

ANIMAL BREEDING NOTES

CHAPTER 19

DIRECT AND MATERNAL GENETIC EFFECTS MODELS

Some traits are affected not only by an animals' ability to perform, but also by the environment provided by its dam. Examples of these traits are birth weight (BW), weaning weight (WW), and first calf calving ease (CE1). Thus, models used to obtain predictions of genetic values for these traits must account for both direct genetic effects (i.e., an animal's own ability to perform), and for maternal effects. Maternal effects are genetic to the dam and environmental to her progeny.

Direct and maternal animal models

If parents and nonparents have **several** records each, a direct and maternal genetic effects model (**DMM**) can be constructed by putting together two simple repeatability models (**SRM**), one for direct genetic effects and another one for maternal effects (**DMM1**):

$$\begin{aligned}
 y &= Xb + Z_{id} u_{id} + Z_{im} u_{im} + Z_{ip} p_{id} + Z_{dp} p_{dm} + (e_{id} + e_{dm}) \\
 E[y] &= Xb
 \end{aligned}$$

$$\text{var} \begin{bmatrix} u_{id} \\ u_{im} \\ \text{-----} \\ p_{id} \\ p_{dm} \\ \text{-----} \\ e_{id} + e_{dm} \end{bmatrix} = \begin{bmatrix} A\sigma_{dd} & A\sigma_{dm} & | & 0 & 0 & | & 0 \\ A\sigma_{md} & A\sigma_{mm} & | & 0 & 0 & | & 0 \\ \text{----} & \text{----} & | & \text{----} & \text{----} & | & \text{-----} \\ 0 & 0 & | & I\sigma_{E_{pd}}^2 & 0 & | & 0 \\ 0 & 0 & | & 0 & I\sigma_{E_{pm}}^2 & | & 0 \\ \text{----} & \text{----} & | & \text{----} & \text{----} & | & \text{-----} \\ 0 & 0 & | & 0 & 0 & | & I(\sigma_{ed}^2 + \sigma_{em}^2) \end{bmatrix}$$

$$= \begin{bmatrix} Ag_{11} & Ag_{12} & | & 0 & 0 & | & 0 \\ Ag_{21} & Ag_{22} & | & 0 & 0 & | & 0 \\ --- & --- & | & --- & --- & | & --- \\ 0 & 0 & | & I\gamma_1 & 0 & | & 0 \\ 0 & 0 & | & 0 & I\gamma_2 & | & 0 \\ --- & --- & | & --- & --- & | & --- \\ 0 & 0 & | & 0 & 0 & | & I \end{bmatrix} \sigma_e^2$$

where

$$g_{11} = \frac{\sigma_{dd}}{(\sigma_{ed}^2 + \sigma_{em}^2)}$$

$$g_{12} = \frac{\sigma_{dm}}{(\sigma_{ed}^2 + \sigma_{em}^2)} = g_{21}$$

$$g_{22} = \frac{\sigma_{mm}}{(\sigma_{ed}^2 + \sigma_{em}^2)}$$

$$\gamma_1 = \frac{\sigma_{E_{pd}}^2}{(\sigma_{ed}^2 + \sigma_{em}^2)}$$

$$\gamma_2 = \frac{\sigma_{E_{pm}}^2}{(\sigma_{ed}^2 + \sigma_{em}^2)}$$

$$\sigma_e^2 = \sigma_{ed}^2 + \sigma_{em}^2$$

and

σ_{dd} = additive direct genetic variance,

σ_{dm} = additive genetic covariance between direct and maternal effects, and

σ_{mm} = additive maternal genetic variance.

where the meaning of subscripts is:

i_d = animal direct genetic effects,
 i_m = animal maternal genetic effects,
 d_m = dam maternal genetic effects,
 i_p = animal permanent environmental effects, and
 d_p = dam permanent environmental effects.

Vectors are defined as:

y = vector of records,
 b = vector of unknown fixed effects,
 u = vector of unknown random additive genetic effects,
 p = vector of unknown random permanent environment effects,
 e = vector of unknown residual effects.

Matrices X and Z are incidence matrices relating records to fixed and to random effects, respectively.

Matrices Z_{i_d} and Z_{i_m} contain **columns of zeroes for animals without records**.

The same, i.e., **all**, animals are represented in vectors u_{i_d} and u_{i_m} , but **only those with records** are included in p_{i_d} and p_{d_m} .

Matrix A is the matrix of additive genetic relationships (i.e., the numerator relationship matrix).

