Genetic Evaluation by Best Linear Unbiased Prediction Using Marker and Trait Information in a Multibreed Population

T. Wang, R. L. Fernando and M. Grossman

Department of Animal Sciences, University of Illinois, Urbana, Illinois 61801

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ABSTRACT

Genetic evaluation by best linear unbiased prediction (BLUP) requires modeling genetic means, variances, and covariances. This paper presents theory to model means, variances, and covariances in a multibreed population, given marker and breed information, in the presence of gametic disequilibrium between the marker locus (ML) and linked quantitative trait locus (MQTL). Theory and algorithms are presented to construct the matrix of conditional covariances between relatives ($\mathbf{G}_v$) for the MQTL effects in a multibreed population and to obtain the inverse of $\mathbf{G}_v$ efficiently. Theory presented here accounts for heterogeneity of variances among pure breeds and for segregation variances between pure breeds. A numerical example was used to illustrate how the theory and algorithms can be used for genetic evaluation by BLUP using marker and trait information in a multibreed population.

GENETIC evaluation by best linear unbiased prediction (BLUP) requires modeling genetic means, variances, and covariances. For genetic evaluation using only trait information, genetic group theory can be used to accommodate heterogeneous genetic means under additive inheritance (Thompson 1979; Quaas 1988; Westell *et al.* 1988). This theory was extended to accommodate heterogeneous genetic variances and covariances among genetic groups (Elzo 1990; Lo *et al.* 1993).

For genetic evaluation using marker and trait information, Fernando and Grossman (1989) proposed a theory to model genetic variances and covariances. They assumed gametic equilibrium between the marker locus and the linked quantitative trait locus, which means that the genetic mean does not depend on marker information. In the presence of gametic disequilibrium, however, genetic means, variances, and covariances do depend on marker information. In the presence of gametic disequilibrium resulting from crossbreeding, Goddard (1992) showed how genetic group theory can accommodate marker information. His model for variances, however, does not accommodate heterogeneous variances among pure breeds and the segregation variance may not be properly modeled (M. E. Goddard, personal communication).

The objective of this paper is to present an alternative approach to model genetic means, variances, and covariances for genetic evaluations by BLUP using marker and trait information in a multibreed population in the presence of gametic disequilibrium. Our approach is to combine covariance theory for a marked quantitative trait locus (Wang *et al.* 1995) and covariance theory for a multibreed population (Lo *et al.* 1993). A numerical example will illustrate the theory and related algorithms.

DEFINITION AND NOTATION

A multibreed population comprises individuals from several breed groups, including purebred and crossbred groups (Lo *et al.* 1993). Founders are assumed to be unrelated, noninbred, and of known breed; parents of nonfounders are assumed to be known. Breed information, denoted **B**, consists of breeds for founders and parentage for nonfounders. Breed information (**B**) for the pedigree in Table 1, for example, consists of breed groups B_1, B_1, B_2 for founders 1, 2, and 3 and parentage $P_{1,2}$, $P_{3,2}$, and $P_{4,5}$ for nonfounders 4, 5, and 6.

Consider a polymorphic marker locus (ML) closely linked to a QTL (MQTL), and assume the genotype at this ML is known for each individual in the pedigree. Information on the genotype will be referred to as marker information, denoted **M**. Following Wang *et al.* (1995), for individual i, let M_i^1 and M_i^2 denote the two alleles at the ML, and let Q_i^1 and Q_i^2 denote the two alleles at the MQTL linked to M_i^1 and M_i^2:

$$\frac{M_i^1 \quad Q_i^1}{\qquad\qquad}$$
$$\frac{\qquad\qquad}{M_i^2 \quad Q_i^2}$$

Further, let v_i^1 and v_i^2 be the additive effects of Q_i^1 and Q_i^2 in individual i, and let u_i be the sum of additive effects of the remaining QTL alleles (RQTL). Assume

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Corresponding author: Rohan L. Fernando, Department of Animal Science, Iowa State University, 225 Kildee Hall, Ames, IA 50011. E-mail: rohan@iastate.edu

TABLE 1

Pedigree of five individuals with marker genotypes

Individual	Sire	Dam	Phenotype	Breed	Marker genotype
1	0	0	10.6	B_1	m_1m_1
2	0	0	10.1	B_1	m_1m_1
3	0	0	13.0	B_2	m_2m_2
4	1	2	14.0	—	m_1m_1
5	3	2	11.0	—	m_1m_2
6	4	5	14.0	—	m_1m_1

A zero in columns 2 or 3 indicates an unknown parent; breed information is required only for founders.

the RQTL are unlinked and in gametic equilibrium with the MQTL and with the ML; thus, u_i is uncorrelated with v_i^1 and with v_i^2. Let $\boldsymbol{v}$ be a vector of v_i^1 and v_i^2 for $i = 1, 2, \ldots, n$, and $\boldsymbol{u}$ be a vector of u_i for $i = 1, 2, \ldots, n$. Suppose J alleles segregate at the MQTL in a multibreed population with allele frequencies $p_{B_l}^j, j = 1, \ldots, J$ in purebred group B_l. Then, v_i^1 and v_i^2 are random variables with sample space $\{\nu_1, \ldots, \nu_j, \ldots, \nu_J\}$, where ν_j is the effect of MQTL allele j in some reference breed group (*e.g.*, one of the pure breeds). Differences in allele frequencies among breed groups give rise to heterogeneous means, variances, and covariances.

To model means, variances, and covariances of additive genetic values (a_i), let $a_i = v_i^1 + v_i^2 + u_i$. In matrix notation, the vector of additive genetic values ($\boldsymbol{a}$) is

$$\boldsymbol{a} = \mathbf{L}\boldsymbol{v} + \boldsymbol{u} \tag{1}$$

where

$$\mathbf{L} = \begin{bmatrix} 1\ 1 & & & \\ & 1\ 1 & & \\ & & \cdots & \\ & & & 1\ 1 \end{bmatrix}$$

is a matrix of order $n \times 2n$. Now, the conditional mean of $\boldsymbol{a}$, given breed ($\mathbf{B}$) and marker ($\mathbf{M}$) information, can be written as $\mathrm{E}(\boldsymbol{a}|\mathbf{BM}) = \mathbf{L}\mathrm{E}(\boldsymbol{v}|\mathbf{BM}) + \mathrm{E}(\boldsymbol{u}|\mathbf{BM})$. As already mentioned, RQTL are unlinked with the ML, so that $\mathrm{E}(\boldsymbol{u}|\mathbf{BM}) = \mathrm{E}(\boldsymbol{u}|\mathbf{B})$ and

$$\mathrm{E}(\boldsymbol{a}|\mathbf{BM}) = \mathbf{L}\mathrm{E}(\boldsymbol{v}|\mathbf{BM}) + \mathrm{E}(\boldsymbol{u}|\mathbf{B}) \tag{2}$$

The second term on the right-hand side of (2) depends only on breed information, so it can be modeled using genetic group theory. The first term, however, depends on breed and marker information, and the modeling of this term is presented here.

The u_i is uncorrelated with both v_i^1 and v_i^2, so that the conditional variance and covariance matrix of $\boldsymbol{a}$, given breed and marker information, can be written as

$$\mathrm{Var}(\boldsymbol{a}|\mathbf{BM}) = \mathbf{L}\mathbf{G}_v\mathbf{L}' + \mathbf{G}_u \tag{3}$$

where $\mathbf{G}_v$ denotes $\mathrm{Var}(\boldsymbol{v}|\mathbf{BM})$ and $\mathbf{G}_u$ denotes $\mathrm{Var}(\boldsymbol{u}|\mathbf{B})$. The second term on the right-hand side of (3) depends only on breed information, so it can be modeled using additive covariance theory for a multibreed population (Lo *et al.* 1993).

