The Covariance Structure of Residual Effects in a Reduced Animal Model for Marker-Assisted Selection

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Abstract For a reduced animal model (RAM) for marker-assisted selection using best linear unbiased prediction, the appropriate structure of covariance matrix of the segregation residual effects is derived for the situation where paternal or maternal origin of marker alleles can not be determined. A RAM approach is then described, in which the covariance structure is taken into account. Formulae for backsolving for non-parent animals are presented. A small numerical example is also given to illustrate the current RAM approach.

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Key words : Marker-assisted selection, Best linear unbiased prediction, Reduced animal model, Covariance, Segregation residual

A large number of genetic polymorphisms such as restriction fragment length polymorphisms¹⁾, variable number of tandem repeats^{6,9)} and random amplified polymorphic DNA¹⁷⁾ are now being detected by molecular techniques. The genetic differences identified at the DNA level are referred to as genetic markers. The use in selection criteria of information on marker loci which are linked to quantitative trait loci (QTLs), that is marker-assisted selection (MAS), is expected to be useful for accelerating genetic progress through increased accuracy of selection, reduced generation interval and increased selection differential^{7,8,12,13)}.

In the field of animal breeding, best linear unbiased prediction (BLUP)⁵⁾ is used for predicting breeding values from data affected by non-genetic nuisance factors, non-random mating, selection and so on. Fernando and Grossman³⁾ showed how marker information

could be utilized in the animal model (AM)-BLUP method. The AM approach permits simultaneous evaluation of fixed effects, effects of alleles at a QTL linked to the marker locus (MQTL) and effects of alleles at the remaining QTLs. As size of data sets becomes large, however, the computational burden in the AM method would dramatically increase. Therefore, Cantet and Smith²⁾ presented the reduced animal model (RAM) version of Fernando and Grossman's AM approach³⁾, by which the total number of equations to be solved could be considerably reduced. However, when there are animals whose paternal or maternal origin of marker alleles is uncertain in the relevant pedigree, the covariance structure of residual effects in Cantet and Smith's RAM²⁾ is no longer true.

The main purpose of this paper is to appropriately define the covariance matrix of segregation residuals in the RAM for the situa-

tion where parental origin of marker alleles can not be determined. The RAM approach in which the covariance matrix has been incorporated is also presented. The results for the covariance structure of the residuals obtained in this study have been used in the RAM procedures for MAS developed by Saito and Iwaisaki^{10,11)}.

Theory

Fernando and Grossman's AM

For simplicity, consider a single polymorphic marker locus. Then the breeding value (a_i) of animal i is written as the sum of additive genetic effects for alleles at the QTLs unlinked to the marker locus (u_i) and additive effects of the MQTL alleles (v_i^1 and v_i^2), that is $a_i = u_i + v_i^1 + v_i^2$. Then the AM³⁾ is written, as follows

$$\begin{aligned} \mathbf{y} &= \mathbf{X}\boldsymbol{\beta} + \mathbf{Z}\mathbf{a} + \mathbf{e} \\ &= \mathbf{X}\boldsymbol{\beta} + \mathbf{Z}\mathbf{u} + \mathbf{Z}\mathbf{P}\mathbf{v} + \mathbf{e}, \end{aligned} \quad (1)$$

where $\mathbf{y}$ is the $n \times 1$ vector of observations, $\boldsymbol{\beta}$ is the $f \times 1$ vector of fixed effects, $\mathbf{a}$ is the $n \times 1$ vector of the total additive genetic merits, $\mathbf{u}$ is the $q \times 1$ vector of additive genetic effects due to QTLs not linked to the marker locus, $\mathbf{v}$ is the $2q \times 1$ vector of additive effects of the MQTL alleles, $\mathbf{e}$ is the $n \times 1$ vector of residual effects, and $\mathbf{X}$, $\mathbf{Z}$ and $\mathbf{P}$ are $n \times f$, $n \times q$ and $q \times 2q$ known incidence matrices, respectively. The expectation and dispersion matrices for the random effects, $\mathbf{u}$, $\mathbf{v}$ and $\mathbf{e}$, are assumed as