The **MME for the DMM1** are:

$$\begin{bmatrix}
 X'X & X'Z_{id} & X'Z_{im} & X'Z_{ip} & X'Z_{dp} \\
 Z_{id}'X & Z_{id}'Z_{id} + A^{-1}g^{11} & Z_{id}'Z_{im} + A^{-1}g^{12} & Z_{id}'Z_{ip} & Z_{id}'Z_{dp} \\
 Z_{im}'X & Z_{im}'Z_{id} + A^{-1}g^{12} & Z_{im}'Z_{im} + A^{-1}g^{22} & Z_{im}'Z_{ip} & Z_{im}'Z_{dp} \\
 Z_{ip}'X & Z_{ip}'Z_{id} & Z_{ip}'Z_{im} & Z_{ip}'Z_{ip} + I\gamma_1^{-1} & Z_{ip}'Z_{dp} \\
 Z_{dp}'X & Z_{dp}'Z_{id} & Z_{dp}'Z_{im} & Z_{dp}'Z_{ip} & Z_{dp}'Z_{dp} + I\gamma_2^{-1}
 \end{bmatrix}
 \begin{bmatrix}
 b \\
 u_{id} \\
 u_{im} \\
 p_{id} \\
 p_{dm}
 \end{bmatrix}
 =
 \begin{bmatrix}
 X'y \\
 Z_{id}'y \\
 Z_{im}'y \\
 Z_{ip}'y \\
 Z_{dp}'y
 \end{bmatrix}$$

Remarks:

$$Z_{id} = [0 \quad Z_{ip}]$$

$$Z_{im} = [0 \quad Z_{dm} \quad 0]$$

\uparrow \uparrow
 parents nonparents
 without
 records

In many instances, **animals (can) have only a single observation per trait**, e.g., BW, WW. In such cases, $Z_{ip} = I$, and because p_{id} is **uncorrelated** to the other random effects in the **DMM1**, it can be placed in the residual term. Thus, the **DMM1** becomes **DMM2**:

$$y = Xb + Z_{id} u_{id} + Z_{im} u_{im} + Z_{dp} p_{dm} + (p_{id} + e_{id} + e_{dm})$$

$$E[y] = Xb$$

$$\text{var} \begin{bmatrix} u_{id} \\ u_{im} \\ \text{-----} \\ p_{dm} \\ p_{id} + e_{id} + e_{dm} \end{bmatrix} = \begin{bmatrix} Ag_{11} & Ag_{12} & | & 0 & 0 \\ Ag_{21} & Ag_{22} & | & 0 & 0 \\ \text{-----} & \text{-----} & | & \text{---} & \text{--} \\ 0 & 0 & | & I\gamma & 0 \\ 0 & 0 & | & 0 & I \end{bmatrix} \sigma_e^2$$

where

$$\sigma_e^2 = \sigma_{E_{pd}}^2 + \sigma_{e_d}^2 + \sigma_{e_m}^2$$

$$g_{11} = \frac{\sigma_{dd}}{\sigma_e^2}$$

$$g_{12} = \frac{\sigma_{dm}}{\sigma_e^2} = g_{21}$$

$$g_{22} = \frac{\sigma_{mm}}{\sigma_e^2}$$

$$\gamma = \frac{\sigma_{E_{pm}}^2}{\sigma_e^2}$$

The **MME for the DMM2** are:

$$\begin{bmatrix} X'X & X'Z_{id} & X'Z_{im} & X'Z_{dp} \\ Z_{id}'X & Z_{id}'Z_{id} + A^{-1}g^{11} & Z_{id}'Z_{im} + A^{-1}g^{12} & Z_{id}'Z_{dp} \\ Z_{im}'X & Z_{im}'Z_{id} + A^{-1}g^{12} & Z_{im}'Z_{im} + A^{-1}g^{22} & Z_{im}'Z_{dp} \\ Z_{dp}'X & Z_{dp}'Z_{id} & Z_{dp}'Z_{im} & Z_{dp}'Z_{dp} + I\gamma^{-1} \end{bmatrix} \begin{bmatrix} b \\ u_{id} \\ u_{im} \\ p_{dm} \end{bmatrix} = \begin{bmatrix} X'y \\ Z_{id}'y \\ Z_{im}'y \\ Z_{dp}'y \end{bmatrix}$$

Remark: $\{g_{ij}\}$ from **DMM2** $\neq \{g_{ij}\}$ from **DMM1** and γ from **DMM2** $\neq \gamma_2$ from **DMM1** because

$$\sigma_e^2 = \begin{cases} \sigma_{e_d}^2 + \sigma_{e_m}^2 & \text{for DMM1} \\ \sigma_{E_{pd}}^2 + \sigma_{e_d}^2 + \sigma_{e_m}^2 & \text{for DMM2} \end{cases}$$

Direct and maternal reduced animal models

The **RAM** corresponding to the **DMM2**, i.e., the **DM2RAM**, is:

$$\begin{bmatrix} y_p \\ y_n \end{bmatrix} = \begin{bmatrix} X_p \\ X_n \end{bmatrix} b + \begin{bmatrix} Z_{pd} \\ \frac{1}{2} P_{np,d} \end{bmatrix} u_{pd} + \begin{bmatrix} Z_{pm} \\ Z_{nm} \end{bmatrix} u_{pm} + \begin{bmatrix} Z_{pdp} \\ Z_{ndp} \end{bmatrix} p_{dm} + \begin{bmatrix} p_{pd} + e_{pd} + e_{pm} \\ \phi_{nd} + p_{nd} + e_{nd} + e_{nm} \end{bmatrix}$$

$$E \begin{bmatrix} y_p \\ y_n \end{bmatrix} = \begin{bmatrix} X_p \\ X_n \end{bmatrix} b$$

