PREDICTED RATES OF INBREEDING AND GENETIC GAIN UNDER MASS SELECTION WITH ADDITIVE MATERNAL EFFECTS

L. Rönnegård and J.A. Woolliams

1 Dep. of Animal Breeding and Genetics, SLU, S-750 07 Uppsala, Sweden
2 Roslin Institute, Midlothian EH25 9PS, UK

INTRODUCTION

As suggested by Woolliams et al. (1999) maternal effects can be included into the theory of expected long-term genetic contributions. In this paper we test the accuracy of predicted gain and inbreeding calculated from expected long-term genetic contributions with maternal genetic effects, by comparing with results from stochastic simulations. We also examine how the predicted rate of inbreeding changes for different mating ratios. Discrete generations are considered here, but the method is general enough to include overlapping generations.

METHODS

We study a model for maternal effects where the phenotype of individual \( i \) is composed of an individual component, \( P_{i,\text{self}} \), and a component caused by the influence of the dam, \( P_{i,\text{maternal}} \) (Willham, 1963): \( P_i = P_{i,\text{self}} + P_{i,\text{maternal}} \). The genetic sub-components of each phenotypic component are assumed to be inherited as a Mendelian inherited trait that is determined by an infinite number of loci, each having an infinitesimal effect, with: \( P_{i,\text{self}} = A_i + E_i \) and \( P_{i,\text{maternal}} = M_d + R_d \), where \( A_i \) and \( M_i \) are the additive direct genetic effects and additive maternal genetic effects, respectively, and where subscripts \( i, s, d \) denote belonging to individual \( i \), sire \( s \) and dam \( d \). \( R_d \) is common environmental maternal effects. (In this paper we study the model for \( V(R_d) = 0 \)). The total phenotypic variance of \( P_i \) will be assumed to be 1 in a randomly selected and unrelated base population, with \( h_a^2 = \text{total direct additive genetic variance} \) and \( h_m^2 = \text{total maternal additive genetic variance} \). In this paper we study the model for \( \rho = 0 \), where \( \rho \) is the direct-maternal genetic correlation of the unselected base population. For each genetic component

\[
A_i = \frac{1}{2}A_s + \frac{1}{2}A_d + a_i \quad \text{where } V(a_i) = \frac{1}{2}h_a^2
\]

\[
M_i = \frac{1}{2}M_s + \frac{1}{2}M_d + m_i \quad \text{where } V(m_i) = \frac{1}{2}h_m^2
\]

Furthermore, the model is studied for mass selection and fixed family size. Random mating is assumed such that covariances between mates are zero.

Expected genetic contributions, gain and rate of inbreeding. The long-term genetic contribution, \( r_{i(q)} \), of individual \( i \) in category \( q \) born at \( t_i \) is defined as the proportion of genes present in individuals in cohort \( t \) derived by descent from \( i \), where \( (t - t_i) \rightarrow \infty \) (Woolliams et al. 1993). The expected long-term genetic contribution \( u_{i(q)} \) is defined as \( u_{i(q)} = E[r_{i(q)} | s_{i(q)} - \bar{s}_q] \), where \( s_{i(q)} \) is a vector of selective advantages for \( i(q) \) and \( \bar{s}_q \) is the average of selected individuals in category \( q \). Let the number of categories be denoted by \( n_c \). In this paper we study a single closed population so that the number of categories is equal to twice the
maximum age. For direct and maternal effects \( s_{i(q)} = \begin{pmatrix} A_{i(q)} \\ M_{i(q)} \end{pmatrix} \) where \( T \) denotes the transpose of matrices. Assuming linear regression on \( s_{i(q)} - \bar{s}_q \) (Wray and Thompson 1990) the expected long-term genetic contribution is: \( \mu_{i(q)} = \alpha_{i(q)} + \beta_q T (s_{i(q)} - \bar{s}_q) \). A general solution to predict the solutions for the coefficients of \( \mu_{i(q)}, \alpha_{i(q)} \) and \( \beta_q \), were derived by Woolliams et al. (1999), but this had not previously been applied to the additive maternal effects.

