Maternal Genetic Effects

A special case of heritable social effects
Maternal effects

- Juvenile traits in mammals depend on “environment provided by the mother”
  - Juvenile growth rate in pigs → milk yield of dam
  - Calving ease in cattle → rump angle and width of dam
  - Juvenile mortality in pigs → maternal behavior

- Maternal effects are a “social environment”
  - Partially heritable → breeding interest
Components of maternally affected traits

- Wilham (1963)
  - \( P_{\text{offspring}} = \text{Direct} + \text{Maternal} \)
    - \( = A_{D, \text{offspring}} + E_{D, \text{offspring}} + A_{M, \text{dam}} + E_{M, \text{dam}} \)

- Two genetic components, \( A_D, A_M \)
  - Three variance components
    - \( \text{Var}(A_D), \text{Var}(A_M), \text{Cov}(A_D, A_M) \)

- Response to selection: \( \Delta P = \Delta A_D + \Delta A_M \)
  - Total breeding value of individual:
    - \( G_i = A_{D,i} + A_{M,i} \)
  - Total genetic variance in trait
    - \( \text{Var}(G) = \text{Var}(A_D) + 2\text{Cov}(A_D, A_M) + \text{Var}(A_M) \)
    - Maternal effects may either increase or decrease the heritable variation
      - Depending on \( \text{Cov}(A_D, A_M) \)
  - Total “heritability”: \( T^2 = \frac{\text{Var}(G)}{\text{Var}(P)} \) (Eaglen and Bijma, JDS 2009)

Better individuals
Better mothers
Maternal effects and heritability

- “total heritability”
  - Willham, 1972; Meyer, 1992; Luo et al., 2002

\[ h_r^2 = \frac{\sigma^2_{AD} + \frac{1}{2} \sigma^2_{ADM} + \frac{1}{2} \sigma^2_{AM}}{\sigma^2_p} \]

- This is the realized heritability of mass selection
- \( h_r^2 \) is the regression coefficient of \( A_D + A_S \) on \( P \)
- \( \Delta G_{mass} = h_r^2 S \)

- \( T^2 \) expresses the heritable variance that can be used for response, irrespective of the selection method

\[ R = i r_{IH} \sigma_{TBV} \]

\[ T^2 = \frac{\sigma^2_{TBV}}{\sigma^2_p} \]
Maternal effects and accuracy

\[ R = i r_{IH} \sigma_{TBV} \]

- \( r_{IH} = \text{corr}(\text{selcrit}, A_D + A_M) \)
- This applies to any selection method

For mass selection

\[ r_{IH} = \frac{\sigma_{AD}^2 + \frac{1}{2} \sigma_{ADM} + \frac{1}{2} \sigma_{AM}^2}{\sigma_p \sigma_{TBV}} \neq \sqrt{h_r^2} \]
Estimating variance components

- **Parameters of interest**
  - $\text{Var}(A_D)$, $\text{Var}(A_M)$, $\text{Cov}(A_D, A_M)$
    - Estimated $\text{Cov}(A_D, A_M)$ often strongly negative → statistical artifact?
      - Koerhuis and Thompson (1997)

- **Where does the info come from?**
  - $\text{Var}(A_M)$: Individuals with the same dam are similar
    - Problem: Full sibs also have $\frac{1}{2}A_D$ in common
      - Confounding of $\text{Var}(A_D)$ with $\text{Var}(A_M)$
    - Problem: Full sibs also have $E_M$ in common ($c^2$)
      - Confounding of $\text{Var}(A_M)$ with $\text{Var}(E_M)$
  - $\text{Cov}(A_D, A_M)$: Similarity between dam and offspring
    - Problem: dam and offspring also have $\text{Cov}(E_D, E_M)$
      - Two distinct traits of the same individual (the dam)

- **Beware of confounding**
  - Not accounting for non-genetic covariances → biased genetic parameter estimates
  - We need to identify all the covariances between relatives
Covariances dam and offspring

Dam: $P_d = A_{D,d} + E_{D,d} + A_{M,gd} + E_{M,gd}$

Off: $P_{off} = \frac{1}{2}A_{D,d} + A_{M,d} + E_{M,d} + \ldots$

$Cov(P_d, P_{off}) = \frac{1}{2} \sigma^2_{A_D} + \frac{1}{4} \sigma_{A_{DM}} + \frac{1}{2} \sigma^2_{A_M} + Cov(E_D, E_M)$

- Relationship matrix in MME
- Residual covariance of dam and offspring record
Covariances full sibs