MEANS OF MQTL EFFECTS

Let i be an individual with sire s and dam d (Figure 1). The conditional expectation of the MQTL effect v_i^{ki} for $k_i = 1$ or 2, given breed ($\mathbf{B}$) and marker ($\mathbf{M}$) information, can be written as $\mathrm{E}(v_i^{ki}|\mathbf{BM}) = \mathrm{E}[\mathrm{E}(v_i^{ki}|Q_i^{ki} \leftarrow B_l,\mathbf{BM})]$, where $Q_i^{ki} \leftarrow B_l$ means that Q_i^{ki} can be traced back to pure breed B_l, or that Q_i^{ki} originates from pure breed B_l. Then,

$$\begin{aligned} \mathrm{E}(v_i^{k_i}|\mathbf{BM}) &= \sum_{l=1}^{L} \mathrm{E}(v_i^{k_i}|Q_i^{k_i} \leftarrow B_l,\mathbf{BM})\mathrm{Pr}(Q_i^{k_i} \leftarrow B_l|\mathbf{BM}) \\ &= \sum_{l=1}^{L} \mu_{B_l} f_{B_l}^{i,k_i} \end{aligned} \tag{4}$$

where $\mu_{B_l} = \mathrm{E}(v_i^{ki}|Q_i^{ki} \leftarrow B_l,\mathbf{BM}) = \sum_{j=1}^{J} p_{B_l}^j \nu_j$ is the mean of additive MQTL effects in pure breed B_l, and $f_{B_l}^{i,k_i} = \mathrm{Pr}(Q_i^{ki} \leftarrow B_l|\mathbf{BM})$ is the conditional probability that MQTL allele Q_i^{ki} originates from pure breed B_l, given breed and marker information. This probability will be also referred to as the conditional breed composition for MQTL allele Q_i^{ki}, given breed and marker information.

Note that the expected value of v_i^{ki} for any individual i in a multibreed population, given breed and marker information, can be written as a linear combination of the means (μ_{B_l}) of additive MQTL effects in pure breeds.

Computation of $f_{B_l}^{i,k_i}$ in (4) is described below. Recall that s and d are the parents of individual i, so that MQTL allele Q_i^{ki} can originate from a pure breed B_l allele in one of four ways:

(1) Q_i^{ki} descended from Q_s^1, and Q_s^1 originated from breed B_l, denoted $(Q_i^{ki} \Leftarrow Q_s^1, Q_s^1 \leftarrow B_l)$

(2) Q_i^{ki} descended from Q_s^2, and Q_s^2 originated from breed B_l, denoted $(Q_i^{ki} \Leftarrow Q_s^2, Q_s^2 \leftarrow B_l)$

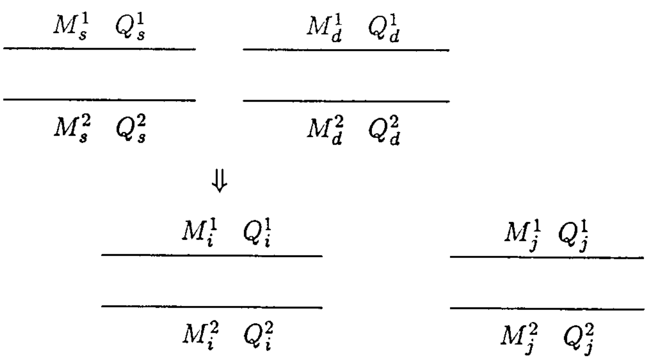

Figure 1.—Chromosomal fragments containing the ML and the MQTL for individuals s, d, i, and j where s and d are parents of i and where j is not a direct descendent of i.

(3) $Q_i^{k_i}$ descended from Q_d^1, and Q_d^1 originated from breed B_l, denoted $(Q_i^{k_i} \Leftarrow Q_d^1, Q_d^1 \leftarrow B_l)$

(4) $Q_i^{k_i}$ descended from Q_d^2, and Q_d^2 originated from breed B_l, denoted $(Q_i^{k_i} \Leftarrow Q_d^2, Q_d^2 \leftarrow B_l)$

where, for example, Q_s^1 and Q_s^2 are the MQTL alleles in parent s. The $f_{B_l}^{i,k_i}$, therefore, can be written as

$$\begin{aligned} f_{B_l}^{i,k_i} &= \Pr(Q_i^{k_i} \leftarrow B_l \,|\, \mathbf{BM}) \\ &= \Pr(Q_i^{k_i} \Leftarrow Q_s^1, Q_s^1 \leftarrow B_l \,|\, \mathbf{BM}) \\ &\quad + \Pr(Q_i^{k_i} \Leftarrow Q_s^2, Q_s^2 \leftarrow B_l \,|\, \mathbf{BM}) \\ &\quad + \Pr(Q_i^{k_i} \Leftarrow Q_d^1, Q_d^1 \leftarrow B_l \,|\, \mathbf{BM}) \\ &\quad + \Pr(Q_i^{k_i} \Leftarrow Q_d^2, Q_d^2 \leftarrow B_l \,|\, \mathbf{BM}) \end{aligned} \tag{5}$$

Note that the sampling of $Q_i^{k_i}$ from parents s and d does not depend on the breed origin of the MQTL alleles in s and d. Thus, (5) can be computed recursively as

$$\begin{aligned} f_{B_l}^{i,k_i} &= \Pr(Q_i^{k_i} \leftarrow B_l \,|\, \mathbf{BM}) \\ &= \Pr(Q_i^{k_i} \Leftarrow Q_s^1 \,|\, \mathbf{BM}) f_{B_l}^{s,1} + \Pr(Q_i^{k_i} \Leftarrow Q_s^2 \,|\, \mathbf{BM}) f_{B_l}^{s,2} \\ &\quad + \Pr(Q_i^{k_i} \Leftarrow Q_d^1 \,|\, \mathbf{BM}) f_{B_l}^{d,1} + \Pr(Q_i^{k_i} \Leftarrow Q_d^2 \,|\, \mathbf{BM}) f_{B_l}^{d,2} \end{aligned} \tag{6}$$

where $\Pr(Q_i^{k_i} \Leftarrow Q_p^{k_p} \,|\, \mathrm{BM})$, for $p = s$ or d and $k_p = 1$ or 2, is the conditional probability that MQTL allele $Q_i^{k_i}$ descended from $Q_p^{k_p}$. The event $Q_i^{k_i} \Leftarrow Q_p^{k_p}$ does not depend on breed information, so $\Pr(Q_i^{k_i} \Leftarrow Q_p^{k_p} \,|\, \mathrm{BM})$ is equal to $\Pr(Q_i^{k_i} \Leftarrow Q_p^{k_p} \,|\, \mathrm{M})$. Wang *et al.* (1995) referred to this as the probability of descent for MQTL alleles (PDQ) and presented a recursive formula for its computation.

