



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

- $\text{Var}(A_D)$, $\text{Var}(A_M)$, $\text{Cov}(A_D, A_M)$

Better individuals

Better mothers

- 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": $T^2 = \text{Var}(G)/\text{Var}(P)$ (Eaglen and Bijma, JDS 2009)



Maternal effects and heritability

- “total heritability”

- Willham, 1972; Meyer, 1992; Luo et al., 2002

$$h_r^2 = \frac{\sigma_{A_D}^2 + 1\frac{1}{2}\sigma_{A_{DM}} + \frac{1}{2}\sigma_{A_M}^2}{\sigma_P^2}$$

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

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

$$R = i r_{IH} \sigma_{TBV}$$

$$T^2 = \frac{\sigma_{TBV}^2}{\sigma_P^2}$$



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

$$r_{IH} = \frac{\sigma_{A_D}^2 + 1\frac{1}{2}\sigma_{A_{DM}} + \frac{1}{2}\sigma_{A_M}^2}{\sigma_P\sigma_{TBV}} \neq \sqrt{h_r^2}$$

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 $\text{Var}(A_M)$

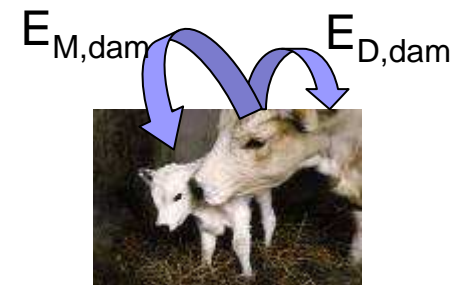
- Problem: Full sibs also have E_M in common (c^2)

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

Diagram illustrating the relationship between the dam's phenotype (P_d) and the offspring's phenotype (P_{off}) through additive genetic effects (A) and residual effects (E):

- The dam's phenotype is composed of additive genetic effects ($A_{D,d}$), residual effects ($E_{D,d}$), additive genetic effects from the sire ($A_{M,gd}$), and residual effects from the sire ($E_{M,gd}$).
- The offspring's phenotype is composed of half the dam's additive genetic effects ($\frac{1}{2}A_{D,d}$), the sire's additive genetic effects ($A_{M,d}$), and the sire's residual effects ($E_{M,d}$).
- Covariances are indicated by arrows:
 - $\frac{1}{4}\sigma_{ADM}$ (Covariance between $A_{D,d}$ and $A_{M,gd}$)
 - σ_{ADM} (Covariance between $A_{D,d}$ and $A_{M,d}$)
 - σ_{EDM} (Covariance between $E_{D,d}$ and $E_{M,d}$)
 - $\frac{1}{2}\sigma_{AD}^2$ (Covariance between $A_{D,d}$ and $\frac{1}{2}A_{D,d}$)
 - $\frac{1}{2}\sigma_{AM}^2$ (Covariance between $A_{M,gd}$ and $A_{M,d}$)

$$Cov(P_d, P_{off}) = \underbrace{\frac{1}{2}\sigma_{AD}^2 + 1\frac{1}{4}\sigma_{ADM} + \frac{1}{2}\sigma_{AM}^2}_{\text{Relationship matrix in MME}} + \underbrace{Cov(E_D, E_M)}_{\text{Residual covariance of dam and offspring record}}$$

Relationship matrix
in MME

Residual covariance of
of dam and offspring record

Covariances full sibs



■ FS1: $P_{\text{off}} = \frac{1}{2}A_{D,s} + \frac{1}{2}A_{D,d} + A_{M,d} + E_{M,d} + \dots$

■ FS2: $P_{\text{off}} = \frac{1}{2}A_{D,s} + \frac{1}{2}A_{D,d} + A_{M,d} + E_{M,d} + \dots$

$$Cov_{FS} = \underbrace{\frac{1}{2}\sigma_{A_D}^2 + \sigma_{A_{DM}} + \sigma_{A_M}^2}_{\text{Relationship matrix}} + \underbrace{\sigma_{E_M}^2}_{\text{"common environment"} c^2}$$



Covariances between relatives

■ Conclusions

- Maternal effect create additional genetic and non-genetic covariances among relatives
- In the MME
 - Genetic covariances → A-matrix in MME
 - Non-genetic covariances
 - Dam-offspring → variance structure of residuals
 - Full-sibs → c^2

Resulting mixed models



- One offspring per dam (no full sibs)

$$\mathbf{y} = \mathbf{X}\mathbf{b} + \mathbf{Z}_D\mathbf{a}_D + \mathbf{Z}_M\mathbf{a}_M + \mathbf{e}$$

- \mathbf{Z}_D is the usual incidence matrix
 - a “1” for each animal, zero elsewhere $\rightarrow \mathbf{Z}_D = \mathbf{I}$
- \mathbf{Z}_M is the incidence matrix for the mother
 - a “1” at the position of the mother $\rightarrow \mathbf{Z}_M = \mathbf{I}$
- $\text{Cov}(e_i, e_j) = \text{Cov}(E_D, E_M)$ when i and j are dam and off.

