Estimation of Variance Components and Prediction of Breeding Values for Scrotal Circumference and Weaning Weight in Limousin Cattle

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ABSTRACT: Variance and covariance components were estimated for yearling scrotal circumference and weaning weight from Limousin field data. Records of 8,226 bulls were used to evaluate 584 sires and 653 maternal grandsires. Data included all herdbook records of bulls with a recorded scrotal circumference and their weaning contemporaries. Analyses were performed by restricted maximum likelihood techniques employing the expected maximization algorithm and fitting both single- and two-trait models. Scrotal circumference was first fitted in a single-trait, sire model to obtain starting values for variances for a later analysis. Likewise, weaning weight was fitted in a single-trait, sire-maternal grandsire model to obtain priors for (co)variances for a later analysis. Scrotal circumference and weaning weight were then fitted together in a two-trait model to estimate variance components. Estimates of variance components were calculated by equating (co)variances obtained from the models to their expectations. Estimates of heritability of scrotal circumference, direct weaning weight, and maternal weaning weight were .46, .25, and .19, respectively. Estimates of genetic correlations between yearling scrotal circumference and direct weaning weight, scrotal circumference and maternal weaning weight, and direct weaning weight and maternal weaning weight were .14, −.22, and −.44, respectively. The estimate of the environmental correlation between scrotal circumference and weaning weight was .61. Genetic parameters obtained were then used in two-trait, reduced animal mixed-model equations for a maternally influenced trait to predict breeding values for animals.

Key Words: Scrotum, Weaning Weight, Genetic Parameters, Cattle

Introduction

Selection of bulls for increased scrotal circumference is considered to be the most rapid method to genetically improve inherent fertility in beef cattle. Scrotal circumference is a moderate to highly heritable trait (Bourdon and Brinks, 1986; Smith et al., 1989a; Kriese et al., 1991) that is easily measured (Lunstra, 1982). Research has shown favorable relationships between scrotal circumference and growth and reproductive traits. Scrotal circumference has also been shown to be favorably correlated with seminal measures (Neely et al., 1982; Smith et al., 1989a), whereas a negative correlation has been reported between scrotal circumference and age at puberty of both males and females (Brinks et al., 1978; Lunstra, 1982; Smith et al., 1989b). Measures of reproductive performance after puberty are also favorably affected by increased scrotal circumference of sire (Smith et al., 1989b).

Phenotypic level of performance for yearling scrotal circumference in the Limousin breed has been shown as lower than in other breeds. Estimates of the breed average have ranged from 29.0 to 30.2 cm for this trait (Lunstra, 1982; Gregory et al., 1991; Keeton et al., 1995). Coupled with later age at puberty of females (Cundiff et al., 1993), this prompted the North American Limousin Foundation to set implementation of scrotal circumference EPD into their national cattle evaluation as a high research priority.

Therefore, objectives of this study were to compute heritability estimates and genetic and environmental correlations for yearling scrotal circumference and
Variance component analysis

<table>
<thead>
<tr>
<th>Trait</th>
<th>No. records</th>
<th>No. contemporary groups</th>
<th>No. sires</th>
<th>No. dams or maternal grandsires</th>
<th>Mean age, d</th>
<th>Mean observation</th>
<th>SD</th>
</tr>
</thead>
<tbody>
<tr>
<td>Scrotal circumference, cm</td>
<td>5,311</td>
<td>547</td>
<td>487</td>
<td>—</td>
<td>374</td>
<td>32.3</td>
<td>2.48</td>
</tr>
<tr>
<td>Weaning weight, kg</td>
<td>8,116</td>
<td>525</td>
<td>584</td>
<td>653</td>
<td>201</td>
<td>253</td>
<td>39.8</td>
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</tbody>
</table>

Prediction of breeding values

<table>
<thead>
<tr>
<th>Trait</th>
<th>No. records</th>
<th>No. contemporary groups</th>
<th>No. sires</th>
<th>Mean age, d</th>
<th>Mean observation</th>
<th>SD</th>
</tr>
</thead>
<tbody>
<tr>
<td>Scrotal circumference, cm</td>
<td>6,547</td>
<td>777</td>
<td>806</td>
<td>5,048</td>
<td>374</td>
<td>32.4</td>
</tr>
<tr>
<td>Weaning weight, kg</td>
<td>9,532</td>
<td>745</td>
<td>905</td>
<td>6,849</td>
<td>203</td>
<td>255</td>
</tr>
</tbody>
</table>

Table 1. Description of data

Materials and Methods

Data. Complete herdbook records on 8,226 purebred Limousin bulls were obtained from the North American Limousin Foundation (Englewood, CO). Records included all bulls with recorded yearling scrotal circumference (SC) and their weaning contemporaries. These data were used to estimate genetic parameters in both single-trait and multi-trait analyses. Recorded information included all pedigree information, age of dam, weaning contemporary group (WCG), weaning age (WAGE), weaning weight (WWT), yearling contemporary group (YCG), yearling age (YAGE), SC, and other information necessary for WCG and YCG formation. Contemporary group formations provided by the association were verified for accuracy with available information. Single-sire contemporary groups and embryo-transfer calves were deleted from analyses. Important age of dam classes (AODC) were previously determined (Keeton et al., 1995) for SC analysis to be 2-, 3-, 4- to 10-, and 11-yr-old dams.

