Phenotypic response to selection for traits with direct and maternal components when generations overlap

J.P. Mueller * and J.W. James
School of Wool and Pastoral Sciences, University of New South Wales, Kensington 2033, Australia

Received September 19, 1984
Communicated by J. S. F. Barker

Summary. Prediction of response to selection for traits with direct and maternal components is described for discrete and overlapping generations. Expected phenotypic response is the sum of direct and maternal contributions, the latter having a genetic and an environmental component. With overlapping generations the selection differentials achieved on these components are added to respective updated vectors containing age-sex distributions with values of previous selection rounds. An example demonstrates that in the early stages, results may be considerably affected by environmental correlations between direct and maternal effects. The method could be helpful in interpreting phenotypic changes in a population selected for traits with maternal effects.

Key words: Selection — Maternal effects — Overlapping generations

Introduction

There are several reasons why accurate prediction of response in traits with direct and maternal components is not straightforward (see review by Willham 1980). Genetic gains in maternal effects are expressed one generation later than genetic gains in direct effects; expression of maternal effects is sex limited; and direct and maternal effects may be genetically and environmentally correlated. The asymptotic rate of response to selection for such traits was first given by Dickerson (1947) and later usually referred to as being proportional to "total additive heritability", defined as the regression of total (direct plus maternal) genotype on phenotype. If we wish to predict phenotypic response, the maternal ability of selected dams of the current generation must be considered, since it affects the next generation of progeny. With non-zero environmental correlation between direct and maternal effects it is not sufficient to consider genetic differentials only. With overlapping generations we also need a description of the flow of genes through the population in order to keep track of contributions made by individuals born at different stages of the program (Hill 1974). Aspects of the design and evaluation of selection programs involving maternal effects were discussed by Koch (1972), Hanrahan (1976); Van Vleck et al. (1977) and Koch et al. (1982). Little has been published on formal methods to describe selection response with maternal effects in a general fashion, although Van Vleck et al. (1977) presented a method for predicting phenotypic response when generations do not overlap (or are equal in both sexes) and where environmental correlations between direct and maternal effects were not taken into account.

Here we shall develop methods for predicting phenotypic changes in a population undergoing selection for a trait influenced by maternal effects, allowing for overlapping generations and environmental correlations between direct and maternal effects.

Theory

The model

Our model is a version of the more general one presented by Willham (1963). The phenotypic value P of an individual is made up of direct (D) and maternal (M) contributions, each
of which has genetic (G) and environmental (E) components. Thus
\[ P = G_D + E_D + G_M + E_M. \]
The prime denotes contributions from the dam of the individual, which are reflected in P. The genetic components in an individual's phenotype are \( G_D + G_M \), whereas its own genotypic value is \( G_D + G_M \). The phenotypic variance is then
\[ \sigma^2 = \sigma_D^2 + \sigma_D^2 + \sigma_M^2 + \sigma_M^2 + \text{cov} (G_D, G_M), \]
where \( \sigma^2 \) denotes variance, and \( \text{cov} (G_D, G_M) \) denotes the covariance between \( G_D \) and \( G_M \). It has been assumed that genetic and environmental effects are independent, and that the same is true for environmental effects on dam and offspring. However, the covariance between environmental effects on direct and maternal values of the one individual, \( \text{cov} (E_D, E_M) \), is not assumed to be zero. It will be assumed that all genetic effects are additive, and that variances and covariances are constant during the selection program.

**Selection differentials**

Selection may be based on arbitrary indices \( I_m \) and \( I_f \) in males and females designed to improve overall genetic merit \( H \), of which \( G_D \) and \( G_M \) for the trait of interest may be components. Genetic selection differentials for any trait are then given by the phenotypic selection differential for the index multiplied by the regression of breeding value for the trait on the index. If \( i_i \) denotes the standardised selection differential, the phenotypic selection differential is \( \sigma_i \), where \( \sigma \) stands for standard deviation. The regression is \( \text{Cov} (G, I) / \sigma_I \). Then the genetic selection differentials for direct effects in males and females are
\[ g_{Dm} = \text{Cov} (G_D, I_m) i_m / \sigma_{I_m} \]
\[ g_{Dr} = \text{Cov} (G_D, I_f) i_f / \sigma_{I_f}. \]

