

Maternal Environmental Effects

- All offspring from same mother share a common maternal environment
 - Non inherited maternal effects
 - Nutrition of offspring influenced by mother
 - Maternal Health
 - » infections (Mastitis)
 - » Injuries (Damaged teats)
 - » Nutrition
 - » Wellbeing
 - Intra-uterine
 - Fetal Alcohol syndrome
 - Number of embryos developing
 - Placental effects
 - Cytoplasmic
 - Extra nuclear environment present in oocyte passed on by maternal lineages
 - Non-inherited social effects
 - Maternal learned behavior
 - Maternal nurturing

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Maternal Environmental Effects

- If Ignored
 - Reduces Response to Selection
- Solution
 - Within Family Selection
 - How to weight the between vs within family information
 - BLUP
 - Estimate and remove the effect

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Common Situation Correlated Residuals

Animals in a common group (pen, herd, or **mother**) share a common environmental effect. Let ρ be the correlation between residuals due to shared environment.

A covariance within groups is reflected in a between group variance
Principle for estimating heritability via ANOVA (between and within sire variances)

ρ is the intra-class environmental correlation

$$\rho = \frac{\sigma_b^2}{\sigma_b^2 + \sigma_e^2}$$

$$\mathbf{R} = (\sigma_b^2 + \sigma_e^2) \begin{bmatrix} 1 & \rho & \rho & \cdots & 0 & 0 & 0 \\ \rho & 1 & \rho & \cdots & 0 & 0 & 0 \\ \rho & \rho & 1 & \cdots & 0 & 0 & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots & \vdots \\ 0 & 0 & 0 & \cdots & 1 & \rho & \rho \\ 0 & 0 & 0 & \cdots & \rho & 1 & \rho \\ 0 & 0 & 0 & \cdots & \rho & \rho & 1 \end{bmatrix} = \begin{bmatrix} \sigma_b^2 + \sigma_e^2 & \sigma_b^2 & \sigma_b^2 & \cdots & 0 & 0 & 0 \\ \sigma_b^2 & \sigma_b^2 + \sigma_e^2 & \sigma_b^2 & \cdots & 0 & 0 & 0 \\ \sigma_b^2 & \sigma_b^2 & \sigma_b^2 + \sigma_e^2 & \cdots & 0 & 0 & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots & \vdots \\ 0 & 0 & 0 & \cdots & \sigma_b^2 + \sigma_e^2 & \sigma_b^2 & \sigma_b^2 \\ 0 & 0 & 0 & \cdots & \sigma_b^2 & \sigma_b^2 + \sigma_e^2 & \sigma_b^2 \\ 0 & 0 & 0 & \cdots & \sigma_b^2 & \sigma_b^2 & \sigma_b^2 + \sigma_e^2 \end{bmatrix}$$

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Solution 1

Model Residual Correlation Structure

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Zu} + \mathbf{e}$$

Weight by inverse of residual covariance matrix \mathbf{R}

$$\begin{bmatrix} \mathbf{X}'\mathbf{R}^{-1}\mathbf{X} & \mathbf{X}'\mathbf{R}^{-1}\mathbf{Z} \\ \mathbf{Z}'\mathbf{R}^{-1}\mathbf{X} & \mathbf{Z}'\mathbf{R}^{-1}\mathbf{Z} + \mathbf{G}^{-1} \end{bmatrix} \begin{bmatrix} \mathbf{b} \\ \mathbf{u} \end{bmatrix} = \begin{bmatrix} \mathbf{X}'\mathbf{R}^{-1}\mathbf{Y} \\ \mathbf{Z}'\mathbf{R}^{-1}\mathbf{Y} \end{bmatrix}$$

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Solution 2

Add another random effect due to shared environment (mother, cage, herd)

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Z}_1\mathbf{d} + \mathbf{Z}_2\mathbf{m}_e + \mathbf{e}$$