Another set of complete herdbook records was obtained from the same source before prediction of breeding values to include all animals with recorded progeny information at that time. This was done to allow inclusion of additional information that had been collected during the time of variance component estimation (approximately 1 yr later). Observations on 9,618 bulls were available. Information available in this second data set was equivalent to information described above. These latter data were used to compute breeding value estimates and to study genetic trend. A description of the data sets appears in Table 1.

Variance Component Estimation. Estimation of genetic parameters was performed for SC and WWT. Fixed effects included in the SC model included AODC, YCG, and YAGE as a covariate. Similarly, fixed effects in the WWT model were AODC, WCG, and WAGE as a covariate. No adjustment to either SC or WWT was performed before analysis. Before estimation of variance components for SC and WWT in a two-trait mixed model, starting values were obtained by single-trait analyses. A sire model was used for the estimation of variance component starting values for SC. The model was as follows:

\[ y = Xb + Zu + e, \]

where \( y \) is a vector of observations, \( X \) and \( Z \) are known incidence matrices relating observations to fixed and random (sire) effects, respectively, \( b \) and \( u \) are unknown vectors of fixed and random (sire) effects, respectively, and \( e \) is a vector of unknown random residual effects. A sire-maternal grandsire model was used for the estimation of variance component starting values for WWT (Bertrand and Benyshek, 1987). The model for this analysis was the same as the sire model, with the addition of an incidence matrix relating observations to random (maternal grandsire) effects and an unknown vector of random (maternal grandsire) effects. Standard errors of heritability estimates were calculated following Falconer (1989).

Final estimation of variance components utilizing a two-trait model precluded the use of animal or reduced animal models, due to computational problems. Therefore, a two-trait model with sire-maternal grandsire effects fitted for WWT and sire effects fitted for SC was used to obtain estimates of genetic parameters. A two-trait analysis was performed to account for potential selection bias. The model was as follows:

\[
\begin{bmatrix}
  y_w \\
  y_s
\end{bmatrix} =
\begin{bmatrix}
  X_w & 0 & b_w \\
  0 & X_s & b_s
\end{bmatrix}
\begin{bmatrix}
  X_w \\
  X_s
\end{bmatrix} =
\begin{bmatrix}
  Z_{wd} & Z_{wm} & 0 & u_{wd} & u_{wm} & e_w \\
  0 & 0 & Z_{sd} & u_{sd} & u_{s} & e_s
\end{bmatrix},
\]

where

\[
y_w (y_s) = \text{vector of WWT (SC) records,}
X_w (X_s) = \text{known incidence matrix relating WWT (SC) records to fixed effects,}
\]

\[
b_w (b_s) = \text{vector of fixed effects affecting WWT (SC) records,}
Z_{wd} (Z_s) = \text{known incidence matrix relating WWT (SC) records to random sire additive effects,}
\]
\( Z_{wm} \) = known incidence matrix relating WWT records to random maternal grandsire additive effects,

\( u_{wd} (u_s) \) = vector of random sire additive effects affecting WWT (SC) records,

\( u_{wm} \) = vector of random maternal grandsire additive effects affecting WWT records, and

\( e_{w} (e_s) \) = vector of random environmental effects peculiar to each WWT (SC) records.

Multiple-trait, mixed-model equations followed Quaas and Pollak (1980), where the variance structure of the random effects was as follows:

\[
\begin{bmatrix}
\begin{bmatrix}
A_{ww}^2 & A_{ws} & A_{ss}
\end{bmatrix} &
\begin{bmatrix}
0 & 0 & 0
\end{bmatrix}
\end{bmatrix}
\]

\( \text{var}(u_{wd}, u_{wm}, u_s, e_w, e_s) = 
\begin{bmatrix}
0 & 0 & 0 & 0 & 0
\end{bmatrix}. \)

where \( A \) is the numerator relationship matrix among sires and maternal grandsires.