**FS1:** \( P_{\text{off}} = \frac{1}{2}A_{D,s} + \frac{1}{2}A_{D,d} + A_{M,d} + E_{M,d} + \ldots \)

\[ \begin{align*}
\frac{1}{2} \sigma^2_{AD} & \quad \sigma^2_{ADM} & \quad \sigma^2_{AM} & \quad \sigma^2_{EM} \\
\end{align*} \]

**FS2:** \( P_{\text{off}} = \frac{1}{2}A_{D,s} + \frac{1}{2}A_{D,d} + A_{M,d} + E_{M,d} + \ldots \)

\[ \begin{align*}
\frac{1}{2} \sigma^2_{AD} & \quad \sigma^2_{ADM} & \quad \sigma^2_{AM} & \quad \sigma^2_{EM} \\
\end{align*} \]

\[ \text{Cov}_{FS} = \left( \frac{1}{2} \sigma^2_{AD} + \sigma^2_{ADM} + \sigma^2_{AM} + \sigma^2_{EM} \right) \]

- Relationship matrix
- "common environment" \( c^2 \)
Covariances between relatives

- Conclusions
  - Maternal effect create additional genetic and non-genetic covariances among relatives
  - In the MME
    - Genetic covariances $\rightarrow$ A-matrix in MME
    - Non-genetic covariances
      - Dam-offspring $\rightarrow$ variance structure of residuals
      - Full-sibs $\rightarrow$ $c^2$
Resulting mixed models

- One offspring per dam (no full sibs)
  \[ y = Xb + Z_D a_D + Z_M a_M + e \]
- \( Z_D \) is the usual incidence matrix
  - a “1” for each animal, zero elsewhere \( \rightarrow Z_D = I \)
- \( Z_M \) is the incidence matrix for the mother
  - a “1” at the position of the mother \( \rightarrow Z_M = I \)
- \( \text{Cov}(e_i, e_j) = \text{Cov}(E_D, E_M) \) when \( i \) and \( j \) are dam and off.

\[
\text{Var}\left[ \begin{bmatrix} a_D \\ a_M \end{bmatrix} \right] =
\begin{bmatrix}
A \sigma_{AD}^2 & A \sigma_{ADS} \\
A \sigma_{ADS} & A \sigma_{AS}^2
\end{bmatrix}
\]

\[
\text{Var}(e) = R \sigma_e^2
\]
\[
R_{ii} = 1
\]
\[
R_{ij} = \rho \text{ when } i \text{ and } j \text{ dam and offspring}
\]
\[
\rho = \frac{\text{Cov}(E_D, E_M)}{\sigma_e^2}
\]
\[
R_{ij} = 0 \text{ elsewhere}
\]

Fit a correlated residual between dam and offspring

Bijma, JAS, 2006
Resulting mixed models

- One litter per dam (full sibs of a single litter)
  \[ y = Xb + Z_D a_D + Z_M a_M + Z_C c + e \]
  - \( Z_C \) has a “1” at the position of the litter, zero elsewhere
    - \( Z_C = I_{n_{\text{litters}}} \)
  - \( e_c \) contains \( E_{M,d} \)
  - The residual of the dam, \( e_{\text{dam}} \) contains \( E_{D,d} \)
  - \( \text{Cov}(e_{\text{c,off}}, e_{\text{dam}}) = \text{Cov}(E_{D}, E_{M}) \)

\[
\text{Var}\left[
\begin{bmatrix}
    e_c \\
    e
\end{bmatrix}
\right] =
\begin{bmatrix}
    \text{I} \sigma_c^2 & \text{B} \sigma_{E_{DM}} \\
    \text{B} \sigma_{E_{DM}} & \text{I} \sigma_e^2
\end{bmatrix}
\]

- \( \text{B} \) connects birth litters of individuals to the records of their dams

Need to fit a correlation between the common environment of the offspring and the residual of the dam

Problem: no software (R?)

Bijma, JAS, 2006
Omitting residual variance structures

Estimated genetic correlation when fitting independent residuals

<table>
<thead>
<tr>
<th></th>
<th>True $r_{g} = 0$</th>
<th>True $r_{g} = 0.3$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$r_{E} = 0$</td>
<td>0</td>
<td>0.3</td>
</tr>
<tr>
<td>$r_{E} = 0.3$</td>
<td>0.3</td>
<td>0.6</td>
</tr>
</tbody>
</table>

Severe bias may occur

Other factors that may solve extreme estimated $r_{g}$
- Fixed effects in the model
- (random) sire by herd effect (cattle)
  - Koerhuise and Thompson (1997)
What data is needed?