We pay special attention to selection based on the trait itself, such as weaning weight. For such traits
\[ \text{Cov} (G_D, P) = \text{Cov} (G_D, G_D) + \text{Cov} (G_D, G_M) = (h_D^2 + r_G h_D h_M / 2) \sigma_P^2 \]
where \( h_D^2 \) and \( h_M^2 \) are the fractions of \( \sigma_P^2 \) due to variation in \( G_D \) and \( G_M \) respectively, and \( r_G \) is the genetic correlation between direct and maternal effects. Thus for selection on phenotype
\[ g_{Dm} = (h_D^2 + r_G h_D h_M / 2) i_m \sigma_P \]
\[ g_{Dr} = (h_D^2 + r_G h_D h_M / 2) i_f \sigma_P. \]

In addition to transmitting genes for direct and maternal effects, selected females also contribute their own maternal ability \( G_M + E_M \) to the phenotype of their progeny. To estimate this contribution, we need the covariance of maternal ability with the index:
\[ \text{Cov} (G_M + E_M, I_f) = \text{Cov} (G_M, I_f) + \text{Cov} (E_M, I_f). \]
Thus this covariance has both genetic and environmental components. The genetic selection differential is
\[ g_{Mf} = \text{Cov} (G_M, I_f) i_f / \sigma_{I_f}, \]
while the environmental selection differential is
\[ e_{Mf} = \text{Cov} (E_M, I_f) i_f / \sigma_{I_f}. \]
Sires pass on to their progeny genes for both direct and maternal effects, the latter being expressed in the maternal ability of their daughters. The maternal genetic selection differential for sires is
\[ g_{Mm} = \text{Cov} (G_M, I_m) i_m / \sigma_{I_m}. \]
For direct selection, differentials for maternal effects can be found as follows.
\[ \text{Cov} (G_M, P) = \text{Cov} (G_M, G_D) + \text{Cov} (G_M, G_M) = (r_G h_D h_M + h_M^2 / 2) \sigma_P^2 \]
\[ \text{Cov} (E_M, P) = \text{Cov} (E_M, E_D) = q_E \sigma_P. \]
The corresponding differentials are:
\[ g_{Mm} = (r_G h_D h_M + h_M^2 / 2) i_m \sigma_P \]
\[ g_{Mf} = (r_G h_D h_M + h_M^2 / 2) i_f \sigma_P \]
\[ e_{Mf} = q_E i_f \sigma_P. \]

**Response with discrete generations**
The total additive response (Dickerson 1947) would be given by
\[ (g_{Dm} + g_{Mm} + g_{Dr} + g_{Mf}) / 2 = (h_D^2 + 3 r_G h_D h_M / 2 + h_M^2 / 2) (i_m + i_f) \sigma_I / 2. \]
In a population with discrete generations, the first generation of selection would give a response as follows. The direct value of the progeny would be increased by \( g_{Dm} + g_{Dr} \) / 2, while the maternal ability of their dams would be increased by \( g_{Mm} + e_{Mf} \). Thus the phenotypic improvement in the progeny would be
\[ (g_{Dm} + g_{Dr}) / 2 + g_{Mf} + e_{Mf}, \]
and thus would differ from the total additive response by
\[ g_{Mf} + (g_{Mm} - g_{Mm}) / 2. \]
After two generations of selection the gain in the direct component would be \( (g_{Dm} + g_{Dr}) \), the gain in maternal effect from the first generation of selection would be \( (g_{Mm} + g_{Mf}) / 2 \) and the effect of selection of dams would be \( g_{Mf} + e_{Mf} \), so the total response to two generations of selection would be
\[ (g_{Dm} + g_{Dr}) + (g_{Mm} + g_{Mf}) / 2 + g_{Mf} + e_{Mf}. \]
Then the change from first to second generation would be the total additive response, as would subsequent gains (Van Vleck et al. 1977).

When generations overlap, the pattern of response can be more complicated, and we now turn to consider how to deal with this.