Estimation of variance components was facilitated by use of the expected maximization (EM) algorithm of restricted maximum likelihood (REML; Henderson, 1984). In this procedure, solutions at one round of the iteration are used as the prior in the next round until a pre-specified level of convergence occurs. Genetic (co)variance components were estimated by \( \hat{e}_{ij} = (u_i^t A^{-1} u_j + tr A^{-1} C_{ij})/q \), (Wright et al., 1991), where \( u_i \) and \( u_j \) were additive random effects, \( q \) was the number of animals represented in \( A \), and \( C_{ij} \) was a submatrix of the generalized inverse of the coefficient matrix corresponding to the \( i \)th and \( j \)th random effect.

Residual variances were estimated by difference:

\[
\begin{align*}
\sigma^2_{ew} &= \left( y_w, y_w - b_w X_w y_w - \hat{u}_{wd} Z_{wd} y_w - \hat{u}_{wm} Z_{wm} y_w \right) / df, \text{ and} \\
\sigma^2_{es} &= \left( y_s, y_s - b_s X_s y_s - \hat{u}_{s} Z_{s} y_s \right) / df.
\end{align*}
\]

Residual covariance estimation has been outlined by Henderson (1984). However, that method was too computationally difficult for these data. Therefore, residual covariance \( \sigma_{es} \) was estimated by the approximation (C. H. Mallinckrodt, personal communication):

\[
\sigma_{es} = \left( e_w, e_s, y_w, y_s \right) / \left( 2 \times (n_{ws} - \text{rank}(X_{ws})) \right),
\]

where

\[
\begin{align*}
e_w (e_s) &= y_w - \hat{y}_w (y_s - \hat{y}_s), \\
\hat{y}_w &= X_w b_w + Z_{wd} \hat{u}_{wd} + Z_{wm} \hat{u}_{wm}, \\
\hat{y}_s &= X_s b_s + Z_{sw} \hat{u}_s,
\end{align*}
\]

\( n_{ws} \) = number of animals with both traits observed, and

\( \text{rank}(X_{12}) \) = rank of the fixed effects matrix after combining fixed effects for both traits.

Transformation of the observation vectors to a standard normal distribution was required for the approximation for the error covariance to compute. This was probably because of the necessity of homogeneity of variances for the approximation.

The Animal Breeders Toolkit software (Golden et al., 1992) was used to assemble and solve the mixed-model equations in all analyses. Convergence of the solutions was set at a level where the (co)variances changed less than \( 0.000025 \) standard deviation unit from one round of iteration to the next. This convergence criterion is equivalent to \( 0.05 \) kg\(^2\) for WWT and \( 0.15 \) cm\(^2\) for SC.

The expectations of the variances and covariances estimated from this model were as follows (Kriese et al., 1991):

\[
\begin{align*}
E(\sigma^2_{sw}) &= 1/4 \sigma^2_{Aw} + 1/4 \sigma^2_{Mw}, \\
E(\sigma^2_{wsw}) &= 1/4 \sigma^2_{Aw} + 1/4 \sigma^2_{Mw}, \\
E(\sigma^2_{mgsw}) &= 1/16 \sigma^2_{Aw} + 1/4 \sigma^2_{Mw} + 1/4 \sigma^2_{Ww}, \\
E(\sigma^2_{mgsws}) &= 1/8 \sigma^2_{Mw} + 1/4 \sigma^2_{Mw} + 1/4 \sigma^2_{Mw}, \\
E(\sigma^2_{sw}) &= 1/4 \sigma^2_{Aw} + 1/4 \sigma^2_{Aw}, \\
E(\sigma^2_{sw}) &= 11/16 \sigma^2_{Aw} + 3/4 \sigma^2_{Mw} + 3/4 \sigma^2_{Ww} + \sigma^2_{ew}, \\
E(\sigma^2_{es}) &= 3/4 \sigma^2_{Aw} + \sigma^2_{ew},
\end{align*}
\]

where

\[
\begin{align*}
A &= \text{additive genetic effects}, \\
M &= \text{maternal genetic effects}, \\
\epsilon_w (\epsilon_s) &= \text{random environmental effects on WWT and SC, and} \\
s (mgs) &= \text{sire and maternal grandsire effects.}
\end{align*}
\]

Prediction of Breeding Values. Prediction of SC breeding values was accomplished using a two-trait, reduced animal, mixed-model method for a maternally influenced trait (Quaas and Pollak, 1980). Fixed effects included in this model were the same as those described for previous models. Evaluation of genetic trend was accomplished by obtaining means of animals’ breeding values by birth years from 1970 to 1989.