Direct effect

Shared Group Environmental effect

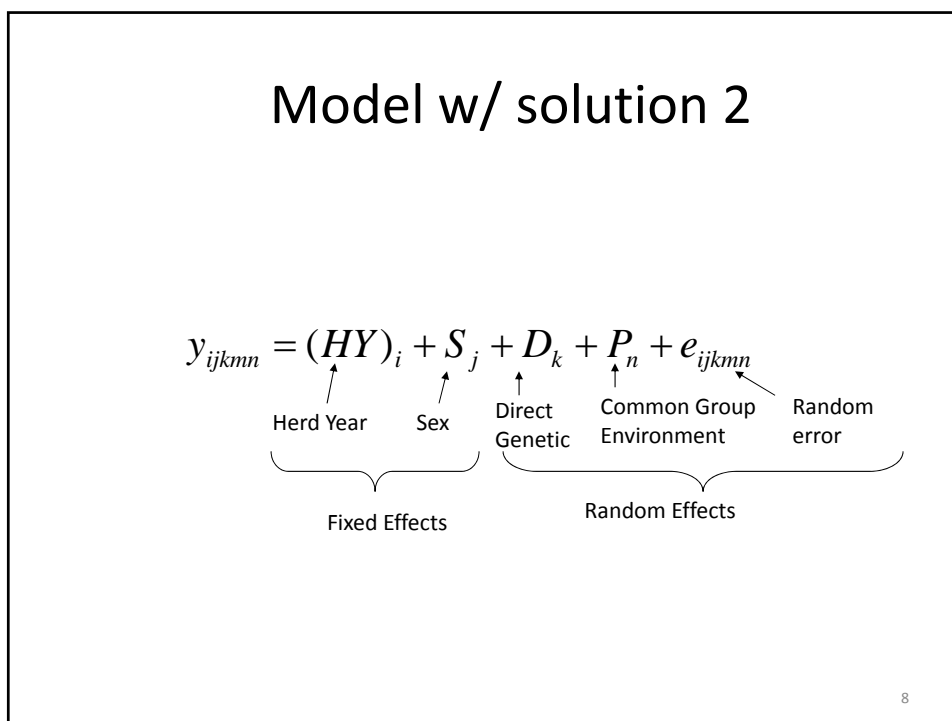
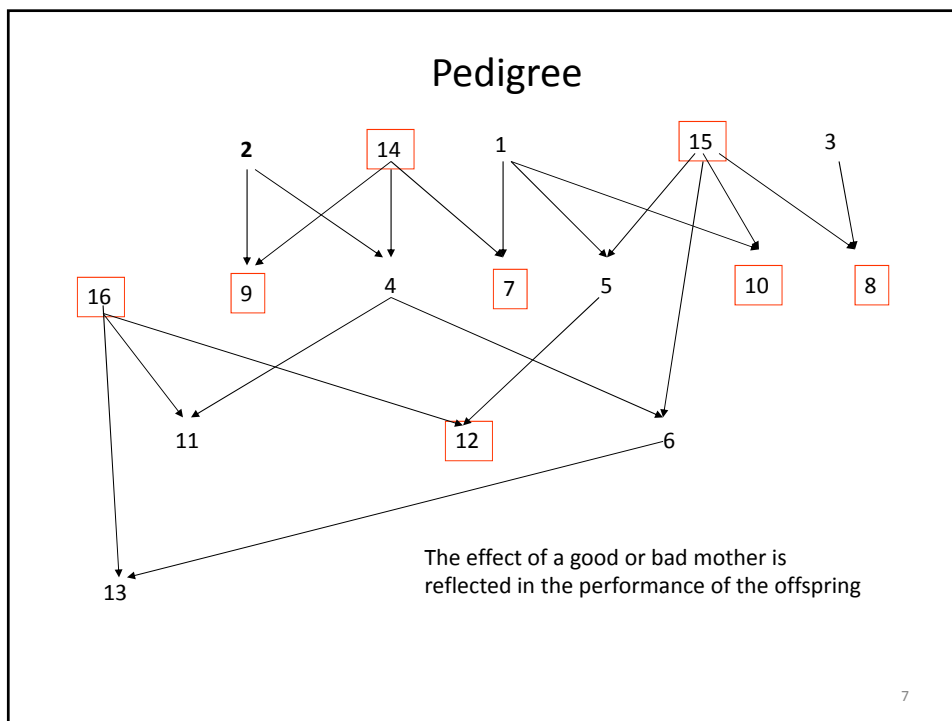
$$V \begin{bmatrix} \mathbf{d} \\ \mathbf{m} \\ \mathbf{e} \end{bmatrix} = \begin{bmatrix} \mathbf{A}\sigma_d^2 & 0 & 0 \\ 0 & \mathbf{I}\sigma_{m_e}^2 & 0 \\ 0 & 0 & \mathbf{I}\sigma_e^2 \end{bmatrix}$$

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Maternal Effects Example

Schaeffer Table 8.7

Animal	Sire	Dam	Year	Sex	Wean Wt
7	14	1	86	M	400
4	14	2	86	F	380
8	15	3	86	M	410
5	15	1	87	F	350
9	14	2	87	M	420
6	15	4	87	F	360
10	15	1	88	M	390
11	16	4	88	F	390
12	16	5	88	M	430
13	16	6	88	F	370



Year sex
86 87 88 m

$$\mathbf{X} = \begin{bmatrix} 1 & 0 & 0 & 1 \\ 1 & 0 & 0 & 0 \\ 1 & 0 & 0 & 1 \\ 0 & 1 & 0 & 0 \\ 0 & 1 & 0 & 1 \\ 0 & 1 & 0 & 0 \\ 0 & 0 & 1 & 1 \\ 0 & 0 & 1 & 0 \\ 0 & 0 & 1 & 1 \\ 0 & 0 & 1 & 0 \end{bmatrix}$$

$$\mathbf{B} = \begin{bmatrix} b_1 \\ b_2 \\ b_3 \\ b_4 \end{bmatrix}$$

} Herd
} Year
← Sex

$$\mathbf{Y} = \begin{bmatrix} 400 \\ 380 \\ 410 \\ 350 \\ 420 \\ 360 \\ 390 \\ 390 \\ 430 \\ 370 \end{bmatrix}$$

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Animal Direct Genetic Effect

Note that sires and dams did not have records and are missing

An	Sire	Dam
7	14	1
4	14	2
8	15	3
5	15	1
9	14	2
6	15	4
10	15	1
11	16	4
12	16	5
13	16	6

$$\mathbf{Z} = \begin{bmatrix} 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 \end{bmatrix}$$

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Maternal Environmental effect

Animal 1 was the mother of animals 7, 5, 10

An	Sire	Dam
7	14	1
4	14	2
8	15	3
5	15	1
9	14	2
6	15	4
10	15	1
11	16	4
12	16	5
13	16	6