$$E \begin{pmatrix} \mathbf{u} \\ \mathbf{v} \\ \mathbf{e} \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \\ 0 \end{pmatrix} \text{ and } \text{Var} \begin{pmatrix} \mathbf{u} \\ \mathbf{v} \\ \mathbf{e} \end{pmatrix} = \begin{pmatrix} \mathbf{A}_u \sigma_u^2 & 0 & 0 \\ 0 & \mathbf{A}_v \sigma_v^2 & 0 \\ 0 & 0 & \mathbf{I} \sigma_e^2 \end{pmatrix},$$

respectively, where $\mathbf{A}_u$ is the numerator relationship matrix for the QTLs not linked to the marker locus, $\mathbf{A}_v$ is the gametic relationship matrix for the MQTL, $\mathbf{I}$ is an identity matrix, and σ_u^2 , σ_v^2 and σ_e^2 are the variance components for $\mathbf{u}$, $\mathbf{v}$ and $\mathbf{e}$, respectively.

For MAS, mixed model methodology used for predicting breeding values requires the inverses of $\mathbf{A}_u$ and $\mathbf{A}_v$. Fernando and Grossman³⁾ presented an algorithm to directly

construct the inverse of $\mathbf{A}_v \sigma_v^2$. In the algorithm, it is assumed that the covariance matrix of residual effects for the MQTL is diagonal. However, if paternal or maternal origin of marker alleles can not be determined, it is not true.

Cantet and Smith's RAM

Cantet and Smith²⁾ described the RAM version of Fernando and Grossman's AM³⁾. If animals can be partitioned into parents and non-parents, eq. (1) can be arranged as

$$\begin{pmatrix} \mathbf{y}_p \\ \mathbf{y}_o \end{pmatrix} = \begin{pmatrix} \mathbf{X}_p \\ \mathbf{X}_o \end{pmatrix} \boldsymbol{\beta} + \begin{pmatrix} \mathbf{Z}_p & 0 \\ 0 & \mathbf{Z}_o \end{pmatrix} \begin{pmatrix} \mathbf{u}_p \\ \mathbf{u}_o \end{pmatrix} + \begin{pmatrix} \mathbf{Z}_p \mathbf{P}_p & 0 \\ 0 & \mathbf{Z}_o \mathbf{P}_o \end{pmatrix} \begin{pmatrix} \mathbf{v}_p \\ \mathbf{v}_o \end{pmatrix} + \begin{pmatrix} \mathbf{e}_p \\ \mathbf{e}_o \end{pmatrix}, \quad (2)$$

where the subscripts p and o refer to animals with progeny and without progeny, respectively. For the RAM, $\mathbf{u}_o$ and $\mathbf{v}_o$ are expressed as a linear function of $\mathbf{u}_p$ and $\mathbf{v}_p$, respectively, as follows

$$\mathbf{u}_o = \mathbf{T}\mathbf{u}_p + \mathbf{m} \quad (3)$$

and

$$\mathbf{v}_o = \mathbf{B}\mathbf{v}_p + \boldsymbol{\varepsilon}, \quad (4)$$

where $\mathbf{T}$ is a matrix relating $\mathbf{u}_o$ to $\mathbf{u}_p$ and has zeros except for .5 in the column pertaining to a known parent, $\mathbf{m}$ is a vector of the Mendelian sampling effects, $\mathbf{B}$ is a matrix relating $\mathbf{v}_o$ to $\mathbf{v}_p$ and contains two non-zero elements in each row if the parental origins of marker alleles are known, as discussed by Fernando and Grossman³⁾, and $\boldsymbol{\varepsilon}$ is a vector of segregation residuals. The Mendelian sampling effects $\mathbf{m}$ follow $E(\mathbf{m}) = \mathbf{0}$ and $\text{Var}(\mathbf{m}) = \mathbf{D}\sigma_u^2$, where $\mathbf{D}$ is the diagonal matrix whose diagonal elements, d_i , equal .5-.25($F_s + F_d$) with the inbreeding coefficients of the sire and the dam, F_s and F_d . And also, the segregation residuals $\boldsymbol{\varepsilon}$ have $E(\boldsymbol{\varepsilon}) = \mathbf{0}$ and $\text{Var}(\boldsymbol{\varepsilon}) = \mathbf{G}_\varepsilon \sigma_v^2$, where $\mathbf{G}_\varepsilon$ is the diagonal matrix and contains the diagonal elements $\mathbf{G}_{\varepsilon i} = 2r(1-r)(1-f_s)$ and $\mathbf{G}_{\varepsilon j} = 2r(1-r)(1-f_d)$, letting r be recombination rate between the marker locus and MQTL and f_s and f_d be the inbreeding coefficients at the MQTL¹⁵⁾ of the

