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ABSORPTION OF EQUATIONS FOR NON-PARENTS FOR AN ANIMAL MODEL WITH MATERNAL EFFECTS AND GENETIC GROUPS¹

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ABSTRACT

Rules for forming the mixed-model equations for the reduced animal model with all relationships and including maternal effects have been set out by Quaas and Pollak. They also have shown how to simplify the mixed-model equations when genetic group effects are included in the model with what has become known as the Q-P transformation. Westell has given rules for calculating the coefficients for the Q-P transformed equations that are associated with the inverse of the numerator relationship matrix and genetic group effects. Those rules can be extended to include maternal effects and genetic groups for maternal as well as direct effects. As with the rules of Quaas and Pollak for the equations for the reduced animal model, a similar set of rules can be obtained for the genetic groups model after the Q-P transformation. The rules are derived easily by examining the algebraic results of absorbing the direct and maternal breeding value equations for non-parents into the parent breeding value, group and fixed effects equations. These rules involve Westell's rules and the inverse elements of the genetic (co)variance matrix for direct and maternal additive genetic effects. The rules make calculation of breeding values for parents for models including direct and maternal genetic group effects nearly as easy as for models without genetic group effects. Back solution for direct and maternal breeding values of non-parents similarly is as simple as when genetic group effects are not in the model.

(Key Words: Genetic Analysis, Transformation, Breeding Value, Genetic Models.)

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Introduction

Quaas and Pollak (1980) introduced the reduced animal model (**RAM**) for genetic evaluation using as a basic model the so-called animal model. The RAM is based on a model containing additive genetic value of the animal with the record. Essentially, RAM results from forming an equivalent model (Henderson, 1985) that gives mixed-model equations (**MME**) that are equivalent to those after absorbing equations for additive genetic values of non-parent animals. The computational advantages often are substantial, with many fewer equations and, more significantly, many fewer solutions and right-hand-sides, which are most efficiently kept in computer memory. Most genetic evaluation programs for beef cattle use RAM (Benyshek et al., 1988) rather than iterating on data, which is based usually on the full set of equations (Schaeffer and Kennedy, 1986a,b; Wiggans et al., 1988a,b).

Quaas and Pollak (1981) showed how to transform the MME when genetic group effects are in the model to calculate breeding values (genetic group effect plus deviation from mean group effect) rather than deviation of additive values from genetic group effect and genetic group effects separately. These equations will be denoted as the Q-P equations. This

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transformation reduces the number of coefficients in the MME and generally increases rate of convergence if the equations are solved by iteration (Van Vleck and Dwyer, 1985).

Westell (1984) discovered some simple rules for calculating the coefficients of the Q-P transformed equations. She augmented the MME to include base animals without records (Henderson, 1977), applied an appropriate Q-P transformation, absorbed the breeding value equations for the base animals, and then observed that the coefficients due to numerator relationships and group effects followed a simple pattern. The result is Westell's rules (Westell, 1984; Westell et al., 1984, 1988; Quaas, 1988). The resulting equations will be called the Q-P-W equations. The assignment of groups by Westell (1984) is similar to a development by Thompson (1979) and is the same as proposed by Robinson (1986). Westell's rules are as simple as Henderson's (1976) rules for calculating the inverse of the numerator relationship matrix. Group effects and numerator relationships are incorporated into genetic evaluations of dairy cattle that use the additive genetic animal model using Westell's rules (Wiggans et al., 1988a,b; Robinson and Chesnais, 1988).

Van Vleck (1990) extended the use of Westell's rules to a model including maternal effects with separate genetic group effects for both direct and maternal effects by including a final female ancestor without records in the solution vector for direct effects and by assigning both of her parents to the genetic group she would have been assigned for a model without maternal effects. Currently neither direct nor maternal genetic group effects are considered with an animal model for genetic evaluations of beef cattle performed routinely in the U.S. (L. L. Benyshek and J. S. Brinks, personal communications, 1989).

The purpose of this note is to show that by absorbing the non-parent equations of the Q-P-W equations that include direct and maternal group effects, coefficients for equations comparable to RAM equations without genetic group effects can be calculated easily.

Results

Mixed-Model Equations for Model with Direct and Maternal Genetic Effects

The mixed model considered by Van Vleck (1990) for animals with a vector of single records, y , is $y = X\beta + Za_1 + ZA_{10}Q_0g_a + Sm_1 + SA_{10}Q_0g_m + Sp + e$, where X associates fixed effects in β with y , Z associates additive genetic effects in a_1 with y , $ZA_{10}Q_0$ associates additive direct group effects in g_a with y , S associates maternal genetic effects in m_1 and nongenetic maternal effects in p with y , $SA_{10}Q_0$ associates maternal group effects in g_m with y , and e is a vector of independent residuals.

