

A SIMPLE METHOD OF COMPUTING RESTRICTED BEST LINEAR UNBIASED PREDICTION OF BREEDING VALUES AND THE APPLICATION TO IMPROVEMENT OF REPRODUCTIVE TRAITS IN GOLDEN HAMSTERS

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SUMMARY

Restricted best linear unbiased prediction (restricted BLUP) is derived by imposing restrictions directly within a multiple trait mixed model. As a result, the restricted BLUP procedure requires the solution of high order simultaneous equations. This paper presents a simple method for computing restricted BLUP of breeding values. The technique is valuable, particularly when a large number of restrictions are imposed in a multiple trait mixed model such as constraints of achieving predetermined relative rates of genetic improvement for all traits. An application of selection experiment for reproductive traits was given for 20 generations in golden hamsters.

Keywords: mixed model, restricted BLUP, reproductive traits, selection, golden hamsters.

INTRODUCTION

Quaas and Henderson (1976) extended the BLUP procedure of Henderson (1973) to allow estimation of breeding values with restriction that a set of linear functions of the estimated breeding values among some or all correlated traits was null (restricted BLUP). Restricted BLUP was derived by imposing restrictions directly on the multiple trait mixed model. Consequently, the restricted BLUP procedure requires the solution of high order simultaneous equations, particularly when a large number of animals are evaluated for many traits. For this reason, computational techniques have been studied for computing restricted BLUP. The objectives of the present paper are to show a simple procedure for computing restricted BLUP of breeding values and to discuss its application.

THEORETICAL APPROACH

Theoretical background. An additive genetic mixed model for q traits is assumed. The model for the i^{th} trait is written as:

$$y_i = X_i b_i + Z_i u_i + e_i$$

where y_i is a vector of observations for the i^{th} trait; b_i is a vector of unknown fixed effects; X_i is a known incidence matrix relating elements of b_i to y_i , u_i is a vector of unknown random additive genetic effects, Z_i is a known incidence matrix relating elements of u_i to y_i , and e_i is a vector of random errors. Let n_j be the number of records on the j^{th} animal; $j = 1, 2, \dots, n$ and $0 \leq n_j \leq q$. The model for all traits is written as:

$$y = Xb + Zu + e, \quad [1]$$

where records are ordered by animals within traits and it is assumed that u and e are multivariate normally distributed with $E(u) = 0$, $E(e) = 0$, $\text{var}(u) = G$, $\text{var}(e) = R$, and $\text{cov}(u, e) = 0$; $G =$

$\mathbf{G}_0 \otimes \mathbf{A}$, where \mathbf{G}_0 is a $q \times q$ additive genetic variance-covariance matrix for the q traits, \mathbf{A} is the additive relationship matrix for the n animals, \otimes is the direct product operation, and \mathbf{R} is an $n \times n$ ($n = \sum n_i$) error variance-covariance matrix for the q traits for the n animals. In restricted BLUP, a set of linear function, $\mathbf{B}'\mathbf{y}$, to predict $\mathbf{K}\mathbf{b} + \mathbf{M}\mathbf{u}$ where \mathbf{K} and \mathbf{M} are any arbitrary matrices, is used which is uncorrelated with some linear function of \mathbf{u} , say $\mathbf{C}'\mathbf{u}$. This is expressed algebraically as $\text{cov}(\mathbf{B}'\mathbf{y}, \mathbf{u}'\mathbf{C}) = \mathbf{B}'\mathbf{Z}\mathbf{G}\mathbf{C} = \mathbf{0}$. If the same restrictions on the predicted breeding values of all animals are imposed, matrix \mathbf{C} is expressed as $\mathbf{C} = \mathbf{C}_0 \otimes \mathbf{I}_n$ where \mathbf{C}_0 is a matrix of order $q \times r$ and is the same as that used by Kempthorne and Nordskog (1959) and Malard (1972), and \mathbf{I}_n is the identity matrix of order $n \times n$. If there are restrictions including no change in r_0 characters and proportional change in r_1 characters, then $r = r_0 + (r_1 - 1)$. The BLUP of \mathbf{u} with this additional constraint, denoted by $\hat{\mathbf{u}}$, is obtained by solving the following equations:

$$\begin{bmatrix} \mathbf{X}'\mathbf{R}^{-1}\mathbf{X} & \mathbf{X}'\mathbf{R}^{-1}\mathbf{Z} & \mathbf{X}'\mathbf{R}^{-1}\mathbf{Z}\mathbf{G}\mathbf{C} \\ \mathbf{Z}'\mathbf{R}^{-1}\mathbf{X} & \mathbf{Z}'\mathbf{R}^{-1}\mathbf{Z} + \mathbf{G}^{-1} & \mathbf{Z}'\mathbf{R}^{-1}\mathbf{Z}\mathbf{G}\mathbf{C} \\ \mathbf{C}'\mathbf{G}\mathbf{Z}\mathbf{R}^{-1}\mathbf{X} & \mathbf{C}'\mathbf{G}\mathbf{Z}\mathbf{R}^{-1}\mathbf{Z} & \mathbf{C}'\mathbf{G}\mathbf{Z}\mathbf{R}^{-1}\mathbf{Z}\mathbf{G}\mathbf{C} \end{bmatrix} \begin{bmatrix} \mathbf{b} \\ \hat{\mathbf{u}} \\ \hat{\mathbf{w}} \end{bmatrix} = \begin{bmatrix} \mathbf{X}'\mathbf{R}^{-1}\mathbf{y} \\ \mathbf{Z}'\mathbf{R}^{-1}\mathbf{y} \\ \mathbf{C}'\mathbf{G}\mathbf{Z}\mathbf{R}^{-1}\mathbf{y} \end{bmatrix} \quad [2]$$

where \mathbf{b} and $\hat{\mathbf{w}}$ are solutions of [2]. If [1] is an animal model, eliminating $\hat{\mathbf{w}}$ gives:

$$\begin{bmatrix} \mathbf{X}'\mathbf{Z}\mathbf{S}\mathbf{Z}\mathbf{X} & \mathbf{X}'\mathbf{Z}\mathbf{S} \\ \mathbf{S}\mathbf{Z}\mathbf{X} & \mathbf{S} + \mathbf{G}^{-1} \end{bmatrix} \begin{bmatrix} \mathbf{b} \\ \hat{\mathbf{u}} \end{bmatrix} = \begin{bmatrix} \mathbf{X}'\mathbf{Z}\mathbf{S}\mathbf{Z}\mathbf{y} \\ \mathbf{S}\mathbf{Z}\mathbf{y} \end{bmatrix} \quad [3]$$

where $\mathbf{S} = \mathbf{Z}\mathbf{R}^{-1}\mathbf{Z} - \mathbf{Z}\mathbf{R}^{-1}\mathbf{Z}\mathbf{G}\mathbf{C}(\mathbf{C}'\mathbf{G}\mathbf{Z}\mathbf{R}^{-1}\mathbf{Z}\mathbf{G}\mathbf{C})\mathbf{C}'\mathbf{G}\mathbf{Z}\mathbf{R}^{-1}\mathbf{Z}$.

Notation and restrictions. When constraints are imposed on some traits, model [1] can be rewritten as:

$$\begin{bmatrix} \mathbf{y}_R \\ \mathbf{y}_N \end{bmatrix} = \begin{bmatrix} \mathbf{X}_R & \mathbf{0} \\ \mathbf{0} & \mathbf{X}_N \end{bmatrix} \begin{bmatrix} \mathbf{b}_R \\ \mathbf{b}_N \end{bmatrix} + \begin{bmatrix} \mathbf{Z}_R & \mathbf{0} \\ \mathbf{0} & \mathbf{Z}_N \end{bmatrix} \begin{bmatrix} \mathbf{u}_R \\ \mathbf{u}_N \end{bmatrix} + \begin{bmatrix} \mathbf{e}_R \\ \mathbf{e}_N \end{bmatrix}$$

where subscript R corresponds to r characters with proportional constraints, including no change, and subscript N corresponds to $q - r_0 - r_1$ characters. Then \mathbf{G}^{-1} and \mathbf{S} are expressed as:

$$\mathbf{G}^{-1} = \mathbf{G}_0^{-1} \otimes \mathbf{A}^{-1} = \begin{bmatrix} g^{11} & \dots & g^{1q} \\ \vdots & & \vdots \\ g^{q1} & \dots & g^{qq} \end{bmatrix} \otimes \mathbf{A}^{-1} = \begin{bmatrix} \mathbf{G}_{RR} & \mathbf{G}_{RN} \\ \mathbf{G}'_{RN} & \mathbf{G}_{NN} \end{bmatrix}, \text{ and } \mathbf{S} = \begin{bmatrix} \mathbf{S}_{RR} & \mathbf{S}_{RN} \\ \mathbf{S}'_{RN} & \mathbf{S}_{NN} \end{bmatrix}$$

where g^{ij} is the ij^{th} element of \mathbf{G}_0^{-1} .

The restricted BLUP from equation [3] are

$$\begin{bmatrix} \mathbf{X}'\mathbf{Z}\mathbf{S}\mathbf{Z}\mathbf{X} & \mathbf{X}'\mathbf{Z}\mathbf{S}_R & \mathbf{X}'\mathbf{Z}\mathbf{S}_N \\ \mathbf{S}'_R\mathbf{Z}\mathbf{X} & \mathbf{S}_{RR} + \mathbf{G}_{RR} & \mathbf{S}_{RN} + \mathbf{G}_{RN} \\ \mathbf{S}'_N\mathbf{Z}\mathbf{X} & \mathbf{S}'_{RN} + \mathbf{G}'_{RN} & \mathbf{S}_{NN} + \mathbf{G}_{NN} \end{bmatrix} \begin{bmatrix} \mathbf{b} \\ \hat{\mathbf{u}}_R \\ \hat{\mathbf{u}}_N \end{bmatrix} = \begin{bmatrix} \mathbf{X}'\mathbf{Z}\mathbf{S}\mathbf{Z}\mathbf{y} \\ \mathbf{S}'_R\mathbf{Z}\mathbf{y} \\ \mathbf{S}'_N\mathbf{Z}\mathbf{y} \end{bmatrix}$$

where $\mathbf{S}_R = [\mathbf{S}_{RR} \ \mathbf{S}_{RN}]$, $\mathbf{S}_N = [\mathbf{S}'_{RN} \ \mathbf{S}_{NN}]$. Premultiplying the second equation in [2] by $\mathbf{C}'\mathbf{G}$ and then subtracting from this product the third equation gives

$$\mathbf{C}'\hat{\mathbf{u}} = (\mathbf{C}_0 \otimes \mathbf{I}_n)' \hat{\mathbf{u}} = \mathbf{0}.$$

Then, using some vector k ,

$$\hat{u}_R = k \otimes \hat{u}_r = (k \otimes I_n) \hat{u}_r, \quad [4]$$

where $\hat{u}_R = [\hat{u}_1' \ \hat{u}_2' \ \dots \ \hat{u}_r']$. Using the above equations, we can get [5].

$$\begin{bmatrix} X'ZSZX & X'ZS_R(k \otimes I_n) & X'ZS_N \\ (k \otimes I_n)'S'_RZX & (k \otimes I_n)'(S_{RR}+G_{RR})(k \otimes I_n) & (k \otimes I_n)'(S_{RN}+G_{RN}) \\ S'_N ZX & (S_{RN}+G_{RN})'(k \otimes I_n) & S_{NN}+G_{NN} \end{bmatrix} \begin{bmatrix} b \\ \hat{u}_r \\ \hat{u}_N \end{bmatrix} = \begin{bmatrix} X'ZSZy \\ (k \otimes I_n)'S'_R Zy \\ S'_N Zy \end{bmatrix} \quad [5]$$

These equations show that computation for formulating BLUP equations are simple. For example, the second row and column of the left hand side of [5] can be transformed as:

$$(k \otimes I_n)'(S_{RR}+G_{RR})(k \otimes I_n) = \sum_i \sum_j k_i k_j S_{ij} + \sum_i \sum_j k_i k_j g^{ij} A^{-1}$$

where k_i is the i^{th} element of k . From the above, restricted BLUP can be computed without directly solving equations [2] or [3] of high order. After solving equations [5], \hat{u}_R can be given using [4]. If constraints are desired changes for all traits, then we eliminate the third equation in [5]. Hence, the size of equations [5] corresponding to random additive effects is reduced to that of single trait BLUP.