VARIANCE OF MQTL EFFECTS

Given random variables X and Y, the variance of X can be written as

$$\mathrm{Var}(X) = \mathrm{E}[\mathrm{Var}(X \,|\, Y)] + \mathrm{Var}[\mathrm{E}(X \,|\, Y)] \tag{7}$$

(Kempthorne and Folks 1971). Using the above formula, the conditional variance of MQTL effect $v_i^{k_i}$ for $k_i = 1$ or 2, given breed and marker information, can be written as

$$\begin{aligned} \mathrm{Var}(v_i^{k_i} \,|\, \mathbf{BM}) &= \mathrm{E}[\mathrm{Var}(v_i^{k_i} \,|\, Q_i^{k_i} \leftarrow B_l, \mathbf{BM})] \\ &\quad + \mathrm{Var}[\mathrm{E}(v_i^{k_i} \,|\, Q_i^{k_i} \leftarrow B_l, \mathbf{BM})] \end{aligned} \tag{8}$$

The first term of (8) can be expressed in terms of conditional breed compositions as

$$\begin{aligned} &\mathrm{E}[\mathrm{Var}(v_i^{k_i} \,|\, Q_i^{k_i} \leftarrow B_l, \mathrm{BM})] \\ &\quad = \sum_{l=1}^{L} \mathrm{Var}(v_i^{k_i} \,|\, Q_i^{k_i} \leftarrow B_l, \mathrm{BM}) \Pr(Q_i^{k_i} \leftarrow B_l \,|\, \mathrm{BM}) \\ &\quad = \sum_{l=1}^{L} \sigma_{v_{B_l}}^2 f_{B_l}^{i,k_i} \end{aligned} \tag{9}$$

where $\sigma_{v_{B_l}}^2 = \mathrm{Var}(v_i^{k_i} \,|\, Q_i^{k_i} \leftarrow B_l, \mathbf{BM}) = \sum_{j=1}^{J} (\nu_j - \mu_{B_l})^2 p_{B_l}^j$ is the variance of the MQTL effects in pure breed B_l. Note that the quantity on the right-hand side of (9) is the mean of variances $\sigma_{v_{B_l}}^2$ of the MQTL effects in the pure breeds, weighted by conditional breed compositions. Purebred variances $\sigma_{v_{B_l}}^2$, for $l = 1, \ldots, L$, can be estimated by maximum likelihood (Weller and Fernando 1991).

The second term of (8) also can be expressed in terms of conditional breed composition as

$$\begin{aligned} \mathrm{Var}[\mathrm{E}(v_i^{k_i} \,|\, Q_i^{k_i} \leftarrow B_l, \mathbf{BM})] &= \sum_{l=1}^{L} f_{B_l}^{i,k_i} \mu_{B_l}^2 - \left(\sum_{l=1}^{L} f_{B_l}^{i,k_i} \mu_{B_l} \right)^2 \\ &= \sum_{l=1}^{L-1} \sum_{l'=l+1}^{L} (\mu_{B_l} - \mu_{B_{l'}})^2 f_{B_l}^{i,k_i} f_{B_{l'}}^{i,k_i} \end{aligned} \tag{10}$$

Note that the quantity on the right-hand side of (10) is the contribution to the variance due to differences in MQTL allele frequencies among pure breeds. Note that $(\mu_{B_l} - \mu_{B_{l'}})^2$ is twice the segregation variance of the MQTL effect for pure breeds l and l' (Lande 1981; Lo *et al.* 1993).

The variance of $v_i^{k_i}$ for any individual i in a multibreed population, therefore, given breed and marker information, is obtained by substituting (9) and (10) into (8):

$$\begin{aligned} \mathrm{Var}(v_i^{k_i} \,|\, \mathrm{BM}) &= \sum_{l=1}^{l=L} \sigma_{v_{B_l}}^2 f_{B_l}^{i,k_i} + \sum_{l=1}^{L-1} \sum_{l'=l+1}^{L} \\ &\quad (\mu_{B_l} - \mu_{B_{l'}})^2 f_{B_l}^{i,k_i} f_{B_{l'}}^{i,k_i} \end{aligned} \tag{11}$$

COVARIANCE BETWEEN RELATIVES FOR MQTL EFFECTS

Following Wang *et al.* (1995), conditional covariances between relatives for additive effects of MQTL alleles, given marker and breed information, will be derived separately for alleles between the two individuals and for alleles within an individual.

Between individuals: Let i be an individual with sire s and dam d, and let j be another individual who is not a direct descendant of i (Figure 1). Given random variables X, Y, and Z, the covariance between X and Y can be written as

$$\mathrm{Cov}(X, Y) = \mathrm{E}[\mathrm{Cov}(X, Y \,|\, Z)] + \mathrm{Cov}[\mathrm{E}(X \,|\, Z), \mathrm{E}(Y \,|\, Z)] \tag{12}$$

(Kempthorne and Folks 1971). Using the above formula, the conditional covariance between relatives for additive MQTL effects $v_i^{k_i}$ and $v_j^{k_j}$, given breed and marker information, can be written as

$$\begin{aligned} \mathrm{Cov}(v_i^{k_i}, v_j^{k_j} \,|\, \mathbf{BM}) &= \mathrm{E}[\mathrm{Cov}(v_i^{k_i}, v_j^{k_j} \,|\, \mathbf{BM}, W)] \\ &\quad + \mathrm{Cov}[\mathrm{E}(v_i^{k_i} \,|\, \mathbf{BM}, W), \mathrm{E}(v_j^{k_j} \,|\, \mathbf{BM}, W)] \end{aligned} \tag{13}$$

where W is a random variable with sample space $\{Q_i^{k_i}{\Leftarrow}Q_s^1,\ Q_i^{k_i}{\Leftarrow}Q_s^2,\ Q_i^{k_i}{\Leftarrow}Q_d^1,\ Q_i^{k_i}{\Leftarrow}Q_d^2\}$. Note that $v_j^{k_j}$ is independent of W because j is not a direct descendant of i (Chang *et al.* 1991). Thus, $\mathrm{E}(v_j^{k_i}|\mathbf{BM},W)$ does not depend on W: $\mathrm{E}(v_j^{k_i}|\mathbf{BM},W) = \mathrm{E}(v_j^{k_i}|\mathbf{BM})$. Therefore, the second term of (13) is null.

The first term of (13) can be expressed in terms of PDQs (Wang *et al.* 1995):

$$\begin{aligned}\mathrm{E}[\mathrm{Cov}(v_i^{k_i},v_j^{k_j}|\mathbf{BM},W)]\\ &= \mathrm{Cov}(v_i^{k_i},v_j^{k_j}|Q_i^{k_i}\Leftarrow Q_s^1,\mathbf{BM})\ \Pr(Q_i^{k_i}\Leftarrow Q_s^1|\mathbf{BM})\\ &+ \mathrm{Cov}(v_i^{k_i},v_j^{k_j}|Q_i^{k_i}\Leftarrow Q_s^2,\mathbf{BM})\ \Pr(Q_i^{k_i}\Leftarrow Q_s^2|\mathbf{BM})\\ &+ \mathrm{Cov}(v_i^{k_i},v_j^{k_j}|Q_i^{k_i}\Leftarrow Q_d^1,\mathbf{BM})\ \Pr(Q_i^{k_i}\Leftarrow Q_d^1|\mathbf{BM})\\ &+ \mathrm{Cov}(v_i^{k_i},v_j^{k_j}|Q_i^{k_i}\Leftarrow Q_d^2,\mathbf{BM})\ \Pr(Q_i^{k_i}\Leftarrow Q_d^2|\mathbf{BM})\end{aligned}$$

The $\mathrm{Cov}(v_i^{k_i},v_j^{k_j}|Q_i^{k_i}{\Leftarrow}Q_p^{k_p},\mathbf{BM}) = \mathrm{Cov}(v_p^{k_p},v_j^{k_j}|\mathbf{BM})$ for $p = s$ or d, so we have

$$\begin{aligned}\mathrm{E}[\mathrm{Cov}(v_i^{k_i},v_j^{k_j}|\mathbf{BM},W)]\\ &= \mathrm{Cov}(v_s^1,v_j^{k_j}|\mathbf{BM})\ \Pr(Q_i^{k_i}\Leftarrow Q_s^1|\mathbf{M})\\ &+ \mathrm{Cov}(v_s^2,v_j^{k_j}|\mathbf{BM})\ \Pr(Q_i^{k_i}\Leftarrow Q_s^2|\mathbf{M})\\ &+ \mathrm{Cov}(v_d^1,v_j^{k_j}|\mathbf{BM})\ \Pr(Q_i^{k_i}\Leftarrow Q_d^1|\mathbf{M})\\ &+ \mathrm{Cov}(v_d^2,v_j^{k_j}|\mathbf{BM})\ \Pr(Q_i^{k_i}\Leftarrow Q_d^2|\mathbf{M})\end{aligned}$$