Response with overlapping generations

As pointed out by Hill (1974), predictions with overlapping generations require a matrix rather than a scalar description because age distributions have to be considered at any one time. Let the direct and maternal genetic values at any one time \( t \) for \( j \) male and \( k \) female age groups be

\[
u_t = (u_{0_t} u_{1_t} \ldots u_{m_j} u_{1t} u_{2t} \ldots u_{kt})
\]

Thus \( u_{0t} \) and \( u_{1t} \) contain mean breeding values for direct and maternal contributions by age-sex groups. If initially \( (t=0) \) all age-sex groups have the same breeding value and we wish to express response as deviation from initial values \( u_0 \) is a vector of zeros. Suppose selection takes place on individuals born at \( t=0 \) so that we have vectors \( d \) with the genic selection differentials of 1 time unit old individuals:

\[
d_d = (g_{0d} 0 \ldots 0 \ g_{0t} 0 \ldots 0)
\]

\[
d_m = (g_{0m} 0 \ldots 0 \ g_{0t} 0 \ldots 0)
\]

The distribution of breeding values (\( u_t \)) at \( t = 1 \) for either direct or maternal genetic contribution is

\[
u_t = P u_{0t} + d
\]

where \( P \) is a "gene flow" matrix (Hill 1974) which updates previous breeding values. With a second round of selection on individuals born at time \( t = 1 \):

\[
u_t = P (P u_{0t} + d) + d
\]

Indeed after \( t \) rounds of selection

\[
u_t = P^t u_{0t} + (I + P + \ldots + P^{t-1}) d
\]

where \( I \) is an identity matrix. If we are interested in the fluctuations of breeding values after one round of selection, then, at time \( t \)

\[
u_t = P^t u_{0t} + P^{t-1} d
\]

We may now describe the general form of the \( P \)-matrix by denoting first with \( p_{1m}, p_{2m} \ldots p_{jm} \) the proportion of genes contributed by 1, 2, \ldots \( j \) time units old males to the next progeny crop, and similarly \( p_{1f}, p_{2f} \ldots p_{kt} \) the proportion of genes contributed by female age groups to the next progeny. The proportion of genes from males, as well as from females must add to 0.5. Then, \( P \) is a square matrix of size \( j + k \) with the first row of each sex exhibiting the proportion of genes contributed by age-sex groups, the remaining rows allowing for ageing.

\[
P =
\begin{bmatrix}
  p_{1m} & p_{2m} & \ldots & p_{j-1m} & p_{jm} & p_{1f} & p_{2f} & \ldots & p_{k-1f} & p_{kf} \\
  1 & 0 & \ldots & 0 & 0 & 0 & 0 & \ldots & 0 & 0 \\
  \vdots & \vdots & & \vdots & \vdots & \vdots & \vdots & & \vdots & \vdots \\
  0 & 0 & \ldots & 1 & 0 & 0 & 0 & \ldots & 0 & 0 \\
  p_{1m} & p_{2m} & \ldots & p_{j-1m} & p_{jm} & p_{1f} & p_{2f} & \ldots & p_{k-1f} & p_{kf} \\
  0 & 0 & \ldots & 0 & 0 & 1 & 0 & \ldots & 0 & 0 \\
  \vdots & \vdots & & \vdots & \vdots & \vdots & \vdots & & \vdots & \vdots \\
  0 & 0 & \ldots & 0 & 0 & 0 & 0 & \ldots & 1 & 0
\end{bmatrix}
\]

In order to consider current generation environmental selection differential we may define a vector \( u_{kt} \), which at any time \( t \) contains the \( e_{mt} \) value in the appropriate female age groups. Let

\[
d_k = (0 \ldots 0 e_{mt} 0 \ldots 0)
\]

and define a matrix \( F \) with zeros everywhere except for the 1's corresponding to ageing in females. It is convenient for the dimensions of these matrices to be compatible with the previous, but with zeros in the blocks corresponding to males. Then,

\[
u_{kt} = F u_{kt} + d_k
\]

and after \( t \) rounds of selection:

\[
u_{kt} = F^t u_{kt} + (I + F + \ldots + F^{t-1}) d_k
\]

In a previously unselected population, \( u_{kt} \) would be a zero vector.

We are now in a position to calculate response to selection. The response in progeny born at time \( t \) will be \( s' u_{dt} \), for direct genetic effects, where \( s' \) is

\[
s' = (p_{1m} p_{2m} \ldots p_{jm} p_{1f} p_{2f} \ldots p_{kf})
\]

Response in maternal effects is \( p' (u_{mt} + u_{kt}) \), where \( p' \) is

\[
p' = (0 \ldots 0 2p_{1f} 2p_{2f} \ldots 2p_{kf})
\]

On summing the two components we get the total response at time \( t \)

\[
R_t = s' u_{dt} + p' (u_{mt} + u_{kt})
\]

If only one cycle of selection is applied, all selected females are lost from the population at time \( t = k + 1 \) and \( u_{kt} \) is zero thereafter. In a continued program, \( u_{kt} \) at this time would have all terms equal to \( e_{mt} \). In either case, all subsequent fluctuations reflect genetic changes only.