The fractional contribution of genetic group effects to breeding values is $A_{10}Q_0g_a$ for additive direct genetic effects and $A_{10}Q_0g_m$ for maternal genetic effects with Q_0 a matrix that assigns base animals to groups (Thompson, 1979; Westell, 1984; Westell et al., 1984, 1988; Robinson, 1986; Quaas, 1988; Wiggans et al., 1988a), where A_{10} is the matrix of the numerator relationships between animals in a_1 (or m_1) and base animals. Non-base animals without records are included in a_1 or m_1 by including corresponding zero columns in Z and S (see Henderson, 1977).

$$E \begin{pmatrix} y \\ a_1 \\ m_1 \\ p \\ e \end{pmatrix} = \begin{pmatrix} X\beta + ZA_{10}Q_0g_a + SA_{10}Q_0g_m \\ 0 \\ 0 \\ 0 \\ 0 \end{pmatrix}$$

For the same animals in a_1 and m_1

$$V \begin{pmatrix} a_1 \\ m_1 \\ p \\ e \end{pmatrix} = \begin{pmatrix} A_{11}\sigma_a^2 & A_{11}\sigma_{am} & 0 & 0 \\ A_{11}\sigma_{am} & A_{11}\sigma_m^2 & 0 & 0 \\ 0 & 0 & I\sigma_p^2 & 0 \\ 0 & 0 & 0 & I\sigma_e^2 \end{pmatrix}$$

where A_{11} is the numerator relationship matrix among animals in a_1 (and m_1), σ_a^2 , σ_m^2 , σ_p^2 , σ_e^2 , are variances for additive direct, additive maternal, nongenetic and nonadditive genetic maternal, and environmental effects and σ_{am} is the covariance between additive direct and additive maternal effects.

$$\text{Let } \begin{pmatrix} \alpha & \lambda \\ \lambda & \gamma \end{pmatrix} = \sigma_e^2 \begin{pmatrix} \sigma_a^2 & \sigma_{am} \\ \sigma_{am} & \sigma_m^2 \end{pmatrix}^{-1} \text{ and } \delta = \sigma_e^2 / \sigma_p^2.$$

$$\text{Let } W = \begin{pmatrix} W_{11} & W_{12} \\ W'_{12} & W_{22} \end{pmatrix} \text{ be the}$$

coefficients due to numerator relationships and group effects as calculated by Westell's rules where the subscript 1 corresponds to breeding value equations and the subscript 2 corresponds to group equations. Also, let $Q = A_{10}Q_0$ to simplify writing equations.

The resulting MME, the Q-P-W equations, (after multiplying left-hand and right-hand sides by σ_e^2) are:

$$\begin{pmatrix} X'X & X'S & X'Z & 0 & X'S & 0 \\ S'X & S'S+I\delta & S'Z & 0 & S'S & 0 \\ Z'X & Z'S & Z'Z+\alpha W_{11} & \alpha W_{12} & Z'S+\lambda W_{11} & \lambda W_{12} \\ 0 & 0 & \alpha W'_{12} & \alpha W_{22} & \lambda W'_{12} & \lambda W_{22} \\ S'X & S'S & S'Z+\lambda W_{11} & \lambda W_{12} & S'S+\gamma W_{11} & \gamma W_{12} \\ 0 & 0 & \lambda W'_{12} & \lambda W_{22} & \gamma W'_{12} & \gamma W_{22} \end{pmatrix} \begin{pmatrix} \hat{\beta} \\ \hat{p} \\ \hat{a}_1+Q\hat{g}_a \\ \hat{g}_a \\ \hat{m}_1+Q\hat{g}_m \\ \hat{g}_m \end{pmatrix} = \begin{pmatrix} X'y \\ S'y \\ Z'y \\ 0 \\ S'y \\ 0 \end{pmatrix}$$

The p equations for animals included in m that are not mothers will have zero coefficients and right-hand sides so that effective number of p equations is the number of mothers with progeny having records rather than the number of elements in m . A non-zero equation in p , however, will be associated with each pair of non-parent equations, for which absorption will be described in the next section.

In the Q-P-W form, all the parts of W with the same multiplier (α , λ or γ) are blocked together. The direct breeding value and direct group effects computationally are a subvector of solutions, as are maternal breeding values and maternal group effects.

Absorption of Non-Parent Equations

Let

$$\hat{a}^* = \begin{pmatrix} \hat{a}_1+Q\hat{g}_a \\ \hat{g}_a \end{pmatrix} \text{ and } \hat{m}^* = \begin{pmatrix} \hat{m}_1+Q\hat{g}_m \\ \hat{g}_m \end{pmatrix}$$

where the top parts of the vectors correspond to breeding values for direct and maternal effects.