Thus, $\mathrm{Cov}(v_i^{k_i},v_j^{k_j}|\mathbf{BM})$ can be computed recursively as

$$\begin{aligned}\mathrm{Cov}(v_i^{k_i},v_j^{k_j}|\mathrm{BM})\\ &= \mathrm{Cov}(v_s^1,v_j^{k_j}|\mathrm{BM})\ \Pr(Q_i^{k_i}\Leftarrow Q_s^1|\mathrm{M})\\ &+ \mathrm{Cov}(v_s^2,v_j^{k_j}|\mathrm{BM})\ \Pr(Q_i^{k_i}\Leftarrow Q_s^2|\mathrm{M})\\ &+ \mathrm{Cov}(v_d^1,v_j^{k_j}|\mathrm{BM})\ \Pr(Q_i^{k_i}\Leftarrow Q_d^1|\mathrm{M})\\ &+ \mathrm{Cov}(v_d^2,v_j^{k_j}|\mathrm{BM})\ \Pr(Q_i^{k_i}\Leftarrow Q_d^2|\mathrm{M}) \qquad (14)\end{aligned}$$

This recursive formula is identical to that used for purbred populations, given marker information (Hoeschele 1993; Wang *et al.* 1995).

Within an individual: For individual i, we present the computation of the covariance between additive effects v_i^1 and v_i^2 of MQTL alleles Q_i^1 and Q_i^2.

Following Mendelian inheritance, the pair of homologous alleles at the MQTL, Q_i^1 and Q_i^2, descended from one of the following pairs of parents: (Q_s^1,Q_d^1), (Q_s^1,Q_d^2), (Q_s^2,Q_d^1), or (Q_s^2,Q_d^2). Let $E_{k_sk_d}$ denote the event that the pair of alleles in i descended from parents, $(Q_i^1{\Leftarrow}Q_s^{k_s},Q_i^2{\Leftarrow}Q_d^{k_d})$ or $(Q_i^1{\Leftarrow}Q_d^{k_d},Q_i^2{\Leftarrow}Q_s^{k})$, for $k_s,k_d = 1$ or 2. Using the formula (12), the covariance between relatives for additive MQTL effects v_i^1 and v_i^2 can be written as

$$\begin{aligned}\mathrm{Cov}(v_i^1,v_i^2|\mathrm{BM}) &= \mathrm{E}[\mathrm{Cov}(v_i^1,v_i^2|\mathbf{BM},W)]\\ &\quad + \mathrm{Cov}[\mathrm{E}(v_i^1|\mathbf{BM},W),\mathrm{E}(v_i^2|\mathbf{BM},W)] \qquad (15)\end{aligned}$$

where W is a random variable with sample space $\{E_{k_sk_d}\}$ for $k_s,k_d = 1$ or 2. The first term in (15) is

$$\begin{aligned}\mathrm{E}[\mathrm{Cov}(v_i^1,v_i^2|\mathrm{BM},W)]\\ &= \sum_{k_s=1}^{2}\sum_{k_d=1}^{2}\mathrm{Cov}(v_s^{k_s},v_d^{k_d}|\mathrm{BM})\Pr(E_{k_sk_d}|\mathrm{BM}) \qquad (16)\end{aligned}$$

Note that event $E_{k_sk_d}$ does not depend on breed information, so that $\Pr(E_{k_sk_d}|\mathbf{BM}) = \Pr(E_{k_sk_d}|\mathbf{M})$. Following Wang *et al.* (1995), $\Pr(E_{k_sk_d}|\mathbf{M})$ can be computed as

$$\begin{aligned}\Pr(E_{k_sk_d}|\mathbf{M}) &= \Pr(Q_i^1\Leftarrow Q_s^{k_s},Q_i^2\Leftarrow Q_d^{k_d}|\mathbf{M})\\ &\quad + \Pr(Q_i^1\Leftarrow Q_d^{k_d},(Q_i^2\Leftarrow Q_s^{k_s}|\mathbf{M})\\ &= \frac{\Pr(Q_i^1\Leftarrow Q_s^{k_s}|\mathbf{M})\Pr(Q_i^2\Leftarrow Q_d^{k_d}|\mathbf{M})}{\Pr(Q_i^1\Leftarrow Q_s^1|\mathbf{M})+\Pr(Q_i^1\Leftarrow Q_s^2|\mathbf{M})}\\ &\quad + \frac{\Pr(Q_i^1\Leftarrow Q_d^{k_d}|\mathbf{M})\Pr(Q_i^2\Leftarrow Q_s^{k_s}|\mathbf{M})}{\Pr(Q_i^1\Leftarrow Q_d^1|\mathbf{M})+\Pr(Q_i^1\Leftarrow Q_d^2|\mathbf{M})} \qquad (17)\end{aligned}$$

The second term in (15) is

$$\begin{aligned}&\mathrm{Cov}[\mathrm{E}(v_i^1|\mathbf{BM},W),\mathrm{E}(v_i^2|\mathbf{BM},W)] =\\ &\mathrm{E}[\mathrm{E}(v_i^1|\mathbf{BM},W)\mathrm{E}(v_i^2|\mathbf{BM},W)] - \mathrm{E}(v_i^1|\mathbf{BM})(v_i^2|\mathbf{BM}) \qquad (18)\end{aligned}$$

where $\mathrm{E}[\mathrm{E}(v_i^1|\mathbf{BM},W)\ \mathrm{E}(v_i^2|\mathbf{BM},W)] = \sum_{k_s=1}^{2}\sum_{k_d=1}^{2}\mathrm{E}(v_s^{k_s}|\mathbf{BM})\ \mathrm{E}(v_d^{k_d}|\mathbf{BM})\ \Pr(E_{k_sk_d}|\mathbf{M})$. Therefore, substituting (16) and (18) into (15), we have

$$\begin{aligned}\mathrm{Cov}(v_i^1,v_i^2|\mathbf{BM}) &= \sum_{k_s=1}^{2}\sum_{k_d=1}^{2}[\mathrm{Cov}(v_s^{k_s},v_d^{k_d}|\mathbf{BM})\\ &\quad + \mathrm{E}(v_s^{k_s}|\mathbf{BM})\mathrm{E}(v_d^{k_d}|\mathbf{BM})]\Pr(E_{k_sk_d}|\mathbf{M})\\ &\quad - \mathrm{E}(v_i^1|\mathbf{BM})\mathrm{E}(v_i^2|\mathbf{BM}) \qquad (19)\end{aligned}$$

In (19), $\mathrm{Cov}(v_s^{k_s},v_d^{k_d}|\mathbf{BM})$ is computed recursively using (14), and means of additive MQTL effects $\mathrm{E}(v_s^{k_s}|\mathrm{BM})$, $\mathrm{E}(v_d^{k_d}|\mathrm{BM})$, $\mathrm{E}(v_i^1|\mathbf{BM})$, and $\mathrm{E}(v_i^2|\mathbf{BM})$ are computed using (4).

TABULAR METHOD TO COMPUTE COVARIANCE MATRIX $\mathbf{G}_v$

Following Wang *et al.* (1995), we show how (11), (14), and (19) can be used to construct recursively the covariance matrix ($\mathbf{G}_v$) between relatives for the MQTL effects by a tabular method.

For each individual in the pedigree, matrix $\mathbf{G}_v$ included a row and a column for each of the two MQTL alleles. Thus, the order of $\mathbf{G}_v$ is $2n$, where n is the number of individuals. Each diagonal element of $\mathbf{G}_v$ is given by (11). Individuals are ordered such that parents precede their progeny, and individuals 1 through b are considered to be unrelated and noninbred. Thus, the upper left submatrix of $\mathbf{G}_v$ is a diagonal matrix of order $2b$, which will be expanded sequentially by the two rows and the two columns corresponding to individual i, for $i = b + 1, \ldots, n$.