↓

1 2 3 4 5 6 ← Mothers only

$$\mathbf{Z}_2 = \begin{bmatrix} 1 & 0 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 & 0 \\ 1 & 0 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 & 0 \\ 1 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 0 & 1 \end{bmatrix}$$

$$\mathbf{I} = \begin{bmatrix} 1 & 0 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 0 & 1 \end{bmatrix}$$

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MME

$$\begin{bmatrix} \mathbf{X}'\mathbf{X} & \mathbf{X}'\mathbf{Z}_1 & \mathbf{X}'\mathbf{Z}_2 \\ \mathbf{Z}_1'\mathbf{X} & \mathbf{Z}_1'\mathbf{Z}_1 + \mathbf{A}^{-1}k_{11} & \mathbf{Z}_1'\mathbf{Z}_2 \\ \mathbf{Z}_2'\mathbf{X} & \mathbf{Z}_2'\mathbf{Z}_1 & \mathbf{Z}_2'\mathbf{Z}_2 + \mathbf{I}k_{22} \end{bmatrix} \begin{bmatrix} \hat{\mathbf{b}} \\ \hat{\mathbf{a}} \\ \hat{\mathbf{p}} \end{bmatrix} = \begin{bmatrix} \mathbf{X}'\mathbf{y} \\ \mathbf{Z}_1'\mathbf{y} \\ \mathbf{Z}_2'\mathbf{y} \end{bmatrix}$$

$$\begin{bmatrix} k_{11} & k_{12} \\ k_{21} & k_{22} \end{bmatrix} = \begin{bmatrix} \sigma_d^2 & 0 \\ 0 & \sigma_{m_e}^2 \end{bmatrix}^{-1} \sigma_e^2$$

$$\begin{bmatrix} k_{11} & k_{12} \\ k_{21} & k_{22} \end{bmatrix} = \begin{bmatrix} 2000 & 0 \\ 0 & 500 \end{bmatrix}^{-1} 6500 = \begin{bmatrix} 3.25 & 0 \\ 0 & 13 \end{bmatrix}$$

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```

proc iml;
start main;
y={400,
380,
410,
350,
420,
360,
390,
390,
430,
370};

Z1={0 0 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 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 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 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 0 1};

X={1001,
1000,
1001,
0100,
0101,
0100,
0011,
0010,
0011,
0010};

Z2={ 1 0 0 0 0 0,
0 1 0 0 0 0,
0 0 1 0 0 0,
1 0 0 0 0 0,
0 1 0 0 0 0,
0 0 0 1 0 0,
1 0 0 0 0 0,
0 0 0 1 0 0,
0 0 0 1 0,
0 0 0 1 0,
0 0 0 0 1};

I= { 1 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 0 1 0,
0 0 0 0 0 1};

```

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```

Ainv={2.5 .5 1 0 0 0 -1 -1 0 0 -1 0 0 0 0 0,
.5 2.5 0 1 0 0 -1 0 0 -1 0 0 -1 0 0 0,
1 0 2 0 0 0 0 -1 0 0 -1 0 0 0 0 0,
0 1 0 3 .5 0 0 .5 -1 -1 0 -1 -1 0 0 0,
0 0 0 .5 1.5 0 0 0 -1 0 0 0 0 0 0 0,
0 0 0 0 0 2.5 0 .5 0 .5 0 .5 0 -1 -1 -1,
-1 -1 0 0 0 0 2 0 0 0 0 0 0 0 0 0,
-1 0 -1 .5 0 .5 0 3 0 0 0 -1 0 -1 0 0,
0 0 0 -1 -1 0 0 0 2 0 0 0 0 0 0 0,
0 -1 0 -1 0 .5 0 0 0 2.5 0 0 0 0 -1 0,
-1 0 -1 0 0 0 0 0 0 0 2 0 0 0 0 0,
0 0 0 -1 0 .5 0 -1 0 0 0 2.5 0 0 0 -1,
0 -1 0 -1 0 0 0 0 0 0 0 0 2 0 0 0,
0 0 0 0 0 -1 0 -1 0 0 0 0 0 2 0 0,
0 0 0 0 0 -1 0 0 0 -1 0 0 0 0 2 0,
0 0 0 0 0 -1 0 0 0 0 0 -1 0 0 0 2};

```

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```

P={2000 0,
   0 500};

K=inv(P)#6500;

LHS=((X`*X)|| (X`*Z1)|| (X`*Z2))
      /((Z1`*X)|| (Z1`*Z1+AINV#K[1,1])|| (Z1`*Z2))
      /((Z2`*X)|| (Z2`*Z1)|| (Z2`*Z2+I#K[2,2]));