$$\text{var} \begin{bmatrix} u_{pd} \\ u_{pm} \\ \text{-----} \\ p_{dm} \\ \text{-----} \\ p_{pd} + e_{pd} + e_{pm} \\ \phi_{nd} + p_{nd} + e_{pd} + e_{pn} \end{bmatrix} = \begin{bmatrix} A_{pp} g_{11} & A_{pp} g_{12} & | & 0 & | & 0 & & 0 \\ A_{pp} g_{12} & A_{pp} g_{22} & | & 0 & | & 0 & & 0 \\ \text{-----} & \text{-----} & | & -- & | & -- & \text{-----} & \\ 0 & 0 & | & I\gamma & | & 0 & & 0 \\ \text{-----} & \text{-----} & | & -- & | & -- & \text{-----} & \\ 0 & 0 & | & 0 & | & I & & 0 \\ 0 & 0 & | & 0 & | & 0 & D_{nd} g_{11} + I & \end{bmatrix} \sigma_e^2$$

where

$$\sigma_e^2 = \sigma_{E_{pd}}^2 + \sigma_{e_d}^2 + \sigma_{e_m}^2$$

$$g_{11} = \frac{\sigma_{dd}}{\sigma_e^2}$$

$$g_{12} = \frac{\sigma_{dm}}{\sigma_e^2} = g_{21}$$

$$g_{22} = \frac{\sigma_{mm}}{\sigma_e^2}$$

$$\gamma = \frac{\sigma_{E_{pm}}^2}{\sigma_e^2}$$

A_{pp} = numerator relationship matrix among parents

$D_n = \text{diag} \{d_{ii}\}$

$D_n = \text{diag} \left\{ 1 - \delta_{s_i} (1/4 a_{s_i s_i}) - \delta_{d_i} (1/4 a_{d_i d_i}) \right\}$

where

$$\delta_{s_i} = \begin{cases} 1 & \text{if } s_i \text{ is known} \\ 0 & \text{else} \end{cases}$$

$$\delta_{d_i} = \begin{cases} 1 & \text{if } d_i \text{ is known} \\ 0 & \text{else} \end{cases}$$

y_p = vector of records of parents

y_n = vector of records of nonparents

b = vector of unknown fixed effects

u_{pd} = vector of unknown random additive direct genetic effects of parents

u_{pm} = vector of unknown random additive maternal genetic effects of parents

p_{dm} = vector of unknown random maternal dam permanent environment effects

p_{pd} = vector of unknown random direct parent permanent environment effects

p_{nd} = vector of unknown random direct nonparent permanent environment effects

ϕ_{nd} = vector of Mendelian sampling of nonparent direct additive genetic effects

where

$$\phi_{n_i d} = \begin{cases} \frac{1}{2} \epsilon_{s_i d} + \frac{1}{2} \epsilon_{d_i d} & \text{if } s_i \text{ and } d_i \text{ are known} \\ \frac{1}{2} u_{d_i d} + \frac{1}{2} \epsilon_{s_i d} + \frac{1}{2} \epsilon_{d_i d} & \text{if } s_i \text{ is known only} \\ \frac{1}{2} u_{s_i d} + \frac{1}{2} \epsilon_{s_i d} + \frac{1}{2} \epsilon_{d_i d} & \text{if } d_i \text{ is known only} \\ u_{n_i d} & \text{if } s_i \text{ and } d_i \text{ are unknown} \end{cases}$$

e_{pd} = vector of unknown random direct (maternal) residual effects of parents

e_{nd} = vector of unknown random direct residual effects of nonparents

e_{nm} = vector of unknown random maternal residual effects of nonparents

X_p = incidence matrix relating parent records to b

X_n = incidence matrix relating nonparent records to b

Z_{pd} = incidence matrix relating parent records to u_{pd}

$P_{np,d}$ = incidence matrix relating nonparent records to u_{pd}

Z_{pm} = incidence matrix relating parent records to u_{pm} ,

Z_{nm} = incidence matrix relating nonparent records to u_{pm}

Z_{pdp} = incidence matrix relating parent records to p_{dm}

Z_{ndp} = incidence matrix relating nonparent records to p_{dm}

Remarks:

(i) The i^{th} row of the Z_{pd} has a 1 in the j^{th} column corresponding the j^{th} parent with a record.

(ii) The i^{th} row of $P_{np,d}$ has a 1 in the s_i^{th} column, for the sire of nonparent i , if s_i is known, and another 1 in the d_i^{th} column, for the dam of nonparent i , if d_i is known.

(iii) The i^{th} rows of Z_{pm} , Z_{nm} , Z_{pdp} and Z_{ndp} have a 1 in the column corresponding to the dam of the i^{th} individual.