- Relationships via the sire
  - Avoid confounding $A_{D,d}$ with $E_{D,d}$

- Direct effect is expressed in offspring
  - 1: $\text{Cov}_S = \frac{1}{4}\text{Var}(A_D)$

- Maternal effect is expressed in grand-offspring via daughter
  - 2: $\text{Cov}_S = (1/16)\text{Var}(A_D) + \frac{1}{4}\text{Var}(A_M) + (1/8)\text{Cov}(A_D,A_M)$

- Covariance is observed in covariance between offspring and grand-offspring
  - 3: $\text{Cov}_S = (1/8)\text{Var}(A_D) + \frac{1}{4}\text{Cov}(A_D,A_M)$

- 3 equations with 3 unknowns $\rightarrow$ can be solved
  - When full sibs or dam-offspring pairs occur in the data $\rightarrow$ account for non-genetic covariances in the model
    - Or remove those data if possible
  - AI: Use sire-mgs-mmgs models to avoid covs from the dam side

- We need sires that have both offspring and maternal grand-offspring
What data is needed

Calving ease in dairy cattle

<table>
<thead>
<tr>
<th>Variable</th>
<th>Full</th>
<th>Subset 1</th>
<th>Subset 2</th>
</tr>
</thead>
<tbody>
<tr>
<td># of records</td>
<td>677,795</td>
<td>98,162</td>
<td>99,328</td>
</tr>
<tr>
<td># of sires</td>
<td>4,635</td>
<td>4,586</td>
<td>2,682</td>
</tr>
<tr>
<td># of herds</td>
<td>19,985</td>
<td>11,363</td>
<td>4,055</td>
</tr>
<tr>
<td># of dams</td>
<td>677,795</td>
<td>98,162</td>
<td>99,328</td>
</tr>
<tr>
<td># of dams with own birth record</td>
<td>101,445</td>
<td>49,081</td>
<td>0</td>
</tr>
<tr>
<td># maternal grandsires</td>
<td>18,467</td>
<td>6,177</td>
<td>17,963</td>
</tr>
</tbody>
</table>
Calving ease in dairy cattle

**Table 6. Estimated genetic parameters**

<table>
<thead>
<tr>
<th>Model/data set</th>
<th>$k_D^2$</th>
<th>$k_M^2$</th>
<th>$r_{G_{DM}}$</th>
<th>$\rho^I$</th>
<th>$T^{2.8}$</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Animal model</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Subset 1a</td>
<td>0.077±0.007</td>
<td>0.028±0.006</td>
<td>-0.11±0.09</td>
<td>-</td>
<td>0.095±0.007</td>
</tr>
<tr>
<td>Subset 1b</td>
<td>0.076±0.008</td>
<td>0.027±0.006</td>
<td>-0.13±0.11</td>
<td>0.003±0.008</td>
<td>0.091±0.012</td>
</tr>
<tr>
<td>Subset 2</td>
<td>0.088±0.007</td>
<td>0.042±0.010</td>
<td>-0.10±0.14</td>
<td>-</td>
<td>0.116±0.013</td>
</tr>
<tr>
<td>Subset 3</td>
<td>0.087±0.007</td>
<td>0.055±0.011</td>
<td>-0.16±0.12</td>
<td>-</td>
<td>0.120±0.014</td>
</tr>
<tr>
<td>Subset 4</td>
<td>0.090±0.007</td>
<td>0.061±0.011</td>
<td>-0.44±0.09</td>
<td>-</td>
<td>0.085±0.012</td>
</tr>
<tr>
<td>Subset 5</td>
<td>0.091±0.007</td>
<td>0.025±0.007</td>
<td>-0.04±0.14</td>
<td>-</td>
<td>0.112±0.012</td>
</tr>
<tr>
<td>Average S2-S5</td>
<td>0.088±0.004</td>
<td>0.040±0.005</td>
<td>-0.24±0.06</td>
<td>-</td>
<td>0.107±0.006</td>
</tr>
</tbody>
</table>

Even with 100,000 records, $r_{A,DM}$ is not very accurate.
Conclusions maternal effects

- Maternal effects are just a special kind of social interactions
  - Fits within the same theoretical framework

- Data analysis is challenging

- Derive the expected covariances among relatives to:
  - Identify possible confounding of genetic and environmental covariances (BIAS)
  - Identify powerful schemes for estimation