Application to selection experiment. Establishment of lines W and R, and results of the first 15 generations of selection using golden hamsters were described by Satoh *et al.* (1997). Lines W and R were crossed at generation 15. Generation 16 was assumed to be base population. The population was maintained by random selection up to generation 25. Five generations of selection from generation 25 were conducted for litter size at birth (LS) and weight at two weeks of standardized litter (LW). The experiment involved three lines: selection based on restricted animal model BLUP of proportional changes in LS and LW (line B), selection based on index for proportional changes in LS and LW (line S) and a randomly selected control (line K). The proportional changes applied in lines B and S for LS and LW were 0.951 and 13.19, respectively. All lines were kept by relaxed selection from generation 30 through 35. To estimate the genetic trend, means of estimated breeding values (EBV) were calculated using data from generation 15 through 35. Genetic parameters used were estimated by bivariate analysis using restricted maximum likelihood fitting an animal model.

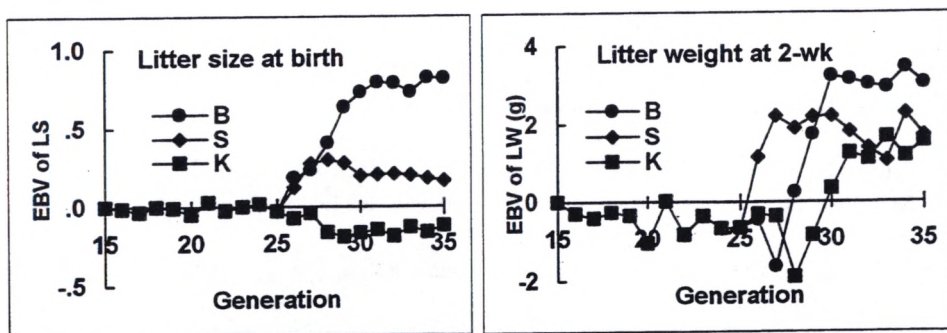


Figure 1. Mean estimated breeding values (EBV) for lines, B = BLUP, S = index and K = control for litter size at birth (LS) and litter weight at 2 weeks of age (LW).

The heritability estimates of LS and LW were 0.05 and 0.15, respectively, and the genetic correlation between them was 0.38. Figure 1 shows the mean estimated breeding values of all females in each line and generation for LS and LW from generation 15 through 35. Line B showed the largest trends for LS and LW from generation 25 till 30. The respective mean advantages of B and S for the last five generations over K were +0.94 and +0.34 for LS, and +1.8g and +0.3g for LW.

DISCUSSION

Henderson and Quaas (1976) derived BLUP of breeding values for multiple traits using records on a large number of relatives. Restricted BLUP was derived by imposing restrictions on multiple trait BLUP (Quaas and Henderson, 1976). Hence, in restricted BLUP, the computing load to get estimates of breeding values can be huge. Lin (1990) showed how restricted BLUP of breeding values can be estimated not only for zero change but also for proportional change in restricted traits. It was, however, assumed that the variance-covariance matrix among predicted breeding values was the same as that among true breeding values. This approach adds bias when estimates of genetic variances and covariances are used instead of the true parameters (Schneeberger *et al.*, 1992). Itoh and Iwaisaki (1990) showed that a canonical transformation technique was applicable to restricted BLUP in order to reduce the number of equations for an animal model. However, the method has a limitation in that models must be identical for all traits and no partially missing observations. Hence, the canonical transformation technique can be used only if models and data structure can meet above condition. The technique developed here needs no conditions to be applied and reduced the number of sets of equations corresponding to random additive effects from q to $q - \text{rank}(C_0)$. Hence, if a large number of restrictions is imposed in a model such as a constraint of achieving predetermined relative changes for all traits (Yamada *et al.*, 1975), the size of equations for random additive effects is the same as that of a single trait model.

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