The **MME for the DM2RAM** are:

$$\left[\begin{array}{cc|cc} X_p'X_p + X_n'R_n^{-1}X_n & & X_p'Z_{pd} + X_n'R_n^{-1}P_{np,d}(\frac{1}{2}) & \\ Z_{pd}'X_p + (\frac{1}{2})P_{np,d}'R_n^{-1}X_n & & Z_{pd}'Z_{pd} + (\frac{1}{2})P_{np,d}'R_n^{-1}P_{np,d}(\frac{1}{2}) + A_{pp}^{-1}g^{11} & \\ Z_{pm}'X_p + Z_{nm}'R_n^{-1}X_n & & Z_{pm}'Z_{pd} + Z_{nm}'R_n^{-1}P_{np,d}(\frac{1}{2}) + A_{pp}^{-1}g^{12} & \\ Z_{pdp}'X_p + Z_{ndp}'R_n^{-1}X_n & & Z_{pdp}'Z_{pd} + Z_{ndp}'R_n^{-1}P_{np,d}(\frac{1}{2}) & \\ & & & \\ & & X_p'Z_{pm} + X_n'R_n^{-1}P_{nd} & \\ & & X_p'Z_{pdp} + X_n'R_n^{-1}Z_{ndp} & \\ Z_{pd}'Z_{pm} + (\frac{1}{2})P_{np,d}'R_n^{-1}Z_{nm} + A_{pp}^{-1}g^{12} & & Z_{pd}'Z_{pdp} + (\frac{1}{2})P_{np,d}'R_n^{-1}Z_{ndp} & \\ Z_{pm}'Z_{pm} + Z_{nm}'R_n^{-1}Z_{nm} + A_{pp}^{-1}g^{22} & & Z_{pm}'Z_{pdp} + Z_{nm}'R_n^{-1}Z_{ndp} & \\ Z_{pdp}'Z_{pm} + Z_{ndp}'R_n^{-1}P_{nd} & & Z_{pdp}'Z_{pdp} + Z_{ndp}'R_n^{-1}Z_{ndp} + I\gamma^{-1} & \end{array} \right]$$

[19-9]

$$\begin{bmatrix} \mathbf{b} \\ \mathbf{u}_{pd} \\ \mathbf{u}_{pm} \\ \mathbf{p}_{dm} \end{bmatrix} = \begin{bmatrix} \mathbf{X}_p' \mathbf{y}_p + \mathbf{X}_n' \mathbf{R}_n^{-1} \mathbf{y}_n \\ \mathbf{Z}_{pd}' \mathbf{y}_p + (\frac{1}{2}) \mathbf{P}_{np,d}' \mathbf{R}_n^{-1} \mathbf{y}_n \\ \mathbf{Z}_{pm}' \mathbf{y}_p + \mathbf{Z}_{nm}' \mathbf{R}_n^{-1} \mathbf{y}_n \\ \mathbf{Z}_{pdp}' \mathbf{y}_p + \mathbf{Z}_{ndp}' \mathbf{R}_n^{-1} \mathbf{y}_n \end{bmatrix}$$

where

$$\mathbf{R}_n^{-1} = (\mathbf{D}_{nd} \mathbf{g}_{11} + \mathbf{I})^{-1}$$

Backsolutions for nonparents in the DM2RAM

(i) Additive direct genetic effects

$$\begin{bmatrix} \hat{\mathbf{u}} \\ \text{---} \\ \hat{\mathbf{e}} \end{bmatrix} = \begin{bmatrix} \hat{\mathbf{u}}_{pd} \\ \hat{\mathbf{u}}_{pm} \\ \hat{\mathbf{p}}_{dm} \\ \text{---} \\ \hat{\mathbf{e}}_p \\ \hat{\mathbf{e}}_n \end{bmatrix}$$

$$\hat{\mathbf{u}}_{nd} = \mathbf{C}_{ud} \mathbf{G}^{-1} \hat{\mathbf{u}} + \mathbf{C}_{ed} \mathbf{R}^{-1} \hat{\mathbf{e}}$$

$$\mathbf{C}_{ud} = \text{cov}(\mathbf{u}_{nd}, [\mathbf{u}_{pd}' \quad \mathbf{u}_{pm}' \quad \mathbf{p}_{dm}'])$$

$$= \text{cov}(\frac{1}{2} \mathbf{P}_{np,d} \mathbf{u}_{pd} + \phi_{nd}, [\mathbf{u}_{pd}' \quad \mathbf{u}_{pm}' \quad \mathbf{p}_{dm}'])$$

$$= \left[\frac{1}{2} \mathbf{P}_{np,d} \mathbf{A}_{pp} \mathbf{g}_{11} \quad \frac{1}{2} \mathbf{P}_{np,d} \mathbf{A}_{pp} \mathbf{g}_{12} \quad 0 \right] \sigma_e^2$$

$$G^{-1} = \left[\begin{array}{cc|c} A_{pp}^{-1} g^{11} & A_{pp}^{-1} g^{12} & 0 \\ A_{pp}^{-1} g^{12} & A_{pp}^{-1} g^{22} & 0 \\ \hline & & \\ 0 & 0 & I\gamma^{-1} \end{array} \right] \sigma_e^{-2}$$

$$\Rightarrow C_{ud} G^{-1} \hat{u} = P_{np,d} \left(\frac{1}{2} \hat{u}_{pd} \right)$$

$$\begin{aligned} C_{ed} &= \text{cov} \left(u_{nd}, \begin{bmatrix} e_p' : \varepsilon_n' \end{bmatrix} \right) \\ &= \text{cov} \left(\frac{1}{2} P_{np,d} u_{pd} + \phi_{nd}, \begin{bmatrix} e_p' : \phi_{nd}' + p_{nd}' + e_{nd}' + e_{nm}' \end{bmatrix} \right) \\ &= \begin{bmatrix} 0 : D_{nd} g_{11} \end{bmatrix} \sigma_e^2 \end{aligned}$$

$$R^{-1} = \left[\begin{array}{c|c} I & 0 \\ \hline -- & ----- \\ 0 & (I + D_{nd} g_{11})^{-1} \end{array} \right] \sigma_e^{-2}$$

$$\Rightarrow C_{ed} R^{-1} \hat{e} = D_{nd} d_{11} (I + D_{nd} g_{11})^{-1} \left[y_n - X_n b^o - P_{np,d} \left(\frac{1}{2} \hat{u}_{pd} \right) - Z_{nm} \hat{u}_{dm} - Z_{ndp} \hat{p}_{dm} \right]$$