To obtain the computing advantages comparable to those with RAM, the equations for direct, \hat{a}^* , and maternal, \hat{m}^* , breeding values of non-parents can be absorbed easily. A set of rules will be developed for calculating elements of the coefficient matrix and right-hand-side vector. Terms that will arise in the absorption of the non-parent equations (those will be contained in the top parts of \hat{a}^* and \hat{m}^*) will be defined here. The absorption will occur as a block for each non-parent corresponding to the animal's additive direct and additive maternal equations. The notation for the inverse of the diagonal block for a non-parent is:

$$\begin{pmatrix} \alpha^* & \lambda^* \\ \lambda^* & \gamma^* \end{pmatrix} = \begin{pmatrix} 1+D\alpha & D\lambda \\ D\lambda & D\gamma \end{pmatrix}^{-1} = \text{DEN} \begin{pmatrix} D\gamma & -D\lambda \\ -D\lambda & 1+D\alpha \end{pmatrix}$$

where $\text{DEN} = 1/[D(\gamma + \alpha D\gamma - \lambda D\lambda)]$

and according to the rules of Westell:

$D = 2$, if both parents are in a_i and the animal is not inbred (if inbred, then adjust as described by Quaas [1976, 1988].

$D = 4/3$, if one parent is in a_i and other parent is proxied by a group and

$D = 1$, if neither parent is in a_i and both parents are proxied by groups.

Terms which arise in the absorption will be assigned briefer symbols as follows:

$$\begin{aligned} \phi_0 &= 1 - \alpha^* \\ \phi_1 &= D(\alpha\alpha^* + \lambda\lambda^*)/2 = (1 - \alpha^*)/2 = \phi_0/2 \\ \phi_2 &= D(\lambda\alpha^* + \gamma\lambda^*)/2 = 0 \\ \phi_3 &= D^2(\alpha\alpha\alpha^* + 2\alpha\lambda\lambda^* + \lambda\lambda\gamma^*)/4 = (D\alpha + \alpha^* - 1)/4 \\ \phi_4 &= D^2(\alpha\lambda\alpha^* + \lambda\lambda\lambda^* + \alpha\gamma\lambda^* + \lambda\gamma\gamma^*)/4 \\ &= D\lambda/4 \\ \phi_5 &= D^2(\lambda\lambda\alpha^* + 2\lambda\gamma\lambda^* + \gamma\gamma\gamma^*)/4 = D\gamma/4 \end{aligned}$$

Note that some of these terms simplify considerable, especially with $\phi_2 = 0$. A reviewer pointed out these simplifications of ϕ_1 and ϕ_3 which further simplify the rules for absorbing equations of non-parents. These terms will change with each non-parent, depending on what D is. Advantage can be taken in computing in the non-inbred case that only three different values of ϕ_0 are possible. Only for an inbred animal, which can occur only if both parents are not proxied, will ϕ_0 not be predetermined.

Examination of the coefficients each non-parent record generates for the Westell form of the Q-P transformed equations leads directly to how to absorb the two equations for each non-parent. Some of the elements come from the least squares portion of MME and some from calculation of W .

For illustration, assume only fixed effect β_k is associated with record y_i of non-parent i that has father, s , and mother, j . If the father is assigned to a group, then s identifies the group of the father. Thus, the coefficients associated with non-parent, i , with record y_i are in Table 1.

TABLE 1. CONTRIBUTIONS TO COEFFICIENT MATRIX AND RIGHT-HAND-SIDE VECTOR ASSOCIATED WITH A NON-PARENT, i , THAT HAS FATHER (OR PROXY), s , AND MOTHER, j , AND THAT HAS RECORD, y_i , CONTAINING FIXED EFFECT, β_k

Equation (row)	Column								Right-hand side
	a_i^*	m_i^*	β_k	p_j	a_s^*	m_s^*	a_j^*	m_j^*	
a_j^*	$1+D\alpha$	$D\lambda$	1	1	$-D\alpha/2$	$-D\lambda/2$	$-D\alpha/2$	$1-D\lambda/2$	y_i
m_i^*	$D\lambda$	$D\gamma$	0	0	$-D\lambda/2$	$-D\gamma/2$	$-D\lambda/2$	$-D\gamma/2$	0
β_k	1	0	1	1	0	0	0	1	y_i
p_j	1	0	1	1	0	0	0	1	y_i
a_s^*	$D\alpha/2$	$-D\lambda/2$	0	0	$D\alpha/4$	$D\lambda/4$	$D\alpha/4$	$1-D\lambda/4$	0
m_s^*	$-D\lambda/2$	$D\gamma/2$	0	0	$D\lambda/4$	$D\gamma/4$	$D\lambda/4$	$D\gamma/4$	0
a_j^*	$-D\alpha/2$	$-D\lambda/2$	0	0	$D\alpha/4$	$D\lambda/4$	$D\alpha/4$	$D\lambda/4$	0
m_j^*	$1-D\lambda/2$	$-D\gamma/2$	1	1	$D\lambda/4$	$D\gamma/4$	$D\lambda/4$	$1+D\gamma/4$	y_i

