MAXIMUM LIKELIHOOD ESTIMATORS OF VARIANCE COMPONENTS FOR DIRECT AND
MATERNAL EFFECTS OF WEANING WEIGHTS OF ROMNEY SHEEP

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SUMMARY

The maximum likelihood (ML) procedure outlined in Wewala, Anderson and Rae (1985) was used to estimate variance components for direct and maternal effects of weaning weights of Romney lambs. In addition, weaning weight adjustment factors were obtained. Large-sample variances for the estimates of the variance components and the estimable functions of the fixed effects in the model were also obtained. The heritability estimate of the direct effects is 0.20. The estimated genetic correlation between the direct and maternal effects of weaning weights is -0.51.

INTRODUCTION

Weaning weight, which is influenced by maternal effects, is a characteristic of economic importance in a dual purpose breed of sheep such as the New Zealand Romney. Evaluation of the direct and maternal genetic variances and the covariance between the effects is essential for the development of optimum selection plans. Hanrahan (1976) examined the influence of maternal genetic effects on the relative efficiency of progeny and performance testing. He concluded that progeny testing is very inefficient when traits are influenced by maternal effects. Weaning weight adjustment factors (for sex, type of birth and rearing, age of dam, age at weaning) are reported by many authors [Blackwell and Henderson (1955); De Baca, Bogart, Calvin and Nelson (1956); Harrington, Whiteman and Morrison (1958); Ch'ang and Rae (1961, 1970); Jury, Johnson and Clarke (1979); and Newman, Wickham, Rae and Anderson (1983)]. Ch'ang and Rae (1972) estimated the genetic correlation between hogget characters and maternal environment for Romney sheep using dam-offspring covariances.

The purpose of this study was to apply the maximum likelihood (ML) procedure outlined in Wewala, Anderson and Rae (1985) to study the maternal effects of weaning weights of Romney lambs. In addition, weaning weight adjustment factors were obtained. Large-sample variances were obtained for the estimates of variance components and estimable functions of fixed effects.

SOURCE OF DATA

Weaning weights (kg) of 2174 Romney lambs were analyzed. The data were from a random-bred experimental flock maintained at Massey University, Palmerston North, New Zealand, for 11 years (1971 to 1981 inclusive).

METHOD OF ANALYSIS

The maximum likelihood procedure for estimating variance components with unbalanced data in a maternal effects model, described in Wewala et al (1985) was used. The method requires observations on parents and offspring. A special design was used where each of a set of sires was mated to several dams and a number of offspring raised from each mating with the assumptions that

(i) observations are available on all animals;
(ii) the phenotypic variance of an observation is \( \sigma_p^2 \), irrespective of the generation;
(iii) the families are independent of each other, where the ith family consists of the ith sire, the dams mated to the ith sire and the
progeny of the ith sire; and
(iv) the sires and the dams within a family are unrelated.

The special structure of the data, together with the above assumptions were exploited to enable derivation of explicit expressions for the inverse and the determinant of the variance-covariance matrix of the observations, both of which arise in the likelihood function and the partial derivatives thereof. Algorithms for generating the likelihood function and the partial derivatives are proposed in Wewala (1984).

However, the data used in this study were not from an experiment especially designed to carry out such an analysis. Therefore the following procedure was adopted for obtaining data suitable for the analysis:

(i) All sires with records, which were born between 1971 and 1981 were included. The number of sires was equivalent to the number of families,
(ii) The records of all dams which produced offspring with records were included, thereby completing information on all families. Animals with no records were deleted.

Altogether there were 73 families giving an average family size of 30. Since the experiment was not especially designed to carry out this analysis, there were a few shortcomings. Some records were used more than once. For example, an animal's record could have been used initially as a progeny record and then subsequently as a parent record. Also, a ewe could have been used in more than one year which means that its record was used more than once. This also violates the assumption that there were no maternal half-sibs. However, the sires did not have progeny in more than one year.