Thus, the prediction of the BV for all nonparents is:

$$\hat{u}_{nd} = P_{np,d} \left(\frac{1}{2} \hat{u}_{pd} \right) + D_{nd} g_{11} (I + D_{nd} g_{11})^{-1} \left[y_n - X_n b^o - P_{np,d} \left(\frac{1}{2} \hat{u}_{pd} \right) - Z_{nm} \hat{u}_{dm} - Z_{ndp} \hat{p}_{dm} \right]$$

and the prediction of the BV for direct effects for the i^{th} nonparent is:

$$\begin{aligned} \hat{u}_{ni,d} &= \frac{1}{2} (\hat{u}_{si,d} + \hat{u}_{di,d}) + \frac{d_{ii} g_{11}}{1 + d_{ii} g_{11}} \left[y_{ni} - b_{ni}^o - \frac{1}{2} (\hat{u}_{si,d} + \hat{u}_{di,d}) - \hat{u}_{di,m} - \hat{p}_{pi,m} \right] \\ &= \frac{1}{2} (\hat{u}_{si,d} + \hat{u}_{di,d}) + \frac{g_{11}}{d^{ii} + g_{11}} \left[y_{ni} - b_{ni}^o - \frac{1}{2} (\hat{u}_{si,d} + \hat{u}_{di,d}) - \hat{u}_{di,m} - \hat{p}_{pi,m} \right] \end{aligned}$$

(ii) Additive maternal genetic effects

$$\begin{aligned}
\hat{\mathbf{u}}_{nm} &= \mathbf{C}_{u_m} \mathbf{G}^{-1} \hat{\mathbf{u}} + \mathbf{C}_{e_m} \mathbf{R}^{-1} \hat{\mathbf{e}} \\
\mathbf{C}_{u_m} &= \text{cov} \left(\frac{1}{2} \mathbf{P}_{np,m} \mathbf{u}_m + \phi_{nm}, [\mathbf{u}_{pd} \text{ } \vdots \text{ } \mathbf{u}_{pm} \text{ } \vdots \text{ } \mathbf{p}_{dm} \text{ } \vdots \text{ } 0] \right) \\
&= \left[\frac{1}{2} \mathbf{P}_{np,m} \mathbf{A}_{pp} \mathbf{g}_{12} \text{ } \vdots \text{ } \frac{1}{2} \mathbf{P}_{np,m} \mathbf{A}_{pp} \mathbf{g}_{22} \text{ } \vdots \text{ } 0 \right] \sigma_e^2 \\
\Rightarrow \mathbf{C}_{u_m} \mathbf{G}^{-1} \hat{\mathbf{u}} &= \mathbf{P}_{np,m} \left(\frac{1}{2} \hat{\mathbf{u}}_{pm} \right) \\
\mathbf{C}_{e_m} &= \text{cov} \left(\frac{1}{2} \mathbf{P}_{np,m} \mathbf{u}_m + \phi_{nm}, [\mathbf{e}_p \text{ } \vdots \text{ } \boldsymbol{\varepsilon}_n \text{ } \vdots \text{ } 0] \right) \\
&= \left[0 \text{ } \vdots \text{ } \mathbf{D}_{nd} \mathbf{g}_{12} \right] \sigma_e^2 \\
\Rightarrow \mathbf{C}_{e_m} \mathbf{R}^{-1} \hat{\mathbf{e}} &= \mathbf{D}_{ng} \mathbf{g}_{12} \left(\mathbf{I} + \mathbf{D}_{nd} \mathbf{g}_{11} \right)^{-1} \left[\mathbf{y}_n - \mathbf{X}_n \mathbf{b}^\circ - \mathbf{P}_{np,d} \left(\frac{1}{2} \hat{\mathbf{u}}_{pd} \right) - \mathbf{Z}_{nm} \hat{\mathbf{u}}_{dm} - \mathbf{Z}_{ndp} \hat{\mathbf{p}}_{dm} \right]
\end{aligned}$$