TABLE 2. ELEMENTS, AFTER SIMPLIFICATION, CONTRIBUTED TO COEFFICIENT MATRIX AND RIGHT-HAND-SIDE VECTOR RESULTING FROM ABSORPTION OF EQUATIONS FOR NON-PARENT, i , THAT HAS FATHER (OR PROXY), s , AND MOTHER, j , AND THAT HAS RECORD, y_i , CONTAINING FIXED EFFECT, β_k

Equation (row)	Column						Right-hand side
	β_k	p_j	a_s^*	m_s^*	a_j^*	m_j^*	
β_k	ϕ_0	ϕ_0	$\phi_0/2$	0	$\phi_0/2$	ϕ_0	$\phi_0 y_i$
p_j		ϕ_0	$\phi_0/2$	0	$\phi_0/2$	ϕ_0	$\phi_0 y_i$
a_s^*			$\phi_0/4$	0	$\phi_0/4$	$\phi_0/2$	$.5\phi_0 y_i$
m_s^*	Symmetric			0	0	0	0
a_j^*					$\phi_0/4$	$\phi_0/2$	$.5\phi_0 y_i$
m_j^*						ϕ_0	$\phi_0 y_i$

Note that the mother of a non-parent is included in a_j and m_j (Van Vleck, 1990) and, thus, j will not identify a group. Further reflection and examination will reveal that no other records or relatives will contribute to the two equations for the non-parent, those for \hat{a}_i^* and \hat{m}_i^* . Thus, the two equations for \hat{a}_i^* and \hat{m}_i^* can be block-absorbed into the other cells shown in Table 1. The results of that absorption are in terms of ϕ 's, α , λ , γ , D and y_i .

Further examination reveals that some of these elements can be simplified. As mentioned earlier, the following equalities can be shown relatively easily by substituting for α^* , λ^* and γ^* terms in D , α , λ and γ . Thus, $\phi_2 = 0$, $D\lambda/4 - \phi_4 = 0$, $D\gamma/4 - \phi_5 = 0$. Table 2 shows the results of these identities and provides rules for computing elements to add to the cells of the coefficient matrix and right-hand sides for each non-parent.

Absorption results in new non-zero entries (fill) in four cells of the coefficient matrix: fixed effect by direct breeding values of father and mother and non-genetic maternal effect by direct breeding values of father and mother, but not for cells associated with maternal breeding value of sire. Only three kinds of coefficients are needed, although all depend on the value of D : $\phi_0 = 1 - \alpha^*$; $\phi_1 = (1 - \alpha^*)/2 = \phi_0/2$ and $D\alpha/4 - \phi_3 = \phi_0/4$. For each non-parent, a set of three coefficients needs to be calculated (ϕ_0 , $\phi_0/2$ and $\phi_0/4$) or taken from the set of three coefficients precalculated, corresponding to the D associated with the non-parent. Table 2 is a set of rules for processing a non-parent record to form the coefficient matrix, corresponding to a reduced animal model with direct and maternal genetic groups.

For completeness, Table 3 provides the rules for processing contributions to the absorbed equations for parents that have records. Some parents may not be base animals and may not have records. Rules for processing contributions of parents without records are in Table 4. The only difference between rules in Table 3 and in Table 4 is that animals without records do not contribute 1's to the cells associated with the least squares parts of the MME.

TABLE 3. ELEMENTS OF COEFFICIENT MATRIX AND RIGHT-HAND-SIDE VECTOR CONTRIBUTED BY A RECORD y_i OF A PARENT, i ; WITH SIRE (OR PROXY GROUP), s ; WITH DAM (OR PROXY GROUP), j . IF THE DAM IS A PROXY GROUP, THEN NOTHING IS ADDED TO RIGHT-HAND-SIDE FOR p_j OR TO ROWS AND COLUMNS ASSOCIATED WITH p_j