Let $\mathbf{G}_{i-1}$ be the upper left submatrix of $\mathbf{G}_v$ expanded up through individual $i - 1$. For individual i, with parents s and d, $\mathbf{G}_{i-1}$ is expanded to $\mathbf{G}_i$ as

$$\mathbf{G}_i = \begin{bmatrix} \mathbf{G}_{i-1} & \mathbf{G}_{i-1}\mathrm{q}_i \\ \mathrm{q}_i' \mathbf{G}_{i-1} & \mathbf{C}_i \end{bmatrix} \tag{20}$$

where

$$\mathbf{C}_i = \begin{bmatrix} \mathrm{Var}(v_i^1 | \mathbf{BM}) & \mathrm{Cov}(v_i^1, v_i^2 | \mathbf{BM}) \\ \mathrm{Cov}(v_i^2, v_i^1 | \mathbf{BM}) & \mathrm{Var}(v_i^2 | \mathbf{BM}) \end{bmatrix} \tag{21}$$

and

$$q_i' = \begin{bmatrix} 0 \ldots 0 & T_i(1,1) & T_i(1,2) & 0 \ldots 0 & T_i(1,3) & T_i(1,4) & 0 \ldots 0 \\ 0 \ldots 0 & T_i(2,1) & T_i(2,2) & 0 \ldots 0 & T_i(2,3) & T_i(2,4) & 0 \ldots 0 \end{bmatrix} \tag{22}$$

Matrix q_i' is of order $2 \times 2\ (i - 1)$, with at most eight nonzero elements that are from:

$$T_i = \begin{bmatrix} \Pr(Q_i^1 \Leftarrow Q_s^1 | \mathbf{M}) & \Pr(Q_i^1 \Leftarrow Q_s^2 | \mathbf{M}) & \Pr(Q_i^1 \Leftarrow Q_d^1 | \mathbf{M}) & \Pr(Q_i^1 \Leftarrow Q_d^2 | \mathbf{M}) \\ \Pr(Q_i^2 \Leftarrow Q_s^1 | \mathbf{M}) & \Pr(Q_i^2 \Leftarrow Q_s^2 | \mathbf{M}) & \Pr(Q_i^2 \Leftarrow Q_d^1 | \mathbf{M}) & \Pr(Q_i^2 \Leftarrow Q_d^2 | \mathbf{M}) \end{bmatrix} \tag{23}$$

These nonzero elements in q' are located in columns $2(s - 1) + 1$, $2(s - 1) + 2$, $2(d - 1) + 1$, and $2(d - 1) + 2$. Diagonal elements in (21) are computed using (11) and off-diagonal elements are computed using (19).

EFFICIENT ALGORITHM TO INVERT COVARIANCE MATRIX G_v

The $\mathbf{q}_i'$ in (22) is sparse, and positions of the nonzero elements can be determined easily; therefore, $\mathbf{G}_v$ can be inverted efficiently (van Arendonk *et al.* 1994; Wang *et al.* 1995).

Following Wang *et al.* (1995), three matrices will be used to described the rules to invert $\mathbf{G}_v$: $\mathbf{D}_i$, $\mathbf{W}_i$, and $\mathbf{\Pi}_i$. The first matrix is

$$\mathbf{D}_i = \mathbf{C}_i - \mathbf{T}_i \mathbf{C}_{s,d} \mathbf{T}_i' \tag{24}$$

where $\mathbf{C}_{s,d}$ is the 4×4 matrix of conditional covariances between s and d, the parents of i, for additive MQTL effects, and T_i is the matrix of PDQs defined in (23). The second matrix is

$$\boldsymbol{W}_i = \begin{bmatrix} -\mathbf{T}_i' \\ \mathbf{I}_2 \end{bmatrix} \mathbf{D}_i^{-1} [-\mathbf{T}_i \ \ \mathbf{I}_2] \tag{25}$$

where $\mathbf{I_2}$ is an identity matrix of order 2. The third matrix is

$$\Pi_i = \begin{bmatrix} (\delta_s^1, \delta_s^1) & (\delta_s^1, \delta_s^2) & (\delta_s^1, \delta_d^1) & (\delta_s^1, \delta_d^2) & (\delta_s^1, \delta_i^1) & (\delta_s^1, \delta_i^2) \\ (\delta_s^2, \delta_s^1) & (\delta_s^2, \delta_s^2) & (\delta_s^2, \delta_d^1) & (\delta_s^2, \delta_d^2) & (\delta_s^2, \delta_i^1) & (\delta_s^2, \delta_i^2) \\ (\delta_d^1, \delta_s^1) & (\delta_d^1, \delta_s^2) & (\delta_d^1, \delta_d^1) & (\delta_d^1, \delta_d^2) & (\delta_d^1, \delta_i^1) & (\delta_d^1, \delta_i^2) \\ (\delta_d^2, \delta_s^1) & (\delta_d^2, \delta_s^2) & (\delta_d^2, \delta_d^1) & (\delta_d^2, \delta_d^2) & (\delta_d^2, \delta_i^1) & (\delta_d^2, \delta_i^2) \\ (\delta_i^1, \delta_s^1) & (\delta_i^1, \delta_s^2) & (\delta_i^1, \delta_d^1) & (\delta_i^1, \delta_d^2) & (\delta_i^1, \delta_i^1) & (\delta_i^1, \delta_i^2) \\ (\delta_i^2, \delta_s^1) & (\delta_i^2, \delta_s^2) & (\delta_i^2, \delta_d^1) & (\delta_i^2, \delta_d^2) & (\delta_i^2, \delta_i^1) & (\delta_i^2, \delta_i^2) \end{bmatrix} \tag{26}$$

where $\delta_a^b = 2(a - 1) + b$ for $a = s$, d, or i, and $b = 1$ or 2. If both parents of individual i are known, then all elements in Π_i are defined. If at least one parent is unknown, then elements in Π_i associated with the unknown parent(s) are not defined.

Rules to invert $\mathbf{G}_v$ are as follows: (1) Set $\mathbf{G}_v^{-1}$ equal to the null matrix of order $2n$. (2) For individual i, $i = 1, \ldots, n$, (a) if both parents are unknown, then (i) add $\mathrm{Var}(v_i^1 | \mathrm{BM})$ to $\mathbf{G}_v^{-1}(\delta_i^1\ \delta_i^1)$ and (ii) add $\mathrm{Var}(v_i^2 | \mathrm{BM})$ to $(\delta_i^2\ \delta_i^2)$; (b) if at least one parent is known, then (i) compute T_i according to (23), (ii) compute D_i according to (24), (iii) compute W_i according to (25), and (iv) for each "defined" element (l, k) in Π_i, add element $\mathrm{W}_i(l, k)$ to $\mathbf{G}_v^{-1}$ at the position given by $\Pi_i(l, k)$.

NUMERICAL EXAMPLE

To illustrate how the theory and algorithms in this paper can be used for genetic evaluation by BLUP using marker and trait information in a multibreed population, we use the pedigree in Table 1. The pedigree consists of six individuals from a multibreed population with two purebred groups, B_1 and B_2, and two crossbred groups, $B_1 \times B_2$ and $B_1B_1 \times B_1B_2$. Individuals are ordered such that parents precede their progeny.