RHS=(X`*Y)/(Z1`*Y)/(Z2`*Y);
C=INV(LHS);
BU=C*RHS;
print BU ;
finish main;
run;
quit;

```

“BLUP Maternal Environmental (2).sas”

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B		\hat{a}	Animal	\hat{p}	Animal
369.87	}	1.81	14	-2.365897	1
363.57		-3.80	1	1.226796	2
375.03		2.783	2	0.0671247	3
40.76	← Sex	-3.56	15	0.5146638	4
		0.13	3	0.9262775	5
		2.63	16	-0.368965	6
		-1.96	7		
		3.46	4		
		-1.57	8		
		-3.88	5		
		3.91	9		
		-0.90	6		
		-6.31	10		
		4.56	11		
		1.22	12		
		0.12	13		

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What to do with the estimates in a breeding program

- Just use estimate of breeding value, permanent environment effect is example of random block factor

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Solution 2

What is R?

$$\begin{bmatrix} \mathbf{X}'\mathbf{R}^{-1}\mathbf{X} & \mathbf{X}'\mathbf{R}^{-1}\mathbf{Z} \\ \mathbf{Z}'\mathbf{R}^{-1}\mathbf{X} & \mathbf{Z}'\mathbf{R}^{-1}\mathbf{Z} + \mathbf{G}^{-1} \end{bmatrix} \begin{bmatrix} \mathbf{b} \\ \mathbf{u} \end{bmatrix} = \begin{bmatrix} \mathbf{X}'\mathbf{R}^{-1}\mathbf{Y} \\ \mathbf{Z}'\mathbf{R}^{-1}\mathbf{Y} \end{bmatrix}$$

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Genetic Parameters

$$\mathbf{G} = \mathbf{A}\sigma_d^2$$

$$\sigma_d^2 = 2000$$

$$\sigma_{m_e}^2 = 500$$

$$\sigma_e^2 = 6500$$

$$\rho = \frac{500}{500 + 6500} = .0714$$

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Answer: Environmental Correlation Matrix
Hint: animals 7, 5, 10 shared Animal 1 as the mother

Shared Maternal Environment

\downarrow $\rho = .0714$ $\sigma_e^2 = 6500 + 500$

An	Sire	Dam
7	14	1
4	14	2
8	15	3
5	15	1
9	14	2
6	15	4
10	15	1
11	16	4
12	16	5
13	16	6

$R =$

\downarrow			$\rho = .0714$		$\sigma_e^2 = 6500 + 500$					
	7	4	8	5	9	6	10	11	12	13
	1	0	0	ρ	0	0	ρ	0	0	0
	0	1	0	0	ρ	0	0	0	0	0
	0	0	1	0	0	0	0	0	0	0
	ρ	0	0	1	0	0	ρ	0	0	0
	0	ρ	0	0	1	0	0	0	0	0
	0	0	0	0	0	1	0	ρ	0	0
	ρ	0	0	ρ	0	0	1	0	0	0
	0	0	0	0	0	ρ	0	1	0	0
	0	0	0	0	0	0	0	0	1	0
	0	0	0	0	0	0	0	0	0	1

$\left. \begin{matrix} 7 \\ 4 \\ 8 \\ 5 \\ 9 \\ 6 \\ 10 \\ 11 \\ 12 \\ 13 \end{matrix} \right\} \sigma_e^2$

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```

proc iml;
start main;

Sig_m=500;
Sig_e=6500+Sig_m;
Sig_g=2000;
LAM=1/2000;

y={400,
  380,
  410,
  350,
  420,
  360,
  390,
  390,
  430,
  370};

X={1 0 0 1,
  1 0 0 0,
  1 0 0 1,
  0 1 0 0,
  0 1 0 1,
  0 1 0 0,
  0 0 1 1,
  0 0 1 0,
  0 0 1 1,
  0 0 1 0};

Z= {0 0 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 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 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 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 0 1};

R= { 1 0 0 .0714 0 0 .0714 0 0 0 0,
     0 1 0 0 .0714 0 0 0 0 0 0,
     0 0 1 0 0 0 0 0 0 0 0,
     .0714 0 0 1 0 0 .0714 0 0 0,
     0 .0714 0 0 1 0 0 0 0 0 0,
     0 0 0 0 0 0 1 0 .0714 0 0,
     .0714 0 0 .0714 0 0 1 0 0 0,
     0 0 0 0 0 .0714 0 1 0 0,
     0 0 0 0 0 0 0 0 1 0,
     0 0 0 0 0 0 0 0 0 1)#Sig_e;

RINV=INV(R);

```

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```

Ainv={2.5 .5 1 0 0 0 -1 -1 0 0 -1 0 0 0 0 0,
      .5 2.5 0 1 0 0 -1 0 0 -1 0 0 -1 0 0 0,
      1 0 2 0 0 0 0 -1 0 0 -1 0 0 0 0 0,
      0 1 0 3 .5 0 0 .5 -1 -1 0 -1 -1 0 0 0,
      0 0 0 .5 1.5 0 0 0 -1 0 0 0 0 0 0 0,
      0 0 0 0 0 2.5 0 .5 0 .5 0 .5 0 -1 -1 -1,
      -1 -1 0 0 0 0 2 0 0 0 0 0 0 0 0 0,
      -1 0 -1 .5 0 .5 0 3 0 0 0 -1 0 -1 0 0,
      0 0 0 -1 -1 0 0 0 2 0 0 0 0 0 0 0,
      0 -1 0 -1 0 .5 0 0 0 2.5 0 0 0 0 -1 0,
      -1 0 -1 0 0 0 0 0 0 0 2 0 0 0 0 0,
      0 0 0 -1 0 .5 0 -1 0 0 0 2.5 0 0 0 -1,
      0 -1 0 -1 0 0 0 0 0 0 0 0 2 0 0 0,
      0 0 0 0 0 -1 0 -1 0 0 0 0 0 2 0 0,
      0 0 0 0 0 -1 0 0 0 -1 0 0 0 0 2 0,
      0 0 0 0 0 -1 0 0 0 0 -1 0 0 0 2};

LHS=(X*RINV*X)/(X*RINV*Z)/((Z*RINV*X)/(Z*RINV*Z+Ainv#LAM));
RHS=(X*RINV*Y)/(Z*RINV*Y);
C=INV(LHS);
BU=C*RHS;
print BU ;