sire and of the dam, respectively.

The proposed covariance matrix

Now, consider the situation where paternal or maternal origin of marker alleles can not be determined. The additive effects of the MQTL alleles of animal i are

$$v_i^1 = b_{i1}^1 v_s^1 + b_{i2}^1 v_s^2 + b_{i3}^1 v_d^1 + b_{i4}^1 v_d^2 + \varepsilon_i^1 \quad (5)$$

and

$$v_i^2 = b_{i1}^2 v_s^1 + b_{i2}^2 v_s^2 + b_{i3}^2 v_d^1 + b_{i4}^2 v_d^2 + \varepsilon_i^2, \quad (6)$$

where the coefficients b_{ik}^l ($l=1$ or 2 and $k=1, 2, 3$ or 4) are the conditional probabilities that the MQTL alleles of animal i are copies of those of its parent, given the marker information (see eqs. [5], [6], [7] and [8] in Wang *et al.*^[5]). In matrix notation eqs. (5) and (6) are rewritten as

$$\mathbf{v}_o = \mathbf{B}^* \mathbf{v}_p + \boldsymbol{\varepsilon}. \quad (7)$$

Then the covariance structure of the segregation residual effects becomes

$$\begin{aligned} & \begin{pmatrix} \text{Var}(\varepsilon_i^1) & \text{Cov}(\varepsilon_i^1, \varepsilon_i^2) \\ \text{Cov}(\varepsilon_i^1, \varepsilon_i^2) & \text{Var}(\varepsilon_i^2) \end{pmatrix} \\ &= \text{Var}([v_i^1 \ v_i^2]') - \mathbf{B}_i^* \text{Var}([v_s^1 \ v_s^2 \ v_d^1 \ v_d^2]') \mathbf{B}_i^{*'} \\ &= \left[\begin{pmatrix} 1 & f_i \\ f_i & 1 \end{pmatrix} - \mathbf{B}_i^* \mathbf{A}_{v_{p(i)}} \mathbf{B}_i^{*'} \right] \sigma_v^2, \end{aligned}$$

where f_i is the conditional inbreeding coefficient of animal i for the MQTL, and $\mathbf{A}_{v_{p(i)}}$ is an appropriate submatrix of $\mathbf{A}_v$ corresponding to the parental MQTL effects of animal i , and

$$\mathbf{B}_i^* = \begin{bmatrix} b_{i1}^1 & b_{i2}^1 & b_{i3}^1 & b_{i4}^1 \\ b_{i1}^2 & b_{i2}^2 & b_{i3}^2 & b_{i4}^2 \end{bmatrix}.$$

Hence, the covariance matrix of the segregation residual effects (denoted as $\mathbf{G}_s^*$) is expressed as a block-diagonal matrix, which is different from that in Cantet and Smith's approach^[2].