Let \( g_{i(q)} \) be a vector of Mendelian sampling terms corresponding to the selective advantages in \( s_{i(q)} \). For maternal effects \( g_{i(q)} = (a_{i(q)}, m_{i(q)}) \). The annual genetic gain is then obtained by extending the expression given by Woolliams et al. (1999) to multiple selective advantages

\[
E[\Delta G] = \sum_{\text{categories } q} n_q E[\mu_{i(q)} g_{i(q)}] = \sum_{q} n_q E[\mu_{i(q)} g_{i(q)}]
\]  

(1)

where \( n_q \) = no. parents in category \( q \). For discrete generations the number of categories is 2 i.e. \( m \) and \( f \) for males and females, with \( n_m \) sires and \( n_f \) dams.

Rates of inbreeding per year are predicted from (Woolliams and Bijma 2000):

\[
E[\Delta F] = \frac{1}{2} n_m E[\mu_{i(m)}^2] + \frac{1}{2} n_f E[\mu_{i(f)}^2] + \frac{1}{8} \sum_{q=m,f} n_q \delta_q
\]  

(2)

where \( \mu_{i(q)} \) is the expected lifetime long-term contribution of individual \( i \) in category \( q \) conditional on its selective advantage, and \( \delta_q \) is a correction factor for deviations of the variance of family size from independent Poisson variances.

**Stochastic simulations.** To examine the accuracy of predictions the stochastic simulation programme described by Bijma and Woolliams (1999) was developed to include maternal effects. The total phenotypic variance of \( P_i \) was assumed to be 1 in a randomly selected and unrelated base population. The direct-maternal genetic correlation of the base population, \( \rho \), is 0 in all the analyses of this paper, therefore, \( \text{Cov}(a_i, m_i) = 0 \). For the base population: \( A_i \) was taken from \( N(0, h_a^2) \), \( M_i \) was simulated as \( M_i = \frac{1}{2} M_d + \frac{1}{2} M_s + m_i \), \( M_d \sim N(0, h_d^2), \) \( M_s \sim N(0, \frac{1}{2} h_s^2), \) and \( P_i = A_i + M_i + E_i \) where \( E_i \sim N(0, \sigma_e^2) \) with \( \sigma_e^2 = 1 - \left( h_a^2 + h_m^2 \right) \). Additive effects in offspring of future generations were then obtained as \( A_i = \frac{1}{2} A_d + \frac{1}{2} A_s + a_i, M_i = \frac{1}{2} M_d + \frac{1}{2} M_s + m_i \) (with \( a_i \sim N(0, \frac{1}{2} h_a^2) \) and \( m_i \sim N(0, \frac{1}{2} h_m^2) \)). Rate of genetic gain (\( \Delta G \)) and rate of inbreeding (\( \Delta F \)) were estimated between cohort \( (t_1 = 10) \) and \( (t_2 = 35) \). Results were averaged over 500 replicates.

**Population studied.** Rates of gain and inbreeding were studied for a population with discrete generations, 25 male parents, 25 female parents, 8 tested offspring per dam, and for which initial direct and maternal heritabilities of the base population summed to 0.4. With this set of populations the final term in equation (2) is \(-0.00125\).
The influence of maternal effects on $\Delta F$ for different mating ratios (= no. dams per sire) was studied for a population with discrete generations, 64 female parents, 8 tested offspring per dam, and the number of male parents ranging from 64 to 2. For these populations the final term in equation (2) is $-0.0005$. The relative $\Delta F$ was calculated as predicted $\Delta F$ for $h_a^2 = 0.4$ ($h_m^2 = 0$) divided by predicted $\Delta F$ for $h_a^2 = 0.4$ ($h_m^2 = 0$).