**THE MODEL**

Let the phenotypic measurement of individual i, which is influenced by the maternal effects of its dam, w, be expressed as

\[ y_i = f_i(\mathbf{g}) + g_{di} + g_{mw} + e_{mw} + e_{di} \]

where
- \( f_i(\mathbf{g}) \) is a linear function of the unknown fixed effects;
- \( g_{di} \) is the direct additively genetic effect of i;
- \( g_{mw} \) is the maternal additively genetic effect of w;
- \( e_{mw} \) represents the residual effect common to the offspring of w; and
- \( e_{di} \) represents the residual effect unique to the individual i.

Assuming that genetic and residual effects are independent and that the residual effects are independent of each other, the covariance between phenotypic values of two related individuals i and i', whose dams are w and w', respectively can be expressed as

\[ a_{ii'} \sigma_{AO}^2 + (a_{i, w'} + a_{i, w}) \sigma_{AOA} + a_{ww'} \sigma_{Am}^2 + b_{ww'} \sigma_{Em}^2 + b_{ii'} \sigma_{Eo}^2 \]

where
- \( \sigma_{AO}^2 \) is the direct additively genetic variance;
- \( \sigma_{Am}^2 \) is the maternal additively genetic variance;
- \( \sigma_{AOA} \) is the covariance between direct additively genetic and maternal additively genetic effects;
- \( \sigma_{Em}^2 \) is the variance of the residual effects common to full-sibs and maternal half-sibs;
- \( \sigma_{Eo}^2 \) is the variance of those residual effects which are unique to the individuals;
- \( a_{ii'} \) is the coefficient of additive relationship between i and i'; and
The vector of fixed effects of the model ($\mathbf{b}$) included a general mean ($\beta_1$); 11 year of birth effects ($\beta_2$ to $\beta_{12}$ for the years 1971 to 1981, respectively); 2 sex effects ($\beta_{13}$ and $\beta_{14}$ for ewe and ram, respectively); 3 birth and rearing rank effects ($\beta_{15}$ to $\beta_{17}$ for single, twin reared as single and twin, respectively); effects of the age of dam ($\beta_{18}$ to $\beta_{21}$ for 2 to 5 years, respectively); and a regression coefficient associated with the age at weaning in days ($\beta_{22}$).

OPTIMIZATION PROCEDURE

A constrained maximization of the likelihood function was carried out to obtain estimable functions of fixed effects and estimates of variance components. Using initial values for the variance components ($\mathbf{Q}^0$), the linear equations given in Wewala et al (1985) were solved to find $\mathbf{Q}^0$ (the elements $Q_{mm}, m = 1, \ldots, 5$ are $Q_{Ao}, Q_{Am}, Q_{AoAm}, Q_{Am^2}$ and $Q_{Em^2}$, respectively). Substituting these solutions for $\mathbf{Q}^0$, the likelihood function was maximised subject to the constraints

(i) $Q_1, Q_2, Q_4, Q_5 \geq 0$ (to avoid negative estimates of variances) and
(ii) $Q_1Q_2 - Q_3^2 \geq 0$ (to ensure that the estimate of the genetic correlation between direct and maternal effects lies within $-1$ and $+1$).

The algorithms given in Wewala (1984) were used to generate the linear equations and the likelihood function.

Routine E04UAF of NAG FORTRAN library [Numerical Algorithms Group (1983)] was used to minimise $-F$ where $F$ is the likelihood function subject to the above constraints. This routine is intended for functions and constraints which have continuous first and second derivatives. However, it is not required to generate the derivatives. The computing routine uses a sequential augmented Lagrangian method, the minimization sub-problems involved being solved by a Quasi-Newton method. The solution values for $\beta_{12}, \beta_{14}, \beta_{17}$ and $\beta_{21}$ were set to zero.