The mixed linear model

$$\boldsymbol{y} = \mathbf{X}_v \boldsymbol{\beta}_v + \mathbf{X}_u \boldsymbol{\beta}_u + \mathbf{Z}_v v^* + \mathbf{Z}_u \boldsymbol{u}^* + \boldsymbol{e} \tag{27}$$

will be used for genetic evaluation by BLUP, where $\boldsymbol{\beta}_v$ is a vector of purebred means for additive MQTL effects, $\boldsymbol{\beta}_u$ is a vector of the fixed effects, $\boldsymbol{v}^*$ and $\boldsymbol{u}^*$ are vectors of additive MQTL and RQTL effects deviated from their respective means, $\boldsymbol{e}$ is a vector of residuals, and X_v, $\mathbf{X}_u$, $\mathbf{Z}_u$, and $\mathbf{Z}_u$ are incidence matrices. For simplicity, assume that $\boldsymbol{\beta}_u$ contains only means of RQTL effects for pure breeds B_1 and B_2, *i.e.*, $\boldsymbol{\beta}_u' = [\eta_{B_1} \eta_{B_2}]$. From the definition of $\boldsymbol{v}^*$ and $\boldsymbol{u}^*$, it follows that each of $\boldsymbol{v}^*$ and $\boldsymbol{u}^*$ has null mean and that $\mathrm{Var}(\boldsymbol{v}^*) = \mathrm{Var}(\boldsymbol{v}) = (\mathbf{G}_v)$ and $\mathrm{Var}(\boldsymbol{u}^*) = \mathrm{Var}(\boldsymbol{u}) = (\mathbf{G}_u)$. Assume also that the residual (e) has null mean and variance $\mathbf{I}\sigma_e^2$.

For this numerical example, the following hypothetical values will be used: $\mu_{B_1} = -0.1$, $\mu_{B_2} = -0.3$, $\sigma_{vB_1}^2 = 0.29$, $\sigma_{vB_2}^2 = 0.81$, $\sigma_{uB_1}^2 = 1.2$, $\sigma_{uB_2}^2 = 1.6$, $\sigma_s^2 = 0.9$, σ_e^2

= 1.0. The estimation of these parameters are discussed in the discussion.

The best linear unbiased estimate (BLUE) of $\boldsymbol{\beta}_u$ and BLUP of $\boldsymbol{v}^*$ and of $\boldsymbol{u}^*$ can be obtained by solving the mixed model equations (Henderson 1973) given below

$$\begin{bmatrix} \mathbf{X}_u' \mathbf{X}_u & \mathbf{X}_u' \mathbf{Z}_v & \mathbf{X}_u' \mathbf{Z}_u \\ \mathbf{Z}_v' \boldsymbol{X}_u & \mathbf{Z}_v' \mathbf{Z}_v + \boldsymbol{G}_v^{-1}/\sigma_e^2 & \mathbf{Z}_v' \mathbf{Z}_u \\ \mathbf{Z}_u' \mathbf{X}_u & \mathbf{Z}_u' \mathbf{Z}_v & \mathbf{Z}_u' \mathbf{Z}_u + \mathbf{G}_u^{-1}/\sigma_e^2 \end{bmatrix} \begin{bmatrix} \boldsymbol{\beta}_u \\ \boldsymbol{v}^* \\ \boldsymbol{u}^* \end{bmatrix} = \begin{bmatrix} \mathbf{X}_u' (\boldsymbol{y} - \mathbf{X}_v \boldsymbol{\beta}_v) \\ \mathbf{Z}_v' (\boldsymbol{y} - \mathbf{X}_v \boldsymbol{\beta}_v) \\ \mathbf{Z}_u' (\boldsymbol{y} - \mathbf{X}_v \boldsymbol{\beta}_v) \end{bmatrix} \tag{28}$$

Construction of the incidence matrices and covariance matrices in (28) are presented in the following sections. To construct X_v and G_v requires conditional breed compositions $f_{B_l}^{i,k_i}$, and their computations are discussed next.

Computing conditional breed compositions $f_{B_l}^{i,k_i}$: Individuals 1 and 2 are founders from pure breed B_1, and 3 is a founder from pure breed B_2. Thus, their breed compositions are

$$\begin{bmatrix} f_{B_1}^{1,1} & f_{B_2}^{1,1} \\ f_{B_1}^{1,2} & f_{B_2}^{1,2} \end{bmatrix} = \begin{bmatrix} 1 & 0 \\ 1 & 0 \end{bmatrix}$$

$$\begin{bmatrix} f_{B_1}^{2,1} & f_{B_2}^{2,1} \\ f_{B_1}^{2,2} & f_{B_2}^{2,2} \end{bmatrix} = \begin{bmatrix} 1 & 0 \\ 1 & 0 \end{bmatrix}$$

and

$$\begin{bmatrix} f_{B_1}^{3,1} & f_{B_2}^{3,1} \\ f_{B_1}^{3,2} & f_{B_2}^{3,2} \end{bmatrix} = \begin{bmatrix} 0 & 1 \\ 0 & 1 \end{bmatrix}$$

For nonfounders 4, 5, and 6, their conditional breed compositions can be computed using recursive formula (6), given PDQs. The PDQs for 4, 5, and 6 (Wang *et al.* 1995) are

$$T_4 = \begin{bmatrix} 0.25 & 0.25 & 0.25 & 0.25 \\ 0.25 & 0.25 & 0.25 & 0.25 \end{bmatrix}$$

$$T_5 = \begin{bmatrix} 0.05 & 0.45 & 0.05 & 0.45 \\ 0.45 & 0.05 & 0.45 & 0.05 \end{bmatrix}$$

and

$$T_6 = \begin{bmatrix} 0.25 & 0.25 & 0.25 & 0.25 \\ 0.5 & 0.5 & 0 & 0 \end{bmatrix}$$

These PDQs are used now to compute conditional breed compositions $f_{B_l}^{i,k_i}$, for i = 4, 5, 6, using (6):

$$\begin{bmatrix} f_{B_1}^{4,1} & f_{B_2}^{4,1} \\ f_{B_1}^{4,2} & f_{B_2}^{4,2} \end{bmatrix} = T_4 \times \begin{bmatrix} f_{B_1}^{1,1} & f_{B_2}^{1,1} \\ f_{B_1}^{1,2} & f_{B_2}^{1,2} \\ f_{B_1}^{2,1} & f_{B_2}^{2,1} \\ f_{B_1}^{2,2} & f_{B_2}^{2,2} \end{bmatrix} = \begin{bmatrix} 1 & 0 \\ 1 & 0 \end{bmatrix}$$

$$\begin{bmatrix} f_{B_1}^{5,1} & f_{B_2}^{5,1} \\ f_{B_1}^{5,2} & f_{B_2}^{5,2} \end{bmatrix} = T_5 \times \begin{bmatrix} f_{B_1}^{3,1} & f_{B_2}^{3,1} \\ f_{B_1}^{3,2} & f_{B_2}^{3,2} \\ f_{B_1}^{2,1} & f_{B_2}^{2,1} \\ f_{B_1}^{2,2} & f_{B_2}^{2,2} \end{bmatrix} = \begin{bmatrix} 0.5 & 0.5 \\ 0.5 & 0.5 \end{bmatrix}$$

and

$$\begin{bmatrix} f_{B_1}^{6,1} & f_{B_2}^{6,1} \\ f_{B_1}^{6,2} & f_{B_2}^{6,2} \end{bmatrix} = T_6 \times \begin{bmatrix} f_{B_1}^{4,1} & f_{B_2}^{4,1} \\ f_{B_1}^{4,2} & f_{B_2}^{4,2} \\ f_{B_1}^{5,1} & f_{B_2}^{5,1} \\ f_{B_1}^{5,2} & f_{B_2}^{5,2} \end{bmatrix} = \begin{bmatrix} 0.75 & 0.25 \\ 1 & 0 \end{bmatrix}$$