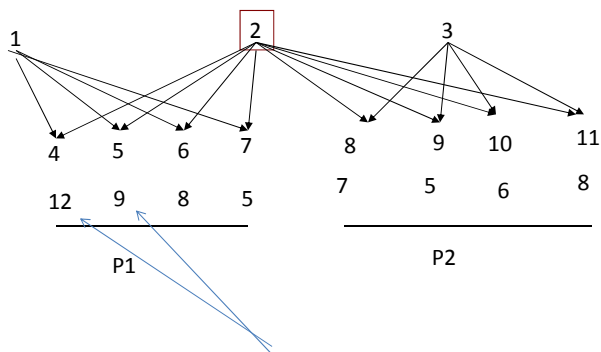
finish main;run;quit;

```

BU	
369.8741	
363.578	
375.0397	
40.76463	
1.813526	14
-3.80565	1
2.783858	2
-3.56012	15
0.13427	3
2.634119	16
-1.96639	7
3.464949	4
-1.5786	8
6 -3.88408	5
3.916292	9
-0.90666	6
-6.31701	10
4.569	11
1.227599	12
0.1258	13

Compare to slide 16 22

Example Impact of maternal environmental effects on breeding program



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```

proc iml;
start main;
Z1={0001000000,
    0000100000,
    0000010000,
    0000001000,
    0000000100,
    0000000010,
    0000000001};
Z2={1 0,
    1 0,
    1 0,
    1 0,
    0 1,
    0 1,
    0 1,
    0 1};
X={1,
    1,
    1,
    1,
    1,
    1,
    1,
    1,
    1};
I={1 0,
    0 1};
A={1 0 0 .5 .5 .5 .5 0 0 0 0,
    0 1 0 .5 .5 .5 .5 .5 .5 .5,
    0 0 1 0 0 0 0 .5 .5 .5 .5,
    .5 .5 0 1 .5 .5 .25 .25 .25 .25,
    .5 .5 0 .5 1 .5 .5 .25 .25 .25 .25,
    .5 .5 0 .5 .5 1 .5 .25 .25 .25 .25,
    .5 .5 .25 .25 .25 .25 1 .5 .5 .5,
    .5 .5 .25 .25 .25 .25 .5 1 .5 .5,
    .5 .5 .25 .25 .25 .25 .5 .5 1 .5,
    .5 .5 .25 .25 .25 .25 .5 .5 .5 1};
AINV=INV(A);

```

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Impact of Relative Magnitude

As ratio gets smaller, permanent environmental effects are more important

```

P={10 0,
  0 100};
K=inv(P)#10;
LHS=((X`*X)|| (X`*Z1)|| (X`*Z2))
      /(((Z1`*X)|| (Z1`*Z1+AINV#K[1,1])|| (Z1`*Z2))
      /(((Z2`*X)|| (Z2`*Z1)|| (Z2`*Z2+I#K[2,2])));
RHS=(X`*Y)/(Z1`*Y)/(Z2`*Y);
C=INV(LHS);
BU=C*RHS;
RMSE=(Y`*Y-BU`*RHS)#(1/6);
print BU ;
finish main;
run;
quit;

```

$\sigma_d^2 = 10$

$\sigma_{m_e}^2 = 100$

$\sigma_e^2 = 10$

Run "BLUP Maternal Environmental.SAS"

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Impact on Choice of Animals for Breeding

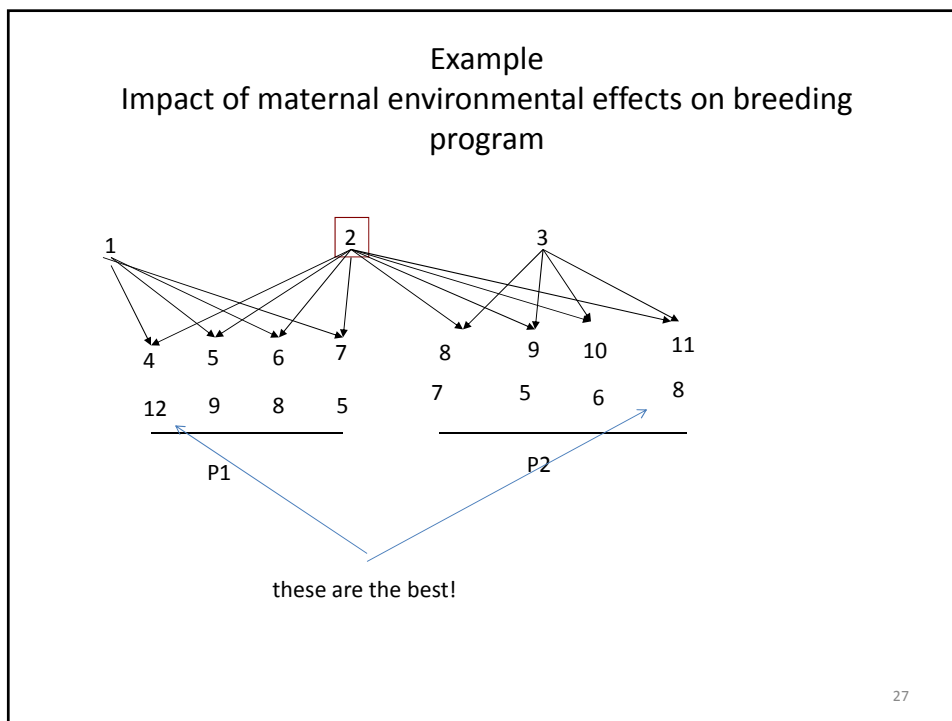
Dam

	4	1.201	1
	5	0.201	
1	6	-0.131	
	7	-1.131	
	8	0.131	
	9	-0.535	
3	10	-0.201	
	11	0.464	2