The RAM approach with the covariance matrix proposed

Using eqs. (3) and (7) in eq. (2), a RAM model is given as

$$\begin{aligned} \begin{pmatrix} \mathbf{y}_p \\ \mathbf{y}_o \end{pmatrix} &= \begin{pmatrix} \mathbf{X}_p \\ \mathbf{X}_o \end{pmatrix} \boldsymbol{\beta} + \begin{pmatrix} \mathbf{Z}_p \\ \mathbf{Z}_o \mathbf{T} \end{pmatrix} \mathbf{u}_p + \begin{pmatrix} \mathbf{Z}_p \mathbf{P}_p \\ \mathbf{Z}_o \mathbf{P}_o \mathbf{B}^* \end{pmatrix} \mathbf{v}_p \\ &+ \begin{pmatrix} \mathbf{e}_p \\ \mathbf{Z}_o \mathbf{m} + \mathbf{Z}_o \mathbf{P}_o \boldsymbol{\varepsilon} + \mathbf{e}_o \end{pmatrix}. \end{aligned} \quad (8)$$

With the appropriate matrices $\mathbf{Z}_t$ and $\mathbf{W}$, eq. (8) is further arranged as

$$\mathbf{y} = \mathbf{X}\boldsymbol{\beta} + \mathbf{Z}_t \mathbf{u}_p + \mathbf{W} \mathbf{v}_p + \boldsymbol{\phi}. \quad (9)$$

For the current RAM, assumptions on the expectation and dispersion parameters for the random effects are

$$\mathbb{E} \begin{pmatrix} \mathbf{u}_p \\ \mathbf{v}_p \\ \boldsymbol{\phi} \end{pmatrix} = \begin{pmatrix} \mathbf{0} \\ \mathbf{0} \\ \mathbf{0} \end{pmatrix} \text{ and } \text{Var} \begin{pmatrix} \mathbf{u}_p \\ \mathbf{v}_p \\ \boldsymbol{\phi} \end{pmatrix} = \begin{pmatrix} \mathbf{A}_{u_p} \sigma_u^2 & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{A}_{v_p} \sigma_v^2 & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{R} \end{pmatrix},$$

where the matrices $\mathbf{A}_{u_p}$ and $\mathbf{A}_{v_p}$ are appropriate submatrices of $\mathbf{A}_u$ and $\mathbf{A}_v$, respectively, and $\mathbf{R}$ is defined as a diagonal matrix, as follows

$$\begin{pmatrix} \mathbf{I}_p \sigma_e^2 & \mathbf{0} \\ \mathbf{0} & \mathbf{D} \sigma_u^2 + \mathbf{P}_o \mathbf{G}_s^* \mathbf{P}_o' \sigma_v^2 + \mathbf{I}_o \sigma_e^2 \end{pmatrix}.$$

Thus, the mixed model equations (MME) for the current RAM are given by

$$\begin{pmatrix} \mathbf{X}'\mathbf{R}^{-1}\mathbf{X} & \mathbf{X}'\mathbf{R}^{-1}\mathbf{Z}_t & \mathbf{X}'\mathbf{R}^{-1}\mathbf{W} \\ \mathbf{Z}_t'\mathbf{R}^{-1}\mathbf{X} & \mathbf{Z}_t'\mathbf{R}^{-1}\mathbf{Z}_t + \mathbf{A}_{u_p}^{-1}\sigma_u^{-2} & \mathbf{Z}_t'\mathbf{R}^{-1}\mathbf{W} \\ \mathbf{W}'\mathbf{R}^{-1}\mathbf{X} & \mathbf{W}'\mathbf{R}^{-1}\mathbf{Z}_t & \mathbf{W}'\mathbf{R}^{-1}\mathbf{W} + \mathbf{A}_{v_p}^{-1}\sigma_v^{-2} \end{pmatrix} \begin{pmatrix} \boldsymbol{\beta}^o \\ \hat{\mathbf{u}}_p \\ \hat{\mathbf{v}}_p \end{pmatrix} = \begin{pmatrix} \mathbf{X}'\mathbf{R}^{-1}\mathbf{y} \\ \mathbf{Z}_t'\mathbf{R}^{-1}\mathbf{y} \\ \mathbf{W}'\mathbf{R}^{-1}\mathbf{y} \end{pmatrix}. \quad (10)$$