Incidence matrices: Incidence matrix $\mathbf{X}_v$ is constructed such that $E(v_i^1) + E(v_i^2) = \mathbf{x}_{v_i}' \boldsymbol{\beta}_v$ where $\mathbf{x}_{v_i}'$, is row i of $\mathbf{X}_v$. From (4),

$$E(v_i^1) + E(v_i^2) = \begin{bmatrix} (f_{B_1}^{i,1} + f_{B_1}^{i,2}) & (f_{B_2}^{i,1} + f_{B_2}^{i,2}) \end{bmatrix} \begin{bmatrix} \mu_{B_1} \\ \mu_{B_2} \end{bmatrix}$$

Thus,

$$\mathbf{X}_v = \begin{bmatrix} 2 & 0 \\ 2 & 0 \\ 0 & 2 \\ 2 & 0 \\ 1 & 1 \\ 1.75 & 0.25 \end{bmatrix}$$

Incidence matrix $\mathbf{X}_u$ is constructed such that $E(u_i) = \mathbf{x}_{u_i}' \boldsymbol{\beta}_u$, where $\mathbf{x}_{u_i}'$ is row i of $\mathbf{X}_u$. From Thompson (1979),

$$E(u_i) = \begin{bmatrix} f_{B_1}^{i} & f_{B_2}^{i} \end{bmatrix} \begin{bmatrix} \eta_{B_1} \\ \eta_{B_2} \end{bmatrix}$$

where $f_{B_1}^i$ and $f_{B_2}^i$ are conditional breed compositions, given breed information only. Thus,

$$\mathbf{X}_u = \begin{bmatrix} 1 & 0 \\ 1 & 0 \\ 0 & 1 \\ 1 & 0 \\ 0.5 & 0.5 \\ 0.75 & 0.25 \end{bmatrix}$$

Matrix $\mathbf{Z}_v = \mathbf{I}_6 \otimes \mathbf{J}_2$ is the Kronecker product of an identity matrix of order 6 and a 2×1 vector of ones. Matrix $\mathbf{Z}_u$ is an identity matrix of order 6.

Constructing $\mathbf{G}_v$: Recall that individuals 1 and 2 are founders from pure breed B_1 and 3 is a founder from pure breed B_2 and that founders are unrelated and noninbred. Thus, the upper-left submatrix of $\mathbf{G}_v$ is diagonal and of order 6, with diagonal elements $\sigma^2_{vB_1}$, $\sigma^2_{vB_1}$, $\sigma^2_{vB_1}$, $\sigma^2_{vB_1}$, $\sigma^2_{vB_2}$, and $\sigma^2_{vB_2}$. For nonfounders 4, 5, and 6, this upper-left submatrix can be expanded by the tabular method using (20).

For individual 4, the matrix $\mathbf{q}_4'$ for use in (20) is

$$\mathbf{q}_4' = \begin{bmatrix} 0.25 & 0.25 & 0.25 & 0.25 & 0 & 0 \\ 0.25 & 0.25 & 0.25 & 0.25 & 0 & 0 \end{bmatrix}$$

The first six elements in rows 7 and 8 of $\mathbf{G}_v$ are computed as $\mathbf{q}_4'\mathbf{G}_3$ (Table 2); columns 7 and 8 are obtained by symmetry. Each of the two diagonal elements of $\mathbf{C}_4$ is computed using (11). Individual 4 is from pure breed B_1; therefore, each diagonal of $\mathbf{C}_4$ is $\sigma^2_{vB_1}$. Parents of 4 are unrelated, so off-diagonal elements of $\mathbf{C}_4$ are null. Thus,

$$\mathbf{C}_4 = \begin{bmatrix} 0.29 & 0 \\ 0 & 0.29 \end{bmatrix}$$

For individual 5, the matrix $\mathbf{q}_5'$ for use in (20) is

$$\mathbf{q}_5' = \begin{bmatrix} 0 & 0 & 0.05 & 0.45 & 0.05 & 0.45 & 0 & 0 \\ 0 & 0 & 0.45 & 0.05 & 0.45 & 0.05 & 0 & 0 \end{bmatrix}$$

Each diagonal element of $\mathbf{C}_5$ is computed using (11): $\mathrm{Var}(v_5^1 | \mathbf{BM}) = (0.29)(0.5) + (0.81)(0.5) + (-0.1 - (-0.3))^2(0.5)(0.5) = 0.559$. The $\mathrm{Var}(v_5^2 | \mathbf{BM})$ happens to have the same value as $\mathrm{Var}(v_5^1 | \mathrm{BM})$. Parents of 5 are unrelated, so off-diagonal elements of $\mathbf{C}_5$ are null. Thus,

$$\mathbf{C}_5 = \begin{bmatrix} 0.559 & 0 \\ 0 & 0.559 \end{bmatrix}$$

For individual 6, the matrix $\mathbf{q}_6'$ for use in (20) is

$$\mathbf{q}_6' = \begin{bmatrix} 0 & 0 & 0 & 0 & 0 & 0 & 0.25 & 0.25 & 0.25 & 0.25 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0.50 & 0.50 & 0 & 0 \end{bmatrix}$$

Parents of 6 are related, so now we have to compute the conditional covariance $\mathrm{Cov}(v_6^1, v_6^2 | \mathbf{BM})$, which requires $\mathrm{Cov}(v_4^{k4}, v_5^{k5} | \mathbf{BM})$, $\mathrm{Pr}(E_{k_4,k_5} | \mathbf{M})$, $\mathrm{E}(v_4^{k4} | \mathbf{BM})$, $\mathrm{E}(v_5^{k5} | \mathbf{BM})$, and $\mathrm{E}(v_6^{k6} | \mathbf{BM})$ for k_4, k_5, $k_6 = 1$ or 2. The $\mathrm{Cov}(v_4^{k4}, v_5^{k5} | \mathrm{BM})$ for k_4, $k_5 = 1$ or 2 have already been computed as $\mathrm{Cov}(v_4^1, v_5^1 | \mathrm{BM}) = \mathrm{Cov}(v_4^1, v_5^2 | \mathrm{BM}) = \mathrm{Cov}(v_4^2, v_5^1 | \mathrm{BM}) = \mathrm{Cov}(v_4^2, v_5^2 | \mathrm{BM}) = 0.036$. The $\mathrm{Pr}(E_{k_4,k_5} | \mathrm{M})$ can be computed using (17); for example,

$$\mathrm{Pr}(E_{11} | \mathbf{M}) = \frac{T_6(1,1)T_6(2,3)}{T_6(1,1) + T_6(1,2)} + \frac{T_6(1,3)T_6(2,1)}{T_6(1,3) + T_6(1,4)} = 0.25$$

Similarly, $\mathrm{Pr}(E_{12} | \mathbf{M}) = \mathrm{Pr}(E_{21} | \mathbf{M}) = \mathrm{Pr}(E_{22} | \mathbf{M}) = 0.25$. The conditional expected values of additive MQTL effects, $\mathrm{E}(v_4^{k4} | \mathrm{BM})$, $\mathrm{E}(v_5^{k5} | \mathrm{BM})$, and $\mathrm{E}(v_6^{k6} | \mathbf{BM})$, are computed using (4) as

$$\begin{aligned} \mathrm{E}(v_4^1 | \mathrm{BM}) &= \mathrm{E}(v_4^2 | \mathrm{BM}) = (-0.1)(1.0) \\ &\quad + (-0.3)(0.0) = -0.1 \\ \mathrm{E}(v_5^1 | \mathrm{BM}) &= \mathrm{E}(v_5^2 | \mathrm{BM}) = (-0.1)(0.5) \\ &\quad + (-0.3)(0.5) = -0.2 \\ \mathrm{E}(v_6^1 | \mathrm{BM}) &= (-0.1)(0.75) + (-0.3)(0.25) = -0.15 \\ \mathrm{E}(v_6^2 | \mathrm{BM}) &= (-0.1)(1.00) + (-0.3)(0.00) = -0.1 \end{aligned}$$