Results and Discussion

Variances and covariances from the models are presented in Table 2. Sire variance for SC increased from the single-trait model to the two-trait model whereas the residual variance remained virtually unchanged. Sire variance for WWT increased <1 kg\(^2\)
Table 2. Estimates of (co)variances from the analyses

<table>
<thead>
<tr>
<th>Model</th>
<th>Variances</th>
<th>Covariances</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$\sigma^2_s$</td>
<td>$\sigma^2_w$</td>
</tr>
<tr>
<td>Single-trait analyses</td>
<td></td>
<td></td>
</tr>
<tr>
<td>SC</td>
<td>.4459</td>
<td>—</td>
</tr>
<tr>
<td>WWT</td>
<td>—</td>
<td>41.90</td>
</tr>
<tr>
<td>Multi-trait analysis</td>
<td></td>
<td></td>
</tr>
<tr>
<td>SC-WWT</td>
<td>.5374</td>
<td>42.44</td>
</tr>
</tbody>
</table>

$^a$Variances for SC = scrotal circumference in square centimeters; (co)variances for WWT = weaning weight in square kilograms; covariances between SC and WWT in centimeters $\times$ kilograms.

$^b$Variances, covariances, heritabilities, and correlations are shown in Table 3. The heritability estimate for SC of .46 $\pm$ .046 resembles values found in previous studies. Bourdon and Brinks (1986) estimated the heritability of age-adjusted SC in Herefords to be .46 $\pm$ .06; Smith et al. (1989a) reported a value of .40 $\pm$ .09 for various breeds; Kriese et al. (1991) reported estimates of SC heritability of .53 and .16 from Hereford and Brangus field data, respectively. The genetic correlation between SC and WWT direct of .14 generally agrees with the value found by Kriese et al. (1991) for Herefords (.08) but is smaller than the value reported by the same authors for Brangus (.34), and is smaller than the .56 reported by Smith et al. (1989a). However, the genetic correlation between SC and WWT maternal of $-$.22 is in contrast to the values found by Kriese et al. (1991) of .20 and .14 for Hereford and Brangus, respectively.

Estimates of the heritabilities of WWT direct and WWT maternal for Limousin of .25 $\pm$ .029 and .19 $\pm$ .026, respectively, are slightly higher than previously reported values of .16 and .15, respectively (Bertrand and Benyshek, 1987). Also, the genetic correlation between WWT direct and WWT maternal of $-$.44 is greater than the $-$.30 reported by Bertrand and Benyshek (1987). However, an estimate of genetic correlation in Senepol cattle between WWT direct and maternal of $-$.57 has been reported in the literature (Wright et al., 1991), in addition to a recent estimate made from Angus experimental data ($-$.57, Shepard et al., 1996). Both of these reports agree closely with our estimate of $-$.44 from these data. Differences between estimates may be attributed to differing levels of genetic variation between populations and to the restricted nature and effects of selected data, or these differences may be due to computational advances in estimation techniques.

At first review, a negative genetic covariance between weaning maternal and scrotal circumference might be surprising because of the large reported negative genetic relationship between age at puberty of females and scrotal circumference of males (Smith et al., 1989b, i.e., that some of the same genes contributing to age at puberty would be contributing to milk yield). However, in these particular data, the
Genetic Parameters of Scrotal Circumference

Figure 1. Distribution of scrotal circumference breeding values for Limousin cattle.

Figure 2. Genetic trend for scrotal circumference in Limousin cattle.

positive genetic covariance between weaning direct and scrotal circumference (.14), together with the large negative genetic covariance between weaning direct and weaning maternal (-.44), forces the relationship between SC and weaning maternal to be negative and intermediate between the two (-.22). Possibilities for these direct/maternal covariances to be artifacts of field data reporting (Mallinckrodt et al., 1992) are recognized but cannot be elucidated in these data.

The environmental correlation between SC and WWT of .59 is larger than previous estimates reported by Kriese et al. (1991) (.43 and .34 for Hereford and Brangus, respectively) and by Smith et al. (1989a) (.30). The magnitude and sign of this correlation indicate that environmental effects manifest themselves in much the same way for these two traits.

Genetic Trend. The distribution of the breeding values is shown in Figure 1, with a range of approximately -2.01 to +2.47 cm. Because these are breeding values and not EPD, the range in EPD would be half of that shown (2.24 cm). No discernable genetic trend in Limousin cattle is evident from Figure 2, signifying that little or no previous selection pressure has been placed on this trait. This is in comparison to significant genetic trend for birth weight (1.0σ), weaning direct (1.35σ), weaning maternal (.76σ), and yearling weight (1.55σ) in this breed over the period from 1971 to 1991 (Anderson, 1994).

Implications

Variances and covariances estimated in this study should be useful in future Limousin breed genetic evaluations. Bulls genetically superior in scrotal circumference should in general also be superior in the direct effects of preweaning growth. Selection of sires for increased scrotal circumference should provide a viable means for making genetic progress in age at puberty and other predictors of inherent fertility in this population, although attention to maintenance of weaning weight maternal performance is warranted. Future research should identify threshold levels for this trait and correlated effects with other economically important indicator traits.

Literature Cited