One from each family

Within Family Selection

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Maternal Genetic Effects

- Inherited Genetic effect of the mother
 - Measured on the offspring
 - An indirect genetic effect
 - Examples
 - Milking ability
 - Mothering ability
 - Social interactions
 - Care
 - Comfort
 - Abuse
- Reference
 - Lynch and Walsh Ch 23
 - Schaeffer: Linear Models and Computing Strategies in Animal Breeding



Maternal Genetic Effects

$$y_{ijkmn} = (HY)_i + S_j + D_k + M_n + e_{ijkmn}$$

↑ Herd Year ↑ Sex ↑ Direct Genetic ↑ Maternal Genetic ↑ Random error

} Fixed Effects } Random Effects

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Maternal Genetic Effects

$$\mathbf{y} = \mathbf{X}\mathbf{b} + \mathbf{Z}_1\mathbf{d} + \mathbf{Z}_2\mathbf{m}_g + \mathbf{e}$$

↑ Direct effect ↑ Maternal Genetic

$$V \begin{bmatrix} \mathbf{d} \\ \mathbf{m} \\ \mathbf{e} \end{bmatrix} = \begin{bmatrix} \mathbf{A}\sigma_d^2 & \mathbf{A}\sigma_{d,m_g} & 0 \\ \mathbf{A}\sigma_{d,m_g} & \mathbf{A}\sigma_{m_g}^2 & 0 \\ 0 & 0 & \mathbf{I}\sigma_e^2 \end{bmatrix}$$

There is a genetic correlation between the animals direct and maternal genetic effect

The are inherited and determined by additive effects in the mother

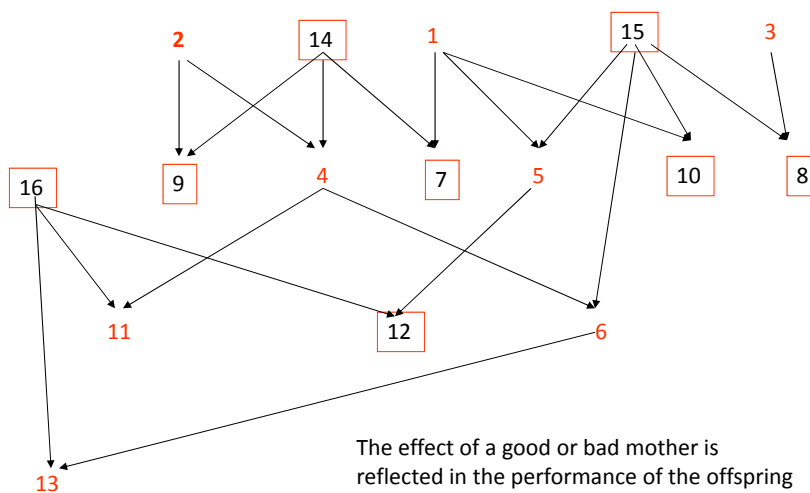
No environmental correlations

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Maternal Effects Example

Animal	Sire	Dam	Year	Sex	Wean Wt
7	14	1	86	M	400
4	14	2	86	F	380
8	15	3	86	M	410
5	15	1	87	F	350
9	14	2	87	M	420
6	15	4	87	F	360
10	15	1	88	M	390
11	16	4	88	F	390
12	16	5	88	M	430
13	16	6	88	F	370

Pedigree



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Year	sex
86 87 88 m	

$$\mathbf{X} = \begin{bmatrix} 1 & 0 & 0 & 1 \\ 1 & 0 & 0 & 0 \\ 1 & 0 & 0 & 1 \\ 0 & 1 & 0 & 0 \\ 0 & 1 & 0 & 1 \\ 0 & 1 & 0 & 0 \\ 0 & 0 & 1 & 1 \\ 0 & 0 & 1 & 0 \\ 0 & 0 & 1 & 1 \\ 0 & 0 & 1 & 0 \end{bmatrix}$$

$$\mathbf{B} = \begin{bmatrix} b_1 \\ b_2 \\ b_3 \\ b_4 \end{bmatrix}$$

}

Herd
Year

←

Sex

$$\mathbf{Y} = \begin{bmatrix} 400 \\ 380 \\ 410 \\ 350 \\ 420 \\ 360 \\ 390 \\ 390 \\ 430 \\ 370 \end{bmatrix}$$

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Animal Direct Genetic Effect

Note that sires and dams did not have records and are missing

An	Sire	Dam
7	14	1
4	14	2
8	15	3
5	15	1
9	14	2
6	15	4
10	15	1
11	16	4
12	16	5
13	16	6

$$\mathbf{Z}_1 = \begin{bmatrix} 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 \end{bmatrix}$$

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Maternal Genetic Effect-identify the mothers of the animal
Animal 1 was the mother of animals 7, 5, 10

An	Sire	Dam
7	14	1
4	14	2
8	15	3
5	15	1
9	14	2
6	15	4
10	15	1
11	16	4
12	16	5
13	16	6