TABLE 2

The conditional covariance matrix ($\mathbf{G}_v$) for MQTL effects

	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	v_6^1	v_6^2
v_1^1	0.290	0.000	0.000	0.000	0.000	0.000	0.073	0.073	0.000	0.000	0.036	0.073
v_1^2	0.000	0.290	0.000	0.000	0.000	0.000	0.073	0.073	0.000	0.000	0.036	0.073
v_2^1	0.000	0.000	0.290	0.000	0.000	0.000	0.073	0.073	0.015	0.131	0.073	0.073
v_2^2	0.000	0.000	0.000	0.290	0.000	0.000	0.073	0.073	0.131	0.015	0.073	0.073
v_3^1	0.000	0.000	0.000	0.000	0.810	0.000	0.000	0.000	0.045	0.365	0.102	0.000
v_3^2	0.000	0.000	0.000	0.000	0.000	0.810	0.000	0.000	0.365	0.045	0.102	0.000
v_4^1	0.073	0.073	0.073	0.073	0.000	0.000	0.290	0.000	0.036	0.036	0.091	0.145
v_4^2	0.073	0.073	0.073	0.073	0.000	0.000	0.000	0.290	0.036	0.036	0.091	0.145
v_5^1	0.000	0.000	0.015	0.131	0.045	0.365	0.036	0.036	0.559	0.000	0.158	0.036
v_5^2	0.000	0.000	0.131	0.015	0.365	0.045	0.036	0.036	0.000	0.549	0.158	0.036
v_6^1	0.036	0.036	0.073	0.073	0.102	0.102	0.091	0.091	0.158	0.158	0.428	0.041
v_6^2	0.073	0.073	0.073	0.073	0.000	0.000	0.145	0.145	0.036	0.036	0.041	0.290

Therefore,

$$\mathrm{Cov}(v_6^1, v_6^2 \mid \mathbf{BM}) = \sum_{k_4=1}^{2} \sum_{k_5=1}^{2} [\mathrm{Cov}(v_4^{k_4}, v_5^{k_5} \mid \mathbf{BM}) + \mathrm{E}(v_4^{k_4} \mid \mathbf{BM})\mathrm{E}(v_5^{k_5} \mid \mathbf{BM})]$$

$$\Pr(\mathrm{E}_{k_4 k_5} \mid \mathbf{M}) - \mathrm{E}(v_6^1 \mid \mathbf{BM})\ \mathrm{E}(v_6^2 \mid \mathbf{BM}) = 0.041$$

Diagonal elements of $\mathbf{C}_6$ are computed using (11) as

$$\begin{aligned} \mathrm{Var}(v_6^1 \mid \mathbf{BM}) &= (0.29)(0.75) + (0.81)(0.25) \\ &\quad + (-0.1 - (-0.3))^2 (0.75)(0.25) = 0.4275 \\ (\mathrm{Var}(v_6^2 \mid \mathbf{BM}) &= (0.29)(1.00) + (0.81)(0.00) \\ &\quad + (-0.1 - (-0.3))^2 (1.00)(0.00) = 0.29) \end{aligned}$$

Thus,

$$\mathbf{C}_6 = \begin{bmatrix} 0.4275 & 0.041 \\ 0.041 & 0.29 \end{bmatrix}$$

The complete G_v is in Table 2.

BLUE and BLUP: The covariance matrix $\mathbf{G}_u$ for additive RQTL effects (Lo *et al.* 1993) is

$$\mathbf{G}_u = \begin{bmatrix} 1.2 & 0 & 0 & 0.6 & 0 & 0.3 \\ 0 & 1.2 & 0 & 0.6 & 0.6 & 0.6 \\ 0 & 0 & 1.6 & 0 & 0.8 & 0.4 \\ 0.6 & 0.6 & 0 & 1.2 & 0.3 & 0.75 \\ 0 & 0.6 & 0.8 & 0.3 & 1.4 & 0.85 \\ 0.3 & 0.6 & 0.4 & 0.75 & 0.85 & 1.9 \end{bmatrix}$$

Now all elements in (28) are available. The BLUE of $\boldsymbol{\beta}_u$ ($\hat{\boldsymbol{\beta}}_u$) and the BLUP of $\boldsymbol{v}^*$ ($\hat{\boldsymbol{v}}^*$) and of $\boldsymbol{u}^*$ ($\hat{\boldsymbol{u}}^*$) were obtained by solving (28):

$$\begin{aligned} \hat{\boldsymbol{\beta}}'_u &= [11.3049, 13.6325] \\ \hat{\boldsymbol{v}}^{*\prime} &= [0.0547, 0.0547, -0.0277, -0.0277, -0.0695, \\ &\quad -0.0695, 0.2773, 0.2773, -0.1570, -0.1570, \\ &\quad 0.2307, 0.3404] \\ \hat{\boldsymbol{u}}^{*\prime} &= [0.12050, -0.12050, 0.0000, 1.0023, -0.2094, \\ &\quad 1.1275] \end{aligned}$$

DISCUSSION

Linear-model methods use only information contained in means, variances, and covariances. When there is gametic disequilibrium between a marker locus (ML) and a closely linked QTL (MQTL), differences between means and between variances provide information on the association between the ML and the MQTL. In the absence of disequilibrium, however, differences between means and between variances do not provide any information on the association between the ML and the MQTL, but differences between covariances do provide information on this association. Some methods that have been proposed for ML-MQTL studies use only information contained in means (Lande and Thompson 1990; Weigel *et al.* 1990; Zhang and Smith 1992; Haley *et al.* 1994). Other methods use information contained in covariances (Fernando and Grossman 1989; Weller *et al.* 1990; Hoeschele 1993; Hoeschele and VanRaden 1993; Wang *et al.* 1995; van Arendonk *et al.* 1994). The method proposed in this paper for genetic evaluation by BLUP uses all information contained in means, variances, and covariances.

The conditional covariance matrix $\mathbf{G}_v$ is a function of purebred means and variances for additive MQTL effects, and $\mathbf{G}_u$ is a function of purebred variances and segregation variances for RQTL effects (Lo *et al.* 1993). Thus, genetic evaluation by BLUP requires purebred means $\boldsymbol{\beta}'_v = [\mu_{B_1}, \mu_{B_2}]$ and variances $(\sigma^2_{vB_1}, \sigma^2_{vB_2})$ for additive MQTL effects and purebred variances $(\sigma^2_{uB_1}, \sigma^2_{uB_2})$ and segregation variance for RQTL effects (σ^2_s). These parameters can be established by maximum likelihood, in principle, based on the theory and algorithms presented here.

For genetic evaluation by BLUP using only trait information in multibreed populations, Elzo (1990) and Lo *et al.* (1993) presented a theory to account for heterogeneity of variances among pure breeds and for segregation variances between pure breeds at the RQTL. Goddard (1992) proposed a method for genetic evaluation by BLUP using marker and trait information in multibreed populations. His model for means is the same as that presented here, but he uses the Westell method of phantom parents (Westell *et al.* 1988) to efficiently set up the mixed model equations. His model for variances, however, does not accommodate heterogeneous variances among pure breeds. Further, his formula, for the variance does not have the second term of (14), and thus the segregation variance is not properly modeled (M. E. Goddard, personal communication). Theory presented in this paper does account for heterogeneity of variances among pure breeds and for segregation variances between pure breeds at the MQTL and at the RQTL.

Theory presented here for use of marker information relies on results from Wang *et al.* (1995). For a purebred population, they gave an exact algorithm to construct $\mathbf{G}_v$ and to compute its inverse for complete marker data. They also proposed two approximate algorithms to construct $\mathbf{G}_v$ and to compute its inverse for incomplete marker data. For a multibreed population, the same approximations can be used to construct $\mathbf{G}_v$ and to compute its inverse forincomplete marker data.

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