.

- Henderson, C. R., 1953. Estimation of Variance and Variance Components. *Biometrics*, 9: 226-252.
- Henderson, C. R., 1986. Recent Development in Variance and Covariance Estimation. *J. Anim. Sci.*, 63: 208-216.
- Kayaalp, G. T. and Y. Bek, 1994. Varyans Unsurları Tahmin Yöntemlerinin Karsılastırmalı Olarak İncelenmesi. *Çukurova Üniv. Ziraat Fak. Dergisi.*, 2:127-142.
- Kaymakci, M. and R. Sonmez, 1996. İleri Koyun Yetiştiriciliği, 1. Baskı, İzmir, 15-52.
- Rao, C. R., 1972. Estimation of Variance Covariance Components in Linear Models. *JASA*, 67:112-115.
- SAS Institute, 1996. SAS Institute Inc., NC, USA.
- Scheffe, H., 1959. The analysis of variance. John Wiley and Sons, New York.
- Searle, R. S., 1971. C. R. Henderson, the Statistician; and his Contributions to Variance Components Estimation. SYMPOSIUM: The Legacy of C.R. Henderson. *J. Dairy Sci.*, 74: 4035-4044.
- Smith, E. J. and T. F. Savage, 1992. Comparison of Four Methods of Variance Component Estimation for Heritability of Embryonic Mortality in Turkeys. *Poultry Sci.*, 71: 229-234.
- Swallow, W. H. and J. F. Monahan, 1984. Monte Carlo Comparison of ANOVA, MIVQUE, REML and Estimators of Variance Components. *Technometrics*, 1: 47-57.
- Swinger, L. A., W. R. Harvey, D. O. Everson, K. E. Gregory, 1964. The variance of interclass correlation involving groups with one observation. *Biometrics*, 20, 818-826.
- Yildiz, N. and H. Bircan, 1991. Arastırma ve Deneme Metodları. Atatürk Üniv. Ziraat Fakültesi Yayınları. Erzurum, 46-50.