Thus, the prediction of BV for maternal effects for all nonparents is:

$$\mathbf{u}_{nm} = \frac{1}{2} \left(\hat{\mathbf{u}}_{s,m} + \hat{\mathbf{u}}_{d,m} \right) + \mathbf{D}_{nd} \mathbf{g}_{12} \left(\mathbf{I} + \mathbf{D}_{nd} \mathbf{g}_{11} \right)^{-1} \left[\mathbf{y}_n - \mathbf{b}_{ni}^\circ - \mathbf{P}_{np,d} \left(\frac{1}{2} \hat{\mathbf{u}}_{pd} \right) - \mathbf{Z}_{nm} \hat{\mathbf{u}}_{dm} - \mathbf{Z}_{ndp} \hat{\mathbf{p}}_{dm} \right]$$

and the prediction of the BV for maternal effects for the i^{th} nonparent is:

$$\begin{aligned}
\hat{\mathbf{u}}_{ni,m} &= \frac{1}{2} \left(\hat{\mathbf{u}}_{s,m} + \hat{\mathbf{u}}_{d,m} \right) + \frac{\mathbf{d}_{ii} \mathbf{g}_{12}}{1 + \mathbf{d}_{ii} \mathbf{g}_{11}} \left[\mathbf{y}_{ni} - \mathbf{b}_{ni}^\circ - \frac{1}{2} \left(\hat{\mathbf{u}}_{s,d} + \hat{\mathbf{u}}_{d,d} \right) - \frac{1}{2} \left(\hat{\mathbf{u}}_{d,m} \right) - \hat{\mathbf{p}}_{d,m} \right] \\
&= \frac{1}{2} \left(\hat{\mathbf{u}}_{s,m} + \hat{\mathbf{u}}_{d,m} \right) + \frac{\mathbf{g}_{12}}{\mathbf{d}^{ii} + \mathbf{g}_{11}} \left[\mathbf{y}_{ni} - \mathbf{b}_{ni}^\circ - \frac{1}{2} \left(\hat{\mathbf{u}}_{s,d} + \hat{\mathbf{u}}_{d,d} \right) - \frac{1}{2} \left(\hat{\mathbf{u}}_{d,m} \right) - \hat{\mathbf{p}}_{d,m} \right]
\end{aligned}$$

Note that:

$$\begin{aligned}
\frac{\mathbf{g}_{12}}{\mathbf{d}^{ii} + \mathbf{g}_{11}} &= \frac{\frac{\mathbf{g}_{12}}{\mathbf{g}_{11}}}{\left(\frac{\mathbf{d}^{ii} + \mathbf{g}_{11}}{\mathbf{g}_{11}} \right)} \\
&= \left(\frac{\mathbf{g}_{12}}{\mathbf{g}_{11}} \right) \left(\frac{\mathbf{g}_{11}}{\mathbf{d}^{ii} + \mathbf{g}_{11}} \right)
\end{aligned}$$

Thus,

$$\hat{u}_{n_i m} = \frac{1}{2}(\hat{u}_{s_i m} + \hat{u}_{d_i m}) + \frac{g_{12}}{g_{11}} \hat{\phi}_{n_i d}$$

where

$$\hat{\phi}_{n_i d} = \frac{g_{11}}{d^{ii} + g_{11}} \left[y_{n_i} - b_{n_i}^o - \frac{1}{2}(\hat{u}_{s_i d} + \hat{u}_{d_i d}) - \frac{1}{2}(\hat{u}_{d_i m}) + \hat{p}_{d_i m} \right]$$

Remarks:

Because nonparent BV (u_i) are defined as $\frac{1}{2}u_s + \frac{1}{2}u_d + \phi$ in **DM2RAM**, the number of effects for a nonparent is 1 more than the number of effects for a parent. For example, if there is one fixed effect, the number of effects for a parent in **DM2RAM** is 4 and for a nonparent is 5. Hence, the number of contributions to the MME is **substantially larger** for a nonparent than for a parent, e.g., for a half-stored LHS matrix:

	No. effects	No. contributions
Parent	4	$4(4 + 1)/2 = 10$
Nonparent	5	$5(5 + 1)/2 = 15$

Since nonparents usually constitute the largest group, it would be advantageous to use an equivalent **DM2RAM** which reduces the number of contributions of nonparents to the MME. Quaas et al. (1984) noticed that:

$$(i) \ P_{np,d} = P_{ns,d} + P_{nd,d}$$

where

$P_{ns,d}$ = incidence matrix relating nonparent BV to their **sire** BV for direct effects

$P_{nd,d}$ = incidence matrix relating nonparent BV to their **dam** BV for direct effects

$$(ii) \ Z_{nm} = P_{nd,d}$$

Thus, the set of equations for nonparents can be written as:

$$y_n = X_n b + \frac{1}{2} P_{ns,d} u_{pd} + \frac{1}{2} P_{nd,d} u_{pd} + P_{nd,d} u_{pm} + Z_{ndp} p_{dm} + \varepsilon_n$$

where

$$\varepsilon_n = \phi_{nd} + p_{nd} + e_{nd} + e_{nm}$$

The model for y_n can be rewritten as:

$$y_n = X_n b + \frac{1}{2} P_{ns,d} u_{pd} + P_{nd} \left(\frac{1}{2} u_{pd} + u_{pm} \right) + Z_{ndp} p_{dm} + \varepsilon_n$$

The equations for parents were:

$$y_p = X_p b + Z_{pd} u_{pd} + Z_{pm} u_{pm} + Z_{pdp} p_{dm} + e_p$$

where

$$e_p = p_{pd} + e_{pd} + e_{pm}$$

The parental model must now be rewritten to match the nonparental model as follows:

$$y_p = X_p b + (Z_{pd} - \frac{1}{2} Z_{pm}) u_{pd} + Z_{pm} \left(\frac{1}{2} u_{pd} + u_{pm} \right) + Z_{pdp} p_{dm} + e_p$$