$Z_2 =$

14	1	2	15	3	16	7	4	8	5	9	6	10	11	12	13
0	1	0	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	0	0	0	1	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
0	0	1	0	0	0	0	0	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	1	0	0	0	0	0	0	0	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	0	0	1	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0

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MME

$$\begin{bmatrix} \mathbf{X}'\mathbf{X} & \mathbf{X}'\mathbf{Z}_1 & \mathbf{X}'\mathbf{Z}_2 \\ \mathbf{Z}_1'\mathbf{X} & \mathbf{Z}_1'\mathbf{Z}_1 + \mathbf{A}^{-1}\mathbf{k}_{11} & \mathbf{Z}_1'\mathbf{Z}_2 + \mathbf{A}^{-1}\mathbf{k}_{12} \\ \mathbf{Z}_2'\mathbf{X} & \mathbf{Z}_2'\mathbf{Z}_1 + \mathbf{A}^{-1}\mathbf{k}_{21} & \mathbf{Z}_2'\mathbf{Z}_2 + \mathbf{A}^{-1}\mathbf{k}_{22} \end{bmatrix} \begin{bmatrix} \hat{\mathbf{b}} \\ \hat{\mathbf{d}} \\ \hat{\mathbf{m}}_g \end{bmatrix} = \begin{bmatrix} \mathbf{X}'\mathbf{y} \\ \mathbf{Z}_1'\mathbf{y} \\ \mathbf{Z}_2'\mathbf{y} \end{bmatrix}$$

$$\begin{bmatrix} k_{11} & k_{12} \\ k_{21} & k_{22} \end{bmatrix} = \begin{bmatrix} \sigma_d^2 & \sigma_{d,m_g} \\ \sigma_{d,m_g} & \sigma_{m_g}^2 \end{bmatrix}^{-1} \sigma_e^2$$

$$\begin{bmatrix} k_{11} & k_{12} \\ k_{21} & k_{22} \end{bmatrix} = \begin{bmatrix} 2000 & -300 \\ -300 & 1200 \end{bmatrix}^{-1} 6500 = \begin{bmatrix} 3.3766 & .8441 \\ .8441 & 5.6288 \end{bmatrix}$$

36

```

proc iml;
start main;

y={400,
380,
410,
350,
420,
360,
390,
390,
430,
370};

X={1001,
1000,
1001,
0100,
0101,
0100,
0011,
0010,
0011,
0010};

Z1={0 0 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 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 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 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 0 1};

Z2={ 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0,
00 1 0 0 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 1 0 0 0 0 0 0 0 0 0 0 0 0 0,
00 1 0 0 0 0 0 0 0 0 0 0 0 0 0,
00 0 0 0 0 0 1 0 0 0 0 0 0 0 0,
0 1 0 0 0 0 0 0 0 0 0 0 0 0 0,
00 0 0 0 0 0 1 0 0 0 0 0 0 0 0,
00 0 0 0 0 0 1 0 0 0 0 0 0 0 0,
00 0 0 0 0 0 0 1 0 0 0 0 0 0 0,
00 0 0 0 0 0 0 0 1 0 0 0 0 0 0,
00 0 0 0 0 0 0 0 0 1 0 0 0 0 0};

```

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```

Ainv={2.5 .5 1 0 0 0 -1 -1 0 0 -1 0 0 0 0,
.5 2.5 0 1 0 0 -1 0 0 -1 0 0 -1 0 0,
1 0 2 0 0 0 0 -1 0 0 -1 0 0 0 0,
0 1 0 3 .5 0 0 .5 -1 -1 0 -1 -1 0 0,
0 0 0 .5 1.5 0 0 0 -1 0 0 0 0 0 0,
0 0 0 0 2.5 0 .5 0 .5 0 .5 0 -1 -1 -1,
-1 -1 0 0 0 2 0 0 0 0 0 0 0 0 0,
-1 0 -1 .5 0 .5 0 3 0 0 0 -1 0 -1 0,
0 0 0 -1 -1 0 0 0 2 0 0 0 0 0 0,
0 -1 0 -1 0 .5 0 0 0 2.5 0 0 0 -1 0,
-1 0 -1 0 0 0 0 0 0 0 2 0 0 0 0,
0 0 0 -1 0 .5 0 -1 0 0 0 2.5 0 0 -1,
0 -1 0 -1 0 0 0 0 0 0 0 2 0 0 0,
0 0 0 0 -1 0 -1 0 0 0 0 0 2 0 0,
0 0 0 0 -1 0 0 0 -1 0 0 0 0 2 0,
0 0 0 0 -1 0 0 0 0 0 -1 0 0 0 2};

```

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```

P={2000 -300,
   -300 1200};

K=inv(P)#6500;
LHS=((X`*X)|(X`*Z1)|(X`*Z2))
//((Z1`*X)|(Z1`*Z1+AINV#K[1,1])|(Z1`*Z2+AINV#K[1,2]))
//((Z2`*X)|(Z2`*Z1+AINV#K[2,1])|(Z2`*Z2+AINV#K[2,2]));
RHS=(X`*Y)/(Z1`*Y)/(Z2`*Y);
C=INV(LHS);
BU=C*RHS;
print BU ;
finish main;
run;
quit;

```

“BLUP Maternal Genetic.sas”