Example

For illustration we take an example in pig breeding also used by Hill (1974). Consider a herd in which boars are mated once and sows twice, having first off-
spring at 12 months of age (or 2 time units). Both female age groups contribute equally to the progeny crop and selection intensity among progeny of first and second parity sows is the same. Then

\[ s' = \begin{pmatrix} 0.5 & 0 & 0.25 & 0.25 \\ 0.5 & 0 & 0.25 & 0.25 \\ 1 & 0 & 0 & 0 \\ 0.5 & 0 & 0.25 & 0.25 \end{pmatrix}, \quad p' = \begin{pmatrix} 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 \\ 0 & 0 & 1 & 0 \end{pmatrix} \]

\[ P = \begin{pmatrix} 0.5 & 0 & 0.25 & 0.25 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 \\ 0 & 0 & 1 & 0 \end{pmatrix}, \quad F = \begin{pmatrix} 0.5 & 0 & 0.25 & 0.25 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 \\ 0 & 0 & 1 & 0 \end{pmatrix}. \]

One out of 40 males and one out of eight females are selected before first mating on body weight gain per day. Phenotypic standard deviation for this trait is 70 g/day. The phenotypic selection differentials are

\[ i_m \sigma_p = (2.34) (70 \text{ g/day}) = 163.8 \text{ g/day} \]
\[ i_t \sigma_r = (1.65) (70 \text{ g/day}) = 115.5 \text{ g/day}. \]

In the original example, growth rate was assumed to be a direct additive trait with heritability 0.3. Suppose we suspect maternal effects to be important and take estimates for \( h_D^2 \), \( h_M^2 \) and \( r_G \) from the literature. For instance, Hohenboken and Brinks (1971) calculated for weaning weight in cattle \( h_D^2 = 0.23 - 0.27 \), \( h_M^2 = 0.34 - 0.40 \) and \( r_G = -0.28 \) yielding a total heritability \( h_I^2 = h_D^2 + h_M^2/2 + 3 r_G h_D h_M/2 = 0.28 - 0.33 \). Assuming a similar pattern would apply in pigs, we will assume for our example \( h_D^2 = 0.2 \), \( h_M^2 = 0.4 \) and \( r_G = -0.236, \) so that \( h_I^2 = 0.3 \), the same as in the original example. The required regressions are

\[ h_D^2 + r_G h_D h_M/2 = 0.1666 \]
\[ r_G h_D h_M + h_M^2/2 = 0.1332. \]

Therefore:

\[ d_D = (27.3 \ 0 \ 19.2 \ 0 \ 0) \quad d_M = (21.8 \ 0 \ 15.4 \ 0 \ 0) \]

We will consider three estimates of environmental covariances:

\[ q_E = 0.35 \quad d_K = (0 \ 0 \ 40 \ 0 \ 0) \]
\[ q_E = 0.00 \quad d_K = (0 \ 0 \ 0 \ 0 \ 0) \]
\[ q_E = -0.35 \quad d_K = (0 \ 0 \ -40 \ 0 \ 0) \]

Results for a single round of selection are shown in Table 1. The asymptotic phenotypic change is that expected for genetic change:

\[ (2.34 + 1.65) (0.3) (70)/(2 + 2.5) = 18.6. \]

In the early stages of the program and until selected sows disappear from the herd the effect of \( q_E \) can be important.

In a continued selection program, responses from previous selection rounds are added to give the cumulative response shown in Fig. 1. Assuming \( q_E = 0.0 \) when it is \(-0.35, \) results in overestimation of phenotypic response by 52% at \( t = 5 \) and 23% at \( t = 10 \) in this case.