RESULTS

The solutions for the fixed effects and the ML estimates of variance components with their standard errors are given in Table 1 and Table 2, respectively. Following Searie (1971), the large sample variance-covariance matrices for $Q^0$ and $Q$ were obtained. The method of obtaining these is given in Wewala et al (1985). Since an explicit expression for the inverse of the variance-covariance matrix was available, explicit expressions for the large-sample variances and covariances were derived [see Wewala (1984)]. The estimate of the genetic correlation between direct and maternal effects ($r_g$) is $-0.507$. The fraction of the selection differential realized if selection is on phenotypic values [Dickerson (1957)],

$$s = (\sigma_{Ao}^2 + 1.5\sigma_{AoAm}^2 + 0.5\sigma_{Am}^2)/\sigma_p^2$$

is 0.206, where $\sigma_p^2$ is the phenotypic variance.
Table 1: Estimable functions of fixed effects and their standard errors for weaning weights of lambs (kg)

<table>
<thead>
<tr>
<th>factor solution ± std. error</th>
<th>sex</th>
<th>factor solution ± std. error</th>
</tr>
</thead>
<tbody>
<tr>
<td>general mean</td>
<td></td>
<td>sex</td>
</tr>
<tr>
<td>$\beta_1^0$</td>
<td>10.31 ± 0.82</td>
<td>$\beta_1^3$</td>
</tr>
<tr>
<td>year-of-birth</td>
<td></td>
<td>birth and rearing rank</td>
</tr>
<tr>
<td>$\beta_2^0$</td>
<td>-3.13 ± 0.73</td>
<td>$\beta_4^5$</td>
</tr>
<tr>
<td>$\beta_3^0$</td>
<td>-0.27 ± 0.51</td>
<td>$\beta_6^5$</td>
</tr>
<tr>
<td>$\beta_4^0$</td>
<td>-0.82 ± 0.54</td>
<td>$\beta_8^5$</td>
</tr>
<tr>
<td>$\beta_5^0$</td>
<td>-0.67 ± 0.47</td>
<td>$\beta_8^6$</td>
</tr>
<tr>
<td>$\beta_6^0$</td>
<td>-0.61 ± 0.48</td>
<td>$\beta_8^7$</td>
</tr>
<tr>
<td>$\beta_7^0$</td>
<td>-0.46 ± 0.42</td>
<td>$\beta_8^9$</td>
</tr>
<tr>
<td>$\beta_8^0$</td>
<td>1.61 ± 0.43</td>
<td>$\beta_8^1$</td>
</tr>
<tr>
<td>$\beta_9^0$</td>
<td>-0.50 ± 0.44</td>
<td>$\beta_8^2$</td>
</tr>
<tr>
<td>$\beta_0^1$</td>
<td>-2.92 ± -0.45</td>
<td>$\beta_8^2$</td>
</tr>
<tr>
<td>$\beta_1^1$</td>
<td>-0.77 ± -0.51</td>
<td>$\beta_8^2$</td>
</tr>
</tbody>
</table>

Note: $\beta_9^0 = \beta_2^0 - \beta_1^2$ and the std. error quoted is the standard error of that contrast.

Table 2: Estimates of variance components and their standard errors for weaning weights of lambs (kg²)

<table>
<thead>
<tr>
<th>variance component</th>
<th>estimate ± std. error</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\sigma_{\alpha_0}^2$</td>
<td>2.55 ± 0.49</td>
</tr>
<tr>
<td>$\sigma_{\alpha_1}^2$</td>
<td>6.44 ± 5.71</td>
</tr>
<tr>
<td>$\sigma_{\alpha_0\alpha_1}^2$</td>
<td>-2.06 ± 2.48</td>
</tr>
<tr>
<td>$\sigma_{\epsilon_0}^2$</td>
<td>0.0 ± 3.56</td>
</tr>
<tr>
<td>$\sigma_{\epsilon_1}^2$</td>
<td>6.11 ± 0.90</td>
</tr>
</tbody>
</table>