Equation (row)	Column								Right-hand side
	β_k	p_j	a_i^*	m_i^*	a_s^*	m_s^*	a_j^*	m_j^*	
β_k	1	1	1					1	y_i
p_j	1	1	1					1	y_i
a_i^*	1	1	$1 + D\alpha$	$D\lambda$	$-D\alpha/2$	$-D\lambda/2$	$-D\alpha/2$	$1 - D\lambda/2$	y_i
m_i^*			$D\lambda$	$D\gamma$	$D\lambda/2$	$-D\gamma/2$	$-D\lambda/2$	$-D\gamma/2$	0
a_s^*			$-D\alpha/2$	$-D\lambda/2$	$D\alpha/4$	$D\lambda/4$	$D\alpha/4$	$D\lambda/4$	0
m_s^*			$-D\lambda/2$	$-D\gamma/2$	$D\lambda/4$	$D\gamma/4$	$D\lambda/4$	$D\gamma/4$	0
a_j^*			$-D\alpha/2$	$-D\lambda/2$	$D\alpha/4$	$D\lambda/4$	$D\alpha/4$	$D\lambda/4$	0
m_j^*	1	1	$1 - D\lambda/2$	$-D\gamma/2$	$D\lambda/4$	$D\gamma/4$	$D\lambda/4$	$1 + D\gamma/4$	y_i

TABLE 4. ELEMENTS OF COEFFICIENT MATRIX CONTRIBUTED BY A PARENT WITHOUT A RECORD, *i*; WITH SIRE (OR PROXY), *s*; WITH DAM (OR PROXY GROUP), *j*

Equation (row)	Column						Right-hand side
	a_i^*	m_i^*	a_s^*	m_s^*	a_j^*	m_j^*	
a_i^*	$D\alpha$	$D\lambda$	$-D\alpha/2$	$-D\lambda/2$	$-D\alpha/2$	$-D\lambda/2$	0
m_i^*	$D\lambda$	$D\gamma$	$-D\lambda/2$	$-D\gamma/2$	$-D\lambda/2$	$-D\gamma/2$	0
a_s^*	$-D\alpha/2$	$-D\lambda/2$	$D\alpha/4$	$D\lambda/4$	$D\alpha/4$	$D\lambda/4$	0
m_s^*	$-D\lambda/2$	$-D\gamma/2$	$D\lambda/4$	$D\gamma/4$	$D\lambda/4$	$D\gamma/4$	0
a_j^*	$-D\alpha/2$	$-D\lambda/2$	$D\alpha/4$	$D\lambda/4$	$D\alpha/4$	$D\lambda/4$	0
m_j^*	$-D\lambda/2$	$-D\gamma/2$	$D\lambda/4$	$D\gamma/4$	$D\lambda/4$	$D\gamma/4$	0

Tables 2, 3 and 4 provide the rules for setting up the equivalent of the RAM equations. The final step is to add the ratio, $\delta = \sigma_e^2/\sigma_p^2$, to the diagonal coefficients of the equations for the nongenetic maternal effects.

The net result of the Q-P transformation, as pointed out by Quaas and Pollak (1980), is fewer equations and thus fewer total coefficients, although the remaining coefficient matrix will be slightly more dense. With one fixed factor (e.g., contemporary groups), after absorption non-zero coefficients result for the following four cells: fixed effect, direct breeding value of sire; fixed effect, direct breeding value of dam; nongenetic maternal effect of dam, direct breeding value of sire; and nongenetic maternal effect of dam, direct breeding value of dam. Absorption leads to contributions to right-hand sides for direct breeding values of sire and dam. If the sire and dam have records, then no new non-zero right-hand sides are generated by absorption of non-parent equations. Absorption of the direct and maternal breeding value equations for non-parents eliminates those two equations, including 13 non-zero (half-stored) coefficients and one non-zero right-hand side. The absorption also results in zero contributions to the (a_s^*, m_s^*) , (m_s^*, m_s^*) , (m_s^*, a_j^*) , and (m_s^*, m_j^*) cells, whereas non-zero coefficients are generated for those cells by a non-parent record. The (a_s^*, m_s^*) and (m_s^*, m_s^*) cells will likely fill anyway, but the other two probably will not. The net result of the absorption of each non-parent with one fixed factor is likely to be a reduction of two equations and solutions and 11 non-zero coefficients.

The effect on computing efficiency will depend on many factors, including memory capacity relative to number of equations. The blocks of coefficients corresponding to genetic groups may be quite dense. If non-parents are not absorbed, the right-hand sides for genetic groups are zero. Westell (1984) has described some computing strategies for a simpler model with the Q-P-W equations. Group solutions seemed to converge more slowly than other classes of solutions. Block iteration is an option because the block size is such that a one-time inversion is not costly. The group equations would be solved last so that the right-hand sides would be adjusted for other effects in those equations.

Backsolutions for Non-Parents

After solutions are obtained for parents, groups and fixed effects, the coefficients of the equations for a non-parent shown in the first two rows of Table 1 can be used to calculate the predicted breeding values for direct and maternal genetic effects. The coefficients to do the initial absorption and the solutions for other effects in the equations are needed. Thus, with the vector of solutions for the equations after absorption, the file of non-parents can be read to calculate solutions for breeding values.