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B		\hat{d}	Animal	\hat{m}_g	Animal
369.40	}	1.567	14	0.09	14
363.10		-2.43	1	-3.65	1
374.56		1.79	15	2.68	15
41.48	←	-3.57	3	1.16	3
		0.07	16	0.10	16
		2.58	7	-0.38	7
		-1.34	4	-1.64	4
		2.67	8	1.55	8
		-1.65	5	0.61	5
		-3.28	9	-0.09	9
		3.15	6	1.16	6
		-1.26	10	1.00	10
		-5.59	11	-0.85	11
		4.13	12	0.36	12
		1.56	13	-0.52	13
		-0.16		0.43	

40

What to do with the estimates in a breeding program

- Selection Index Give a weight to each effect and combine in an index

$$I_i = w_1 \hat{d}_i + w_2 \hat{m}_i$$

Weights are dependent on the economic impact of each trait on overall profits

41

Incorporation of both Maternal Effects Maternal Genetic and Maternal Environment

Add another random effect for common maternal environment

$$\mathbf{y} = \mathbf{X}\mathbf{b} + \mathbf{Z}_1\mathbf{d} + \mathbf{Z}_2\mathbf{m}_g + \mathbf{Z}_3\mathbf{m}_e + \mathbf{e}$$

$$V \begin{bmatrix} \mathbf{d} \\ \mathbf{m} \\ \mathbf{p} \\ \mathbf{e} \end{bmatrix} = \begin{bmatrix} \mathbf{A}\sigma_d^2 & \mathbf{A}\sigma_{d,m_g} & 0 & 0 \\ \mathbf{A}\sigma_{d,m_g} & \mathbf{A}\sigma_{m_g}^2 & 0 & 0 \\ 0 & 0 & \mathbf{I}\sigma_{m_e}^2 & 0 \\ 0 & 0 & 0 & \mathbf{I}\sigma_e^2 \end{bmatrix}$$

Question: what is an alternative approach?

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MME

$$\begin{bmatrix} \mathbf{X}'\mathbf{X} & \mathbf{X}'\mathbf{Z}_1 & \mathbf{X}'\mathbf{Z}_2 & \mathbf{X}'\mathbf{Z}_3 \\ \mathbf{Z}_1'\mathbf{X} & \mathbf{Z}_1'\mathbf{Z}_1 + \mathbf{A}^{-1}\mathbf{k}_{11} & \mathbf{Z}_1'\mathbf{Z}_2 + \mathbf{A}^{-1}\mathbf{k}_{12} & \mathbf{Z}_1'\mathbf{Z}_3 \\ \mathbf{Z}_2'\mathbf{X} & \mathbf{Z}_2'\mathbf{Z}_1 + \mathbf{A}^{-1}\mathbf{k}_{21} & \mathbf{Z}_2'\mathbf{Z}_2 + \mathbf{A}^{-1}\mathbf{k}_{22} & \mathbf{Z}_2'\mathbf{Z}_3 \\ \mathbf{Z}_3'\mathbf{X} & \mathbf{Z}_3'\mathbf{Z}_1 & \mathbf{Z}_3'\mathbf{Z}_2 & \mathbf{Z}_3'\mathbf{Z}_3 + \mathbf{I}k_{33} \end{bmatrix} \begin{bmatrix} \hat{\mathbf{b}} \\ \hat{\mathbf{d}} \\ \hat{\mathbf{m}}_g \\ \hat{\mathbf{m}}_e \end{bmatrix} = \begin{bmatrix} \mathbf{X}'\mathbf{y} \\ \mathbf{Z}_1'\mathbf{y} \\ \mathbf{Z}_2'\mathbf{y} \\ \mathbf{Z}_3'\mathbf{y} \end{bmatrix}$$

$$\begin{bmatrix} k_{11} & k_{12} \\ k_{21} & k_{22} \end{bmatrix} = \begin{bmatrix} \sigma_d^2 & \sigma_{d,m_g} \\ \sigma_{d,m_g} & \sigma_{m_g}^2 \end{bmatrix}^{-1} \sigma_e^2 \quad k_{33} = \frac{\sigma_e^2}{\sigma_{m_e}^2} = \frac{6500}{130} = 50$$

$$\begin{bmatrix} k_{11} & k_{12} \\ k_{21} & k_{22} \end{bmatrix} = \begin{bmatrix} 2000 & -300 \\ -300 & 1200 \end{bmatrix}^{-1} 6500 = \begin{bmatrix} 3.3766 & .8441 \\ .8441 & 5.6288 \end{bmatrix}$$

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For this example, all other matrices as previously defined

$$\mathbf{Z}_3 = \begin{bmatrix} 1 & 0 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 & 0 \\ 1 & 0 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 & 0 \\ 1 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 0 & 1 \end{bmatrix} \quad \mathbf{I} = \begin{bmatrix} 1 & 0 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 0 & 1 \end{bmatrix}$$

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SAS Program Changes

```

I6=I(6); *IDENTITY MATRIX;
P={2000 -300,
  -300 1200};
K=inv(P)#6500;
K33=(6500/130);
LHS=((X`*X) ||(X`*Z1)      ||(X`*Z2)      ||(X`*Z3))
      //((Z1`*X)|| (Z1`*Z1+GINV#K[1,1])|| (Z1`*Z2+GINV#K[1,2])|| (Z1`*Z3))
      //((Z2`*X)|| (Z2`*Z1+GINV#K[2,1])|| (Z2`*Z2+GINV#K[2,2])|| (Z2`*Z3))
      //((Z3`*X)|| (Z3`*Z1