Ch'ang and Rae (1972) estimated the genetic correlation between hogget characters and maternal environment by using dam-offspring covariance components. In addition, they estimated that fraction of the contribution from maternal sources to dam-offspring covariance ($M_1$), where

$$M_1 = \frac{(1.5\sigma_{\alpha_0\alpha_1}^2 + 0.5\sigma_{\epsilon_0}^2)}{\sigma_{\epsilon_1}^2}.$$

The source of data for the study of Ch'ang and Rae (1972) is the same as that for this study. However, their data was obtained in the period 1955 - 1965. A comparison of some estimates from Ch'ang and Rae (1972) and this study is given in Table 3. The estimate of the standard deviation was obtained from Ch'ang and Rae (1970).
Table 3: A comparison of estimates obtained from this study and that of Ch'ang and Rae (1970, 1972)

<table>
<thead>
<tr>
<th>Estimate of</th>
<th>Ch'ang and Rae (1970, 1972)</th>
<th>this study</th>
</tr>
</thead>
<tbody>
<tr>
<td>standard deviation</td>
<td>7.70</td>
<td>7.90</td>
</tr>
<tr>
<td>heritability (of direct effects)</td>
<td>0.30</td>
<td>0.20</td>
</tr>
<tr>
<td>genetic correlation ($r_g$)</td>
<td>-0.76</td>
<td>-0.51</td>
</tr>
<tr>
<td>$M_i$</td>
<td>-0.134</td>
<td>0.01</td>
</tr>
</tbody>
</table>

The magnitudes of the heritability and the genetic correlation are lower than those for the study of Ch'ang and Rae (1972). The difference between the estimates of the standard deviation is negligible. There is a considerable difference between the estimates of $M_i$.

Ch'ang and Rae (1961, 1970) studied the effects of type of birth and rearing, age-of-dam, year-of-birth, sex and age at weaning, on weaning weights of sheep. Jury, Johnson and Clarke (1979) obtained adjustment factors for environmental sources of variation for weaning weights of Romney lambs using 12 commercial flocks participating in the National Flock Recording Scheme (Sheeplan) of New Zealand. Adjustment factors were estimated for birth-rearing rank, sex, age-of-dam and age at weaning. Newman, Wickham, Rae and Anderson (1983) obtained least squares estimates for the factors affecting weaning weights of lambs.

Adjustment factors obtained in this study for birth-rearing rank, dam age and age at weaning where a maternal effects model is assumed are almost identical to the average adjustment factors obtained by Jury et al (1979). However, there is a large difference in the estimated adjustment factors for sex. The adjustment factors obtained by Newman et al (1983) are also similar to the adjustment factors obtained in this study with the exception of the adjustment for sex. The estimate of the adjustment factor obtained for sex by Jury et al (1979), by Newman et al (1983) and that used by Sheeplan are similar.

DISCUSSION

The proportions of genetic variation explained by the direct and maternal effects are comparatively large (19.6% and 49.4% for direct genetic effects and maternal genetic effects, respectively). This means that substantial improvement of direct and maternal genetic effects are possible. However, the negative genetic correlation of $-0.507$ observed between direct and maternal effects implies that simultaneous improvement of direct and maternal genetic effects may be difficult. The estimate of the variance of the residual effects common to a litter (that is full-sibs and maternal half-sibs) is zero.

The estimate of heritability obtained for weaning weight of Romney lambs (0.2) is much lower than the estimate (0.3) obtained by Ch'ang and Rae (1972). The adjustment factors obtained for Romney lamb weaning weights are similar to the adjustment factors obtained by Ch'ang and Rae (1961, 1970) and the average adjustment factors obtained by Jury et al (1979), with the exception of the adjustment factors for sex.
The analysis of the sheep data shows that the ML method developed in Wewala et al (1985) for estimating genetic parameters in mixed models involving maternal effects is computationally feasible. The results obtained are also generally satisfactory.

REFERENCES