For a particular D associated with animal *i*, calculate as for absorption

$$\begin{pmatrix} \alpha^* & \lambda^* \\ \lambda^* & \gamma^* \end{pmatrix} = \begin{pmatrix} 1+D\alpha & D\lambda \\ D\lambda & D\gamma \end{pmatrix}^{-1}$$

Then for, *s*, the sire or proxy group for the sire and, *j*, the dam and, *k*, the indicator of the fixed effect level:

$$\begin{pmatrix} \hat{a}_i^* \\ \hat{m}_i^* \end{pmatrix} = \begin{pmatrix} \alpha^* & \lambda^* \\ \lambda^* & \gamma^* \end{pmatrix} \begin{pmatrix} y_i - \hat{\beta}_k - \hat{p}_j - \hat{m}_j^* + D\alpha(\hat{a}_s^* + \hat{a}_j^*)/2 + D\lambda(\hat{m}_s^* + \hat{m}_j^*)/2 \\ D\lambda(\hat{a}_s^* + \hat{a}_j^*)/2 + D\gamma(\hat{m}_s^* + \hat{m}_j^*)/2 \end{pmatrix}$$

Multiple Traits

Obviously, extension of these rules to multiple traits can follow the same steps as was shown by Quaas and Pollak (1980). The terms will become more complex and will involve the environmental variances and covariances among the traits. If records are available for some traits and not for other traits for a non-parent, the inverse of the associated environmental variance-covariance matrix will involve only the traits with records. As in the Quaas and Pollak (1980) development, records of some traits may include maternal effects and others may not. The potential number of combinations of traits, missing records and maternal effects is such that no effort will be made here to develop a general set of rules. An obvious approach to a particular combination of traits and maternal effects is to set up symbolically the Westell equations for a non-parent and follow through the absorption, as was done here, or to develop rules from an equivalent model as done by Quaas and Pollak (1980) for the animal model without genetic group effects.

Example

The example is based on Figure 1. Animals C₁, C₂ and C₃ are non-parents. Animal S does not have a record but has two collateral descendants. Animals P₁ and P₂ do not have records but are included because they contribute maternal effects to records of animals B and C₁. Genetic groups have been assigned as proxy parents for nearest ancestors without records. Proxy parents of P₁ (also P₂) are assigned to the genetic group that P₁ (also P₂) would have been assigned for a model without maternal effects as suggested by Van Vleck (1990). Assume $\sigma_a^2 = 4$, $\sigma_{am} = .5$, $\sigma_m^2 = 1$, $\sigma_p^2 = 2$ and $\sigma_e^2 = 10$. Then $\alpha = 2.6$, $\lambda = 1.3$, $\gamma = 10.6$ and $\delta = 5.0$, where .F indicates a repeating fraction, .FFFF...F.

The direct and maternal solutions for an animal often are paired for computational convenience. Thus, for this example, the vector of solutions is:

$$(\hat{\mu} \hat{p}_B \hat{p}_{P_1} \hat{p}_{P_2} \hat{a}_B^* \hat{m}_B^* \hat{a}_{P_1}^* \hat{m}_{P_1}^* \hat{a}_{P_2}^* \hat{m}_{P_2}^* a_S^* \hat{m}_S^* \hat{g}_{a1} \hat{g}_{m1} \hat{g}_{a2} \hat{g}_{m2} \hat{a}_{C_1}^* \hat{m}_{C_1}^* \hat{a}_{C_2}^* \hat{m}_{C_2}^* \hat{a}_{C_3}^* \hat{m}_{C_3}^*)'$$

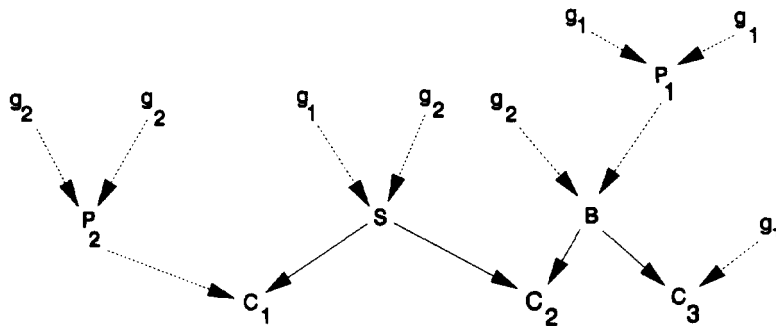


Figure 1. Diagram for example. Animals B, C₁, C₂ and C₃ have records of 130, 100, 110 and 120. Animals P₁, P₂, and B contribute maternal effects to records of B, C₁, C₂ and C₃. Genetic groups (g₁ or g₂) are assigned as shown: parents of most recent female ancestor without records are assigned to the group that female ancestor would have been assigned if no maternal effects influence the trait.