**RESULTS AND DISCUSSION**

**Gain and inbreeding.** As the proportion of the total additive genetic variance attributed to maternal effects increased the predicted genetic gain ($\Delta G$) decreased (as expected from Willham, 1963) and the predicted rate of inbreeding ($\Delta F$) increased (Table 1).

<table>
<thead>
<tr>
<th>[ $h_a^2$, $h_m^2$ ]</th>
<th>Predicted $^b$</th>
<th>Simulated $^c$</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$\Delta G$</td>
<td>$\Delta F$</td>
</tr>
<tr>
<td>[0.4; 0]</td>
<td>0.423</td>
<td>0.0137</td>
</tr>
<tr>
<td></td>
<td>+0.013</td>
<td>+0.0003</td>
</tr>
<tr>
<td>[0.3; 0.1]</td>
<td>0.388</td>
<td>0.0163</td>
</tr>
<tr>
<td></td>
<td>+0.019</td>
<td>+0.0013</td>
</tr>
<tr>
<td>[0.2; 0.2]</td>
<td>0.344</td>
<td>0.0182</td>
</tr>
<tr>
<td></td>
<td>+0.029</td>
<td>+0.0017</td>
</tr>
<tr>
<td>[0.1; 0.3]</td>
<td>0.291</td>
<td>0.0193</td>
</tr>
<tr>
<td></td>
<td>+0.029</td>
<td>+0.0012</td>
</tr>
<tr>
<td>[0; 0.4]</td>
<td>0.229</td>
<td>0.0198</td>
</tr>
<tr>
<td></td>
<td>+0.019</td>
<td>+0.0002</td>
</tr>
</tbody>
</table>

$^a$ Direct and maternal heritabilities of base population. $^b$ Deviations from simulation results on every second line. $^c$ Standard deviations on every second line.

**Expected contributions.** Comparisons of predicted and simulated $\beta_q$ showed fairly good agreement. As expected the predicted regression on $A$ was the same for males and females but the gene flow attributable to $M$ was greater for females.

**Predicted $\Delta G$ and $\Delta F$.** The percentage overestimation of $\Delta G$ grew as the genetic variance became dominated by the maternal additive effects, but $\Delta F$ was overestimated only when there was both additive genetic and maternal additive variance present. Two possible explanations of these biases are that the predictions were not corrected for the effect of finite population size on the intraclass correlation of full and half sibs (see Appendix A in Bijma et al. (2000)), and that the model for expected genetic contributions is linear in the breeding values. The effect of finite population size increases with increased maternal heritability because individuals are selected increasingly on the mother's performance.

**Mating ratio.** As the mating ratio increased for a fixed number of dams the terms for $\Delta F$ become dominated by the $\alpha_m^2$ in both cases with the result that $R(\Delta F)$ tends to 1.
difference between the rates of inbreeding (\( \Delta F \)), when the total additive genetic variance is due to direct effects compared to when the total additive genetic variance is due to maternal effects, decreases as the mating ratio increases (Figure 1). This may be explained by the change in full-sib and half-sib structures. As the mating ratio increases the number of half-sibs increases and the impact of selection on dam performance decreases.

**Figure 1.** Relative \( \Delta F \) for different values of mating ratio. Relative \( \Delta F = \) predicted \( \Delta F \) for \( h_m^2 = 0.4 \) and \( h_a^2 = 0 \) divided by predicted \( \Delta F \) for \( h_m^2 = 0 \) and \( h_a^2 = 0.4 \). Mating ratio=number of mate parents divided by number of female parents.

**CONCLUSIONS**
We have predicted \( \Delta F \) which, to our knowledge, has not been predicted earlier with maternal effects included.

Selection for direct genetic effects with large weights on family information gives poor predictions (Bijma and Woolliams, 1999) and large \( h_m^2 \) give large full-sib family correlations. Predictions of \( \Delta F \) and \( \Delta G \) from mass selection with maternal effects were, therefore, surprisingly accurate.

**REFERENCES**