Let

$$u_{pdm} = \frac{1}{2} u_{pd} + u_{pm}$$

Thus, the equivalent **DM2RAM**, i.e., the **EDM2RAM**, is:

$$\begin{bmatrix} y_p \\ y_n \end{bmatrix} = \begin{bmatrix} X_p \\ X_n \end{bmatrix} b + \begin{bmatrix} Z_{pd} - \frac{1}{2} Z_{pm} \\ \frac{1}{2} P_{ns,d} \end{bmatrix} u_{pd} + \begin{bmatrix} Z_{pm} \\ P_{nd} \end{bmatrix} u_{pdm} + \begin{bmatrix} Z_{pdp} \\ Z_{ndp} \end{bmatrix} p_{dm} + \begin{bmatrix} e_p \\ \varepsilon_n \end{bmatrix}$$

$$E \begin{bmatrix} y_p \\ y_n \end{bmatrix} = \begin{bmatrix} X_p \\ X_n \end{bmatrix}$$

$$\text{var} \begin{bmatrix} \mathbf{u}_{pd} \\ \mathbf{u}_{pdm} \\ \text{---} \\ \mathbf{p}_{dm} \\ \text{---} \\ \mathbf{e}_p \\ \boldsymbol{\varepsilon}_n \end{bmatrix} = \begin{bmatrix} \mathbf{A}_{pp} \mathbf{g}_{11} & \mathbf{A}_{pp} (\frac{1}{2} \mathbf{g}_{11} + \mathbf{g}_{12}) & | & \mathbf{0} & | & \mathbf{0} & | & \mathbf{0} \\ \mathbf{A}_{pp} (\frac{1}{2} \mathbf{g}_{11} + \mathbf{g}_{12}) & \mathbf{A}_{pp} (\frac{1}{4} \mathbf{g}_{11} + \mathbf{g}_{12} + \mathbf{g}_{22}) & | & \mathbf{0} & | & \mathbf{0} & | & \mathbf{0} \\ \text{---} & \text{---} & | & \text{---} & | & \text{---} & | & \text{---} \\ \mathbf{0} & \mathbf{0} & | & \mathbf{I}_\gamma & | & \mathbf{0} & | & \mathbf{0} \\ \text{---} & \text{---} & | & \text{---} & | & \text{---} & | & \text{---} \\ \mathbf{0} & \mathbf{0} & | & \mathbf{0} & | & \mathbf{I} & | & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & | & \mathbf{0} & | & \mathbf{0} & | & \mathbf{D}_{nd} \mathbf{g}_{11} + \mathbf{I} \end{bmatrix} \sigma_e^2$$

Example:

A numerical example for the **EDM2RAM** with the dataset used for the **AM** and **RAM** models for direct additive genetic effects only (Chapter 16) is shown in the output of the SAS IML program for this chapter.

Remarks:

- (i) The **MME** for the **EDM2RAM** are more sparse than those for **DM2RAM**.
- (ii) There will be a covariance between \mathbf{u}_{pd} and \mathbf{u}_{pdm} even if \mathbf{g}_{12} is zero.

The **MME** for the **EDM2RAM** are:

$$\begin{bmatrix} \mathbf{X}_p' \mathbf{X}_p + \mathbf{X}_n' \mathbf{R}_n^{-1} \mathbf{X}_n & | & \mathbf{X}_p' (\mathbf{Z}_{pd} - \frac{1}{2} \mathbf{Z}_{pm}) + \mathbf{X}_n' \mathbf{R}_n^{-1} \mathbf{P}_{ns,d} (\frac{1}{2}) & | \\ (\mathbf{Z}_{pd}' - \frac{1}{2} \mathbf{Z}_{pm}') \mathbf{X}_p + (\frac{1}{2}) \mathbf{P}_{ns,d}' \mathbf{R}_n^{-1} \mathbf{X}_n & | & (\mathbf{Z}_{pd}' - \frac{1}{2} \mathbf{Z}_{pm}') (\mathbf{Z}_{pd} - \frac{1}{2} \mathbf{Z}_{pm}) + (\frac{1}{2}) \mathbf{P}_{ns,d}' \mathbf{R}_n^{-1} \mathbf{P}_{ns,d} (\frac{1}{2}) + \mathbf{A}_{pp}^{-1} * \mathbf{g}^{11} & | \\ \mathbf{Z}_{pm}' \mathbf{X}_p + \mathbf{P}_{nd}' \mathbf{R}_n^{-1} \mathbf{X}_n & | & \mathbf{Z}_{pm}' (\mathbf{Z}_{pd} - \frac{1}{2} \mathbf{Z}_{pm}) + \mathbf{P}_{nd}' \mathbf{R}_n^{-1} \mathbf{P}_{ns,d} (\frac{1}{2}) + \mathbf{A}_{pp}^{-1} * \mathbf{g}^{12} & | \\ \mathbf{Z}_{pdp}' \mathbf{X}_p + \mathbf{Z}_{ndp}' \mathbf{R}_n^{-1} \mathbf{X}_n & | & \mathbf{Z}_{pdp}' (\mathbf{Z}_{pd} - \frac{1}{2} \mathbf{Z}_{pm}) + \mathbf{Z}_{ndp}' \mathbf{R}_n^{-1} \mathbf{P}_{ns,d} (\frac{1}{2}) & | \end{bmatrix}$$