For calculation of W, and of α^* , λ^* , γ^* , the values of D are 2 for C_1 and C_2 , 4/3 for C_3 and B, and 1 for S, P_1 , and P_2 . Then for W calculated in order of B, P_1 , P_2 , S, g_1 , g_2 , C_1 , C_2 , C_3 :

W =	2.17	-.67	0	.50	.33	-.67	0	-1	-.67
		1.33	0	0	-1.0	.33	0	0	0
			1.50	.50	0	-1	-1	0	0
				2	-.5	-.5	-1	-1	0
					1.58	.25	0	0	-.67
Symmetric						1.58	0	0	0
							2	0	0
								2	0
									1.33

The full set of coefficients for equations including non-parents in order of the solution vector is:

4.0	2.0	1.0	1.0	1.0	2.0	0	1.0	0	1.0	0	0	0	0	0	0	1.0	0	1.0	0	1.0	0
	7.0	0	0	0	2.0	0	0	0	0	0	0	0	0	0	0	0	0	1.0	0	1.0	0
		6.0	0	1.0	0	0	1.0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
			6.0	0	0	0	0	1.0	0	0	0	0	0	0	0	1.0	0	0	0	0	0
				6.7	-2.8	-1.7	1.8	0	1.3	-.6	.8	-.4	-1.7	.8	0	0	-2.6	1.3	-1.7	.8	
					25.1	.8	-7.1	0	0	-.6	5.3	-.4	3.5	.8	-7.1	0	0	2.3	-10.6	1.8	-7.1
						3.5	-1.7	0	0	0	0	-2.6	1.3	.8	-.4	0	0	0	0	0	0
							15.2	0	0	0	0	1.3	-10.6	-.4	3.5	0	0	0	0	0	0
								4.0	-2.0	1.3	-.6	0	0	-2.6	1.3	-2.6	1.3	0	0	0	0
									17.0	-.6	5.3	0	0	1.3	-10.6	2.3	-10.6	0	0	0	0
										5.3	-2.6	-1.3	.6	-1.3	.6	-2.6	1.3	-2.6	1.3	0	0
											21.3	.6	-5.3	.6	-5.3	1.3	-10.6	1.3	-10.6	0	0
												4.2	-2.1	.6	-.3	0	0	0	0	-1.7	.8
													16.8	-.3	2.6	0	0	0	0	.8	-7.1
														4.2	-2.1	0	0	0	0	0	0
															16.8	0	0	0	0	0	0
																6.3	-2.6	0	0	0	0
																	21.3	0	0	0	0
																		6.3	-2.6	0	0
																			21.3	0	0
																				4.5	-1.7
																					14.2

The right-hand-side vector is shown in the left column of Table 5.

Two Lagrange multiplier equations were used to obtain an inverse of the coefficient matrix and a direct set of solutions to the equations. These solutions are shown in the second column of Table 5. The constraint equations were $\hat{g}_{a1} + \hat{g}_{a2} = 0$ and $\hat{g}_{m1} + \hat{g}_{m2} = 0$.

The rules shown in Tables 2, 3 and 4 were used to set up the reduced equations for the same example.

For parent with record, B, with sire in group 2 and dam, P_1 ; the D value is 4/3 so that $\alpha^* = .231$, $\lambda^* = .029$, $\gamma^* = .074$, and $\phi_0 = .769$. Contributions to right-hand sides: 130 to μ , p_{P_1} , \hat{a}_B^* , $\hat{m}_{P_1}^*$.

Contributions to the coefficient matrix are (without repeating the symmetrical off-diagonal terms):

1 to (μ with μ , p_{P_1} , a_B^* , $m_{P_1}^*$), with (p_{P_1} with p_{P_1} , a_B^* , $m_{P_1}^*$)

4.556 to (a_B^* , a_B^*)

-1.778 to (a_B^* with $m_{P_1}^*$, $a_{P_1}^*$, g_{a2})

1.889 to (a_B^* , $m_{P_1}^*$)

TABLE 5. RIGHT-HAND-SIDE VECTORS AND SOLUTION VECTORS FOR EXAMPLE FOR FULL SET OF EQUATIONS AND AFTER USE OF RULES TO OBTAIN EQUATIONS AFTER ABSORPTION OF EQUATIONS FOR NON-PARENTS.^a