$$\text{Var} \begin{bmatrix} \mathbf{a}_D \\ \mathbf{a}_M \end{bmatrix} = \begin{bmatrix} \mathbf{A}\sigma_{A_D}^2 & \mathbf{A}\sigma_{A_{DS}} \\ \mathbf{A}\sigma_{A_{DS}} & \mathbf{A}\sigma_{A_S}^2 \end{bmatrix}$$

$$\text{Var}(\mathbf{e}) = \mathbf{R}\sigma_e^2$$

$$\mathbf{R}_{ii} = 1$$

$$\mathbf{R}_{ij} = \rho \text{ when } i \text{ and } j \text{ dam and offspring}$$

$$\rho = \text{Cov}(E_D, E_M) / \sigma_e^2$$

$$\mathbf{R}_{ij} = 0 \text{ elsewhere}$$

Fit a correlated residual
between dam and offspring

Resulting mixed models



- One litter per dam (full sibs of a single litter)

$$\mathbf{y} = \mathbf{X}\mathbf{b} + \mathbf{Z}_D\mathbf{a}_D + \mathbf{Z}_M\mathbf{a}_M + \mathbf{Z}_C\mathbf{e}_c + \mathbf{e}$$

Common environment among full sibs

- \mathbf{Z}_C has a “1” at the position of the litter, zero elsewhere

□ $\mathbf{Z}_c = \mathbf{I}_{n_litters}$

- \mathbf{e}_c contains $E_{M,d}$

- The residual of the dam, \mathbf{e}_{dam} contains $E_{D,d}$

- $\text{Cov}(\mathbf{e}_{c,off}, \mathbf{e}_{dam}) = \text{Cov}(E_D, E_M)$



$$\text{Var} \begin{bmatrix} \mathbf{e}_c \\ \mathbf{e} \end{bmatrix} = \begin{bmatrix} \mathbf{I}\sigma_c^2 & \mathbf{B}\sigma_{E_{DM}} \\ \mathbf{B}\sigma_{E_{DM}} & \mathbf{I}\sigma_e^2 \end{bmatrix}$$

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?)



Omitting residual variance structures

Estimated genetic correlation when fitting independent residuals

	True $r_g = 0$	True $r_g = 0.3$
$r_F = 0$	0	0.3
$r_E = 0.3$	0.3	0.6

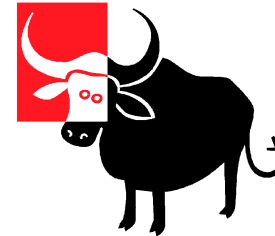
Severe bias may occur

Other factors that may solve extreme estimated r_g

- Fixed effects in the model
- (random) sire by herd effect (cattle)
 - Koerhuisse 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: $Cov_S = \frac{1}{4}Var(A_D)$
- Maternal effect is expressed in grand-offspring via daughter
 - 2: $Cov_S = (1/16) Var(A_D) + \frac{1}{4}Var(A_M) + (1/8)Cov(A_D, A_M)$
- Covariance is observed in covariance between offspring and grand-offspring
 - 3: $Cov_S = (1/8)Var(A_D) + \frac{1}{4}Cov(A_D, A_M)$
- 3 equations with 3 unknowns → can be solved
 - When full sibs or dam-offspring pairs occur in the data → 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 3. Descriptive statistics of the data

Variable	Full	Subset 1 ¹	Subset 2 ²
# of records	677,795	98,162	99,328
# of sires	4,633	4,586	2,683
# of herds	19,985	11,363	4,055
# of dams	677,795	98,162	99,328
# of dams with own birth record	101,445	49,081	0
# maternal grandsires	18,167	6,174	17,963

Calving ease in dairy cattle

Table 6. Estimated genetic parameters¹

Model/dataset	h_D^2	h_M^2	$r_{G_{DM}}$	ρ^1	T^2
<u>Animal model</u>					
Subset 1a	0.077±0.007	0.028±0.006	-0.11±0.09	-	0.095±0.007
Subset 1b	0.076±0.008	0.027±0.006	-0.13±0.11	0.003±0.008	0.091±0.012
Subset 2	0.088±0.007	0.042±0.010	-0.10±0.14	-	0.116±0.013
Subset 3	0.087±0.007	0.055±0.011	-0.16±0.12	-	0.120±0.014
Subset 4	0.090±0.007	0.061±0.011	-0.44±0.09	-	0.085±0.012
Subset 5	0.091±0.007	0.025±0.007	-0.04±0.14	-	0.112±0.012
Average S2-S5	0.088±0.004	0.040±0.005	-0.24±0.06	-	0.107±0.006

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