[19-15]

$$\begin{array}{c|c}
 X_p' Z_{pm} + X_n' R_n^{-1} P_{nd} & X_p' Z_{pdp} + X_n' R_n^{-1} Z_{ndp} \\
 (Z_{pd}' - \frac{1}{2} Z_{pm}') Z_{pm} + (\frac{1}{2}) P_{ns,d}' R_n^{-1} P_{nd} + A_{pp}^{-1} * g^{12} & (Z_{pd}' - \frac{1}{2} Z_{pm}') Z_{pdp} + (\frac{1}{2}) P_{ns,d}' R_n^{-1} Z_{ndp} \\
 Z_{pm}' Z_{pm} + P_{nd}' R_n^{-1} P_{nd} + A_{pp}^{-1} * g^{22} & Z_{pm}' Z_{pdp} + P_{nd}' R_n^{-1} Z_{ndp} \\
 Z_{pdp}' Z_{pm} + Z_{ndp}' R_n^{-1} P_{nd} & Z_{pdp}' Z_{pdp} + Z_{ndp}' R_n^{-1} Z_{ndp} + I \gamma^{-1}
 \end{array}$$

$$\begin{bmatrix} b \\ u_{pd} \\ u_{pdm} \\ p_{dm} \end{bmatrix} = \begin{bmatrix} X_p' y_p + X_n' R_n^{-1} y_n \\ (Z_{pd}' - \frac{1}{2} Z_{pm}') y_p + (\frac{1}{2}) P_{ns,d}' R_n^{-1} y_n \\ Z_{pm}' y_p + P_{nd}' R_n^{-1} y_n \\ Z_{pdp}' y_p + Z_{ndp}' R_n^{-1} y_n \end{bmatrix}$$

The solutions to the MME for the **DM2RAM** and the **EDM2RAM** are related as follows:

$$\begin{bmatrix} \hat{u}_{pd} \\ \hat{u}_{pm} \\ \hat{p}_{dm} \end{bmatrix} = \begin{bmatrix} I & 0 & 0 \\ -\frac{1}{2} I & I & 0 \\ 0 & 0 & I \end{bmatrix} \begin{bmatrix} \hat{u}_{pd} \\ \hat{u}_{pdm} \\ \hat{p}_{dm} \end{bmatrix}$$

↓
DM2RAM

↓
EDM2RAM

Remarks:

(i) Approximations to **DM2RAM** and **EDM2RAM** can be obtained (e.g., sire-dam (**DM2SDM**), sire-maternal grandsire (**DM2SMM**), etc.) by means of procedures similar to those used for the approximations to **RAM**.

(ii) Maternal and permanent environment effects (i.e., u_{pdm} and p_{dm}) can be combined into a single

effect. However, $\text{var} \begin{bmatrix} u_{pd} \\ u_{pdm} + p_{dm} \end{bmatrix}$ is rather difficult to invert. An easier alternative is to put

$\begin{bmatrix} Z_{pdp} \\ Z_{ndp} \end{bmatrix} p_{dm}$ in the residual. This is equivalent to absorbing p_{dm} into b , u_{pd} and u_{pdm} .

The new residual term is:

$$\begin{bmatrix} e_p^* \\ e_n^* \end{bmatrix} - \begin{bmatrix} Z_{pdp} p_{dm} + e_p \\ Z_{ndp} p_{dm} + e_n \end{bmatrix}$$

and its variance is:

$$\begin{aligned} \text{var} \begin{bmatrix} e_p^* \\ e_n^* \end{bmatrix} &= \begin{bmatrix} Z_{pdp} Z_{pdp}' \gamma + I & 0 \\ 0 & Z_{ndp} Z_{ndp}' \gamma + D_{nd} g_{11} + I \end{bmatrix} \sigma_e^2 \\ &= \begin{bmatrix} R_p^* & 0 \\ 0 & R_n^* \end{bmatrix} \sigma_e^2 \end{aligned}$$

Both R_p^* and R_n^* are block diagonal matrices. The elements of the i^{th} block of R_p^* are equal to:

$$\begin{cases} \sigma_{E_{p_m}}^2 + \sigma_{E_{p_d}}^2 + \sigma_{e_d}^2 + \sigma_{e_m}^2 & \text{diagonals} \\ \sigma_{E_{p_m}}^2 + \sigma_{E_{p_d}}^2 & \text{offdiagonals} \end{cases}$$

and those of the i^{th} block of R_n^* are equal to:

$$\begin{cases} \sigma_{E_{p_m}}^2 + \sigma_{E_{p_d}}^2 + \sigma_{e_d}^2 + \sigma_{e_m}^2 + d_{ii} \sigma_{dd} & \text{diagonals} \\ \sigma_{E_{p_m}}^2 + \sigma_{E_{p_d}}^2 & \text{offdiagonals} \end{cases}$$

References

Quaas, R. L., R. D. Anderson, and A. R. Gilmour. 1984. BLUP School Handbook. Use of Mixed Linear Models for Prediction and for Estimation of (Co) Variance Components. AGBU, University of New England, Australia.