Symbolic solution	Before absorption		Absorbed equations	
	Right-hand sides	Solutions	Right-hand sides	Solutions
μ	460	115.33	397.3	115.33
p,B	230	-.49	184.0	-.49
p,P ₁	130	.24	130.0	.24
p,P ₂	100	.24	83.3	.24
A*,B	130	-.09	222.0	-.09
m*,B	230	-.18	184.0	-.18
A*,P ₁	0	7.60	0	7.60
m*,p ₁	130	13.30	130.0	13.30
a*,P ₂	0	-7.29	41.7	-7.29
m*,P ₂	100	-13.15	83.3	-13.15
a*,S	0	-.49	87.5	-.49
m*,S	0	-.06	0	-.06
g ₁ ,a	0	7.60	46.2	7.60
g ₁ ,m	0	13.30	0	13.30
g ₂ ,a	0	-7.60	0	-7.60
g ₂ ,m	0	-13.30	0	-13.30
a*,C ₁	100	-3.65		
m*,C ₁	0	-6.57		
a*,C ₂	110	-1.02		
m*,C ₂	0	-.21		
a*,C ₃	120	4.12		
m*,C ₃	0	6.60		
Lagrange	0	.00	0	0
multipliers	0	.00	0	0

^ap_k is permanent maternal environmental effect for animal k. a*,k is direct breeding value, a+Qg_a, for animal k. m*,k is maternal breeding value, m+Qg_m, for animal k. g_i are group effects, direct = a and maternal = m.

$$\begin{aligned}
 &.889 \text{ to } (a_B^*, g_{m2}), (m_B^* \text{ with } a_{P_1}^*, g_{a2}), (a_{P_1}^*, \text{ with } a_{P_1}^*, g_{a2}), (g_{a2}, g_{a2}) \\
 &14.222 \text{ to } (m_B^*, m_B^*) \\
 &-7.111 \text{ to } (m_B^* \text{ with } m_{P_1}^*, g_{m2}) \\
 &-.444 \text{ to } (a_{P_1}^* \text{ with } m_{P_1}^*, g_{m2}), (m_{P_1}^*, g_{a2}), (g_{a2}, g_{m2}) \\
 &4.556 \text{ to } (m_{P_1}^*, m_{P_1}^*) \\
 &3.556 \text{ to } (m_{P_1}^*, g_{m2}), (g_{m2}, g_{m2}).
 \end{aligned}$$

For parent without record, P₁, with sire and dam both in group 1; the D value is 1 so that $\alpha^* = .286$, $\lambda^* = .036$, $\gamma^* = .098$, and $\phi_0 = .714$. Contributions to right-hand sides: none.

Contributions to coefficient matrix:

$$\begin{aligned}
 &2.667 \text{ to } (a_{P_1}^*, a_{P_1}^*), (g_{a1}, g_{a1}) \\
 &-1.333 \text{ to } (a_{P_1}^*, m_{P_1}^*), (g_{a1}, g_{m1}) \\
 &-2.667 \text{ to } (a_{P_1}^*, g_{a1}) \\
 &1.333 \text{ to } (a_{P_1}^*, g_{m1}), (m_{P_1}^*, g_{a1}) \\
 &10.667 \text{ to } (m_{P_1}^*, m_{P_1}^*), (g_{m1}, g_{m1}) \\
 &-10.667 \text{ to } (m_{P_1}^*, g_{m1}).
 \end{aligned}$$

The accumulated right-hand sides are in the third column of Table 5 and the solutions using the same two Lagrange multiplier constraints as for the full set of equations are in the last column of Table 5. The solutions for the parent animals must be, and are, the same as for the full set of equations. If the non-parent block of the full set of equations had been absorbed as a block, the result naturally would be the same.

Back solutions can be obtained from the solutions for parent breeding values, nongenetic maternal effects and fixed effects.

For C_1 with $D\alpha/2 = 2.6$, $D\lambda/2 = -1.3$, $D\gamma/2 = 10.6$:

$$\begin{pmatrix} a_{c_1}^* \\ m_{c_1}^* \end{pmatrix} = \begin{pmatrix} .1667 & .0208 \\ .0208 & .0495 \end{pmatrix} \begin{pmatrix} 100-115.3343-.2432+13.1459-2.6667(.4963+7.2948)+1.3333(.0608+13.1459) \\ 1.3333(7.7811)-10.6667(13.2067) \end{pmatrix}$$

so that $a_{c_1}^* = -3.64$ and $m_{c_1}^* = -6.58$, the same as for the full model except for differences caused by rounding in the example to four decimal places.

Implications

The rules described here for absorbing non-parent equations will allow animal model evaluations that include maternal effects and genetic groups for both direct and maternal effects to be done essentially as easily as reduced animal model evaluations are now done that do not consider genetic group effects. Because the genetic group effects attempt to account for selection on ancestors that do not have records, the evaluations with group effects should be more accurate than evaluations not considering such selection effects. The advantages of the reduced animal model are retained. The number of equations is reduced by twice the number of non-parents (which often make up a large part of a data set). The memory requirements for efficient computing are reduced because the non-parent solutions are not needed in the basic analysis. Non-parent solutions are easily obtained from a single pass of the non-parent records after solutions for the reduced equations have reached a satisfactory degree of convergence.

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