The parameters used in this example are arbitrary and give inconsistent heritability estimates from paternal half sib (HS) or dam offspring (DO) covariances. For the above parameters:

\[ h_{DS}^2 = 4 \text{ Cov (HS)}/\sigma_D^2 = 0.2 \]
\[ h_{DO}^2 = 2 \text{ Cov (DO)}/\sigma_D^2 = h_D^2 + 5 r_G h_D h_M/2 + 2 q_E + h_M^2 = 1.13 (q_E = 0.35), 0.43 (q_E = 0.0) \text{ or} -0.26 (q_E = -0.35). \]

**Table 1.** Expected response at time of birth in successive time units after one round of selection on pigs born at time \( t = 0 \), assuming different environmental covariances \( (q_E) \) between direct and maternal effects. Parameters and age structure are given in the text. Pigs growth rate in g/day

<table>
<thead>
<tr>
<th>Time</th>
<th>Direct effects</th>
<th>Direct and maternal effects</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>( q_E = -0.35 )</td>
</tr>
<tr>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>2</td>
<td>33.8</td>
<td>6.1</td>
</tr>
<tr>
<td>3</td>
<td>8.8</td>
<td>-7.5</td>
</tr>
<tr>
<td>4</td>
<td>25.3</td>
<td>21.2</td>
</tr>
<tr>
<td>5</td>
<td>15.0</td>
<td>17.5</td>
</tr>
<tr>
<td>6</td>
<td>21.2</td>
<td>19.0</td>
</tr>
<tr>
<td>7</td>
<td>17.6</td>
<td>18.5</td>
</tr>
<tr>
<td>8</td>
<td>19.6</td>
<td>18.7</td>
</tr>
<tr>
<td>9</td>
<td>18.5</td>
<td>18.6</td>
</tr>
<tr>
<td>10</td>
<td>19.1</td>
<td>18.6</td>
</tr>
</tbody>
</table>

**Fig. 1.** Expected cumulative response to selection on growth rate in pigs assuming different environmental covariances \( (q_E) \) between direct and maternal effects. Assumptions are given in the text.
Thus, the dam offspring heritability would take values outside the 0 to 1 range with \( q_E = \pm 0.35 \). However, even if both \( h^2_{RO} \) and \( h^2_{DO} \) were measured in the population and were equal so that we would not suspect maternal effects, one could still make errors in response predictions because of compensating values of \( r_{RO} \), \( h^2_{RO} \), and \( q_E \). For example, suppose \( h^2_{RO} = h^2_{DO} = h^2 = 0.3 \) and \( r_{RO} = -0.471 \), \( q_E = -0.05 \) and \( h^2_M = 0.6 \). That gives the same expected response as before (\( h^2 = 0.3 \)) with deviations in the first four progeny crops (\( t = 2 \) to 5) of 33%, 24%, 20% and 12%.

**Discussion**

The proposed prediction method describes phenotypic response to selection as the sum of direct and maternal contributions, the latter having a genetic and an environmental component. The selection differentials achieved on these components are added to respective updated vectors containing age-sex distributions with values of previous selection rounds. The procedure is an extension of the discrete generation model described by Van Vleck et al. (1977). In their equation, response to selection in a continued program at time \( t \) is given by the sum of \( t \) times the genetic response in direct effects, \( t-1 \) times the genetic response in maternal effects and the maternal genetic selection differential for selected females, the latter accounting for the current generation maternal ability. This differs from our approach in that we use the phenotypic selection differential to account for maternal ability in the current generation, and this amounts to taking consideration of environmental covariance between direct and maternal effects. In one set of examples, describing early response to selection in Van Vleck et al. (1977), \( q_E \) is equal to \(-0.35\). This would introduce an appreciable reduction in expected responses using our method.

In general, response prediction errors due to \( q_E \) will take the sign of the difference between assumed and true \( q_E \). The shorter the evaluation period of a program, the larger the effects of non-zero \( q_E \), because with increasing time genetic contributions become relatively more important compared to current generation effects. It follows that the shorter the female generation interval, and the higher the female selection intensity, the higher is the weight on possible environmental covariances. Consequently, estimates of realised heritability from long term selection experiments can be poor predictors of short term response.

If the evidence indicating negative covariances (Koch 1972) reflects the true situation we would expect responses to selection to be initially very slow. Although several studies have shown slow and even negative response to weaning weight selection (see the review by Barlow 1978) it is not always clear which components restricted response. The response equations derived in this paper could help to explain why initial phenotypic changes in a population selected for traits with maternal influences sometimes do not agree with expectations from genetic changes, and may be useful in the interpretation of experiments involving such traits.

**Acknowledgement.** J. P. M. is gratefully for the support received from the Instituto Nacional de Tecnología Agropecuaria, INTA (Argentina).

**References**


