Chapter 31
Maternal Effects

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Many traits are influenced by the environment contributed by the dam. This is particularly true for traits measured early in life and for species in which the dam nurses the young for several weeks or months. Examples are 3 month weights of pigs, 180 day weights of beef calves, and weaning weights of lambs. In fact, genetic merit for maternal ability can be an important trait for which to select. This chapter is concerned with some models for maternal effects and with BLUP of them.

1 Model For Maternal Effects

Maternal effects can be estimated only through the progeny performance of a female or the progeny performance of a related female when direct and maternal effects are uncorrelated. If they are correlated, maternal effects can be evaluated whenever direct can be. Because the maternal ability is actually a phenotypic manifestation, it can be regarded as the sum of a genetic effect and an environmental effect. The genetic effect can be partitioned at least conceptually into additive, dominance, additive $\times$ additive, etc. components. The environmental part can be partitioned, as is often done for lactation yield in dairy cows, into temporary and permanent environmental effects. Some workers have suggested that the permanent effects can be attributed in part to the maternal contribution of the dam of the dam whose maternal effects are under consideration.

Obviously if one is to evaluate individuals for maternal abilities, estimates of the underlying variances and covariances are needed. This is a difficult problem in part due to much confounding between maternal and direct genetic effects. BLUP solutions are probably quite sensitive to errors in estimates of the parameters used in the prediction equations. We will illustrate these principles with some examples.

2 Pedigrees Used In Example

Individual No.	Sex	Sire	Dam	Record
1	Male	Unknown	Unknown	6
2	Female	Unknown	Unknown	9
3	Female	1	2	4
4	Female	1	2	7
5	Male	Unknown	Unknown	8
6	Male	Unknown	Unknown	3
7	Male	6	3	6
8	Male	5	4	8

This gives an **A** matrix as follows:

$$\begin{pmatrix} 1 & 0 & .5 & .5 & 0 & 0 & .25 & .25 \\ & 1 & .5 & .5 & 0 & 0 & .25 & .25 \\ & & 1 & .5 & 0 & 0 & .5 & .25 \\ & & & 1 & 0 & 0 & .25 & .5 \\ & & & & 1 & 0 & 0 & .5 \\ & & & & & 1 & .5 & 0 \\ & & & & & & 1 & .125 \\ & & & & & & & 1 \end{pmatrix}.$$

The corresponding dominance relationship matrix is a matrix with 1's in the diagonals, and the only non-zero off-diagonal element is that for $d_{34} = .25$.

For our first example we assume a model with both additive direct and additive maternal effects. We assume that $\sigma_e^2 = 1$, σ_a^2 (direct) $= .5$, σ_a^2 (maternal) $= .4$, covariance direct with maternal $= .2$. We assume $\mathbf{X}\boldsymbol{\beta} = \mathbf{1}\mu$. In all of our examples we have assumed that the permanent environmental contribution to maternal effects is negligible. If one does not wish to make this assumption, a vector of such effects can be included. Its variance is $\mathbf{I}\sigma_p^2$, and is assumed to be uncorrelated with any other variables. Then permanent environmental effects can be predicted only for those animals with recorded progeny. Then the incidence matrix excluding **p** is

$$\begin{pmatrix} 1 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 1 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 1 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 \\ 1 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 \\ 1 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 1 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 1 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 \\ 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 \end{pmatrix} \tag{1}$$

Cols. 2-9 represent **a** and cols 10-17 represent **m**. This gives the following OLS equations.

$$
\left(\begin{array}{ccccccccccccccccc}
8 & 1 & 1 & 1 & 1 & 1 & 1 & 1 & 1 & 0 & 2 & 1 & 1 & 0 & 0 & 0 & 0 \\
 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
 & & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
 & & & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 \\
 & & & & 1 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 \\
 & & & & & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
 & & & & & & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
 & & & & & & & 1 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 \\
 & & & & & & & & 1 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 \\
 & & & & & & & & & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
 & & & & & & & & & & 2 & 0 & 0 & 0 & 0 & 0 & 0 \\
 & & & & & & & & & & & 1 & 0 & 0 & 0 & 0 & 0 \\
 & & & & & & & & & & & & 1 & 0 & 0 & 0 & 0 \\
 & & & & & & & & & & & & & 0 & 0 & 0 & 0 \\
 & & & & & & & & & & & & & & 0 & 0 & 0 \\
 & & & & & & & & & & & & & & & 0 & 0 \\
 & & & & & & & & & & & & & & & & 0
\end{array}\right)
\begin{pmatrix} \hat{\mu} \\ \hat{\mathbf{a}} \\ \hat{\mathbf{m}} \end{pmatrix}
=
\begin{pmatrix} 51 \\ 6 \\ 9 \\ 4 \\ 7 \\ 8 \\ 3 \\ 6 \\ 8 \\ 0 \\ 11 \\ 6 \\ 8 \\ 0 \\ 0 \\ 0 \\ 0 \end{pmatrix}. \qquad (2)
$$

$$
\mathbf{G} = \begin{pmatrix} .5\mathbf{A} & .2\mathbf{A} \\ .2\mathbf{A} & .4\mathbf{A} \end{pmatrix}.
$$

Adding the inverse of **G** to the lower 16 × 16 submatrix of (31.2) gives the mixed model equations, the solution to which is

$$
\begin{aligned}
\hat{\mu} &= 6.386, \\
\hat{\mathbf{a}} &= (-.241,\ .541,\ -.269,\ .400,\ .658,\ -1.072,\ -.585,\ .709)', \\
\hat{\mathbf{m}} &= (.074,\ -.136,\ -.144,\ .184,\ .263,\ -.429,\ -.252,\ .296)'.
\end{aligned}
$$

In contrast, if covariance $(\mathbf{a}, \mathbf{m}') = \mathbf{0}$, the maternal predictions of 5 and 6 are 0. With $\sigma^2_a = .5$, $\sigma^2_m = .4$, $\sigma^2_{am} = 0$ the solution is

$$
\begin{aligned}
\hat{\mu} &= 6.409, \\
\hat{\mathbf{a}} &= (-.280,\ .720,\ -.214,\ .440,\ .659,\ -1.099,\ -.602,\ .742)', \\
\hat{\mathbf{m}} &= (.198,\ -.344,\ -.029,\ .081,\ 0,\ 0,\ -.014,\ .040)'.
\end{aligned}
$$

Note now that 5 and 6 cannot be evaluated for **m** since they are males and have no female relatives with progeny.

3 Additive And Dominance Maternal And Direct Effects

If we assume that additive and dominance affect both direct and maternal merit, the incidence matrix of (31.1) is augmented on the right by the last 16 columns of (31.1) giving an 8 × 33 matrix. Assume the same additive direct and maternal parameters as before and let the dominance parameters be .3 for direct variance, .2 for maternal, and .1 for their covariance. Then

$$\mathbf{G} = \begin{pmatrix} .5\mathbf{A} & .2\mathbf{A} & \mathbf{0} & \mathbf{0} \\ .2\mathbf{A} & .4\mathbf{A} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & .3\mathbf{D} & .1\mathbf{D} \\ \mathbf{0} & \mathbf{0} & .1\mathbf{D} & .2\mathbf{D} \end{pmatrix}.$$

The solution is

$$\begin{aligned} \hat{\mu} &= 6.405, \\ \mathbf{a}\text{ direct} &= (-.210,\ .478,\ -.217,\ .350,\ .545,\ -.904,\ -.503,\ .588)', \\ \mathbf{a}\text{ maternal} &= (.043,\ -.083,\ -.123,\ .156,\ .218,\ -.362,\ -.220,\ .243)', \\ \mathbf{d}\text{ direct} &= (-.045,\ .392,\ -.419,\ .049,\ .242,\ -.577,\ .069,\ .169)', \\ \mathbf{d}\text{ maternal} &= (-.015,\ -.078,\ -.078,\ .119,\ .081,\ -.192,\ .023,\ .056)'. \end{aligned}$$

Quadratics to compute to estimate variances and covariances by MIVQUE would be

$$\begin{aligned} &\hat{\mathbf{a}}(\text{direct})'\mathbf{A}^{-1}\hat{\mathbf{a}}(\text{direct}), \\ &\hat{\mathbf{a}}(\text{direct})'\mathbf{A}^{-1}\hat{\mathbf{a}}(\text{maternal}), \\ &\hat{\mathbf{a}}(\text{maternal})'\mathbf{A}^{-1}\hat{\mathbf{a}}(\text{maternal}), \\ &\hat{\mathbf{d}}(\text{direct})'\mathbf{D}^{-1}\hat{\mathbf{d}}(\text{direct}), \\ &\hat{\mathbf{d}}(\text{direct})'\mathbf{D}^{-1}\hat{\mathbf{d}}(\text{maternal}), \\ &\hat{\mathbf{d}}(\text{maternal})'\mathbf{D}^{-1}\hat{\mathbf{d}}(\text{maternal}), \\ &\hat{\mathbf{e}}'\hat{\mathbf{e}}. \end{aligned}$$

Of course the data of our example would be quite inadequate to estimate these variances and covariances.