Backsolving for non-parents

The additive genetic effects due to QTLs unlinked to the marker locus and the additive effects of the MQTL alleles for animals with no progeny can be predicted^[2] by the following equations

$$\begin{pmatrix} \hat{\mathbf{u}}_o \\ \hat{\mathbf{v}}_o \end{pmatrix} = \begin{pmatrix} \mathbf{T} & \mathbf{0} \\ \mathbf{0} & \mathbf{B}^* \end{pmatrix} \begin{pmatrix} \hat{\mathbf{u}}_p \\ \hat{\mathbf{v}}_p \end{pmatrix} + \begin{pmatrix} \hat{\mathbf{m}} \\ \hat{\boldsymbol{\varepsilon}} \end{pmatrix}, \quad (11)$$

where

$$\begin{pmatrix} \hat{\mathbf{m}} \\ \hat{\boldsymbol{\varepsilon}} \end{pmatrix} = \begin{pmatrix} \mathbf{I}_o + \mathbf{D}^{-1}\alpha_u & \mathbf{P}_o \\ \mathbf{P}_o' & \mathbf{P}_o' \mathbf{P}_o + \mathbf{G}_s^* \alpha_v \end{pmatrix}^{-1} \begin{pmatrix} \boldsymbol{\phi}_o \\ \mathbf{P}_o' \boldsymbol{\phi}_o \end{pmatrix}$$

with $\alpha_u = \sigma_e^2 / \sigma_u^2$, $\alpha_v = \sigma_e^2 / \sigma_v^2$ and $\boldsymbol{\phi}_o = \mathbf{y}_o - \mathbf{X}_o \boldsymbol{\beta}^o - \mathbf{T} \hat{\mathbf{u}}_p - \mathbf{P}_o \mathbf{B}^* \hat{\mathbf{v}}_p$.

Numerical example

We use a small example including five animals, four parents and one non-parent, as given in Table 1. The recombination rate and the variance components are assumed as $r=.1$, $\sigma_u^2=.3$, $\sigma_v^2=.05$ and $\sigma_e^2=.8$, respectively. We also assume

$$\mathbf{X} = \begin{pmatrix} 1 & 1 & 1 & 0 & 0 \\ 0 & 0 & 0 & 1 & 1 \end{pmatrix}'$$

Note that parental origins of marker alleles for animal 5 can not be determined.

Then the gametic relationship matrix for the MQTL is obtained as

$$\begin{pmatrix} v_1^1 & v_1^2 & v_2^1 & v_2^2 & v_3^1 & v_3^2 & v_4^1 & v_4^2 & v_5^1 & v_5^2 \\ \left(\begin{array}{cccccc} 1 & 0 & 0 & 0 & .9 & 0 & .1 & 0 & .05 & .05 \\ & 1 & 0 & 0 & .1 & 0 & .9 & 0 & .05 & .05 \\ & & 1 & 0 & 0 & .9 & 0 & .9 & .81 & .81 \\ & & & 1 & 0 & .1 & 0 & .1 & .09 & .09 \\ & & & & 1 & 0 & .18 & 0 & .059 & .059 \\ & & & & & 1 & 0 & .82 & .819 & .819 \\ & & & & & & 1 & 0 & .059 & .059 \\ & & & & & & & 1 & .819 & .819 \\ \text{Sym.} & & & & & & & & 1 & .666 \\ & & & & & & & & & 1 \end{array} \right) \end{pmatrix}$$

The matrices $\mathbf{Z}_t$ and $\mathbf{W}$ in eq. (9) are given as

$$\mathbf{Z}_t = \begin{pmatrix} 1 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 \\ 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 1 \\ 0 & 0 & .5 & .5 \end{pmatrix}$$

and

Table 1. Example data with pedigree of five animals

Animal	Sire	Dam	Genotype	Observation
1	—	—	M_1M_2	80
2	—	—	M_3M_4	120
3	1	2	M_1M_3	90
4	1	2	M_2M_3	110
5	3	4	M_3M_3	115

$$\mathbf{W} = \begin{pmatrix} 1 & 1 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 1 & 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 1 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 1 & 1 \\ 0 & 0 & 0 & 0 & .1 & .9 & .1 & .9 \end{pmatrix},$$

respectively. The covariance matrix for the residual vector ϕ is calculated as

$$\mathbf{R} = \text{diag}(.8 \ .8 \ .8 \ .8 \ .968),$$

where $d_5=.5$ and $\mathbf{G}_{\epsilon_5}^* = \begin{pmatrix} .257 & -.077 \\ -.077 & .257 \end{pmatrix}$ with

$$\mathbf{B}_5^* = \begin{pmatrix} .05 & .45 & .05 & .45 \\ .05 & .45 & .05 & .45 \end{pmatrix}.$$

Thus, solving the resulting MME given as eq. (10) leads to

$$\hat{\beta}^o = (.97.0672 \ 112.084)',$$

$$\hat{\mathbf{u}}_p = (-4.97651 \ 4.97651 \ -.92367 \ -.17615)'$$

and

$$\hat{\mathbf{v}}_p = (-.97606 \ -.77672 \ .76733 \ .98546 \ -1.02 \ .74218 \ -.81568 \ .78703)'.$$

Back-solutions for the non-parent are

$$\hat{\mathbf{u}}_o = (-.19761)'$$

and

$$\hat{\mathbf{v}}_o = (.61750 \ .61750)'.$$

These solutions are completely equal to those obtained by the AM approach that accounts for the situation where parental origin of marker alleles can not be determined.

Discussion

Fernando and Grossman³⁾ first presented the methodology for an application of BLUP to MAS in animal breeding. Denoting the numbers of fixed effects, animals in the pedigree file, and MQTLs by N_f , N_q and N_m , respectively, the number of equations required in their AM approach becomes $N_f + N_q(2N_m + 1)$. Hence, the application of the AM approach would be limited to relatively small data sets. Then Cantet and Smith²⁾ developed a RAM version of the AM procedure for MAS, which is one strategy for making the BLUP evaluation computationally efficient. The system of equations required in the RAM approach is of order $N_f + N_q \cdot (2N_m + 1)$, where $N_q \cdot$ is the number of parent animals. Thus, the RAM procedure

could be especially useful in species where the fraction of non-parents is high and when the number of MQTLs is high.

Fernando and Grossman³⁾ also proposed a recursive algorithm to obtain the covariance matrix for the MQTL effects and presented a simple method to get its inverse, in which information on the parental origins of marker alleles in addition to information on marker genotypes are required. Cantet and Smith's RAM approach²⁾ was described for the situation discussed by Fernando and Grossman³⁾. In the RAM, consequently, the covariance matrix of residual effects for the MQTL, or the segregation residuals, has been defined as diagonal. The parental origin of marker alleles, however, may not be always known. Accordingly, Wang *et al.*¹⁵⁾ extended Fernando and Grossman's work³⁾ to situations where paternal or maternal origin of marker alleles can not be determined and some marker genotypes are uninformative. In this study, the covariance matrix of the segregation residual effects in the RAM for such a situation has been given as block-diagonal, in which the covariance of segregation residuals within an animal is defined appropriately.

Therefore, the RAM approach described herein is an extension of Cantet and Smith's work²⁾. Fortunately, the covariance matrix for the residual effects in the current model remains diagonal. When the algorithm¹⁵⁾ to invert the gametic relationship matrix for the MQTL alleles is used, the calculation of the matrix required is for parents only.

Finally, the BLUP methodology for MAS including the current procedure requires the information of recombination rate between the marker locus and the MQTL and the variance components. However, true values of these parameters are usually unknown. Those values could be estimated, for instance, by the likelihood-based procedures^{4, 14, 16)}, assuming that effects of MQTL alleles follow normality.

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マーカー依存型選抜のための縮約個体モデルにおける 残差効果の共分散構造

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マーカー依存型選抜のための縮約個体モデル-BLUP 法に関して、個々の親から子へのマーカー遺伝子の由来が特定できない場合を取り上げて、モデルにおける分離残差効果の共分散構造を示した。あわせて、当該共分散構造を考慮に入れた BLUP 法の方法論を記述し、後代を生産していない個体に関する解を得るための方程式を与えるとともに、簡単な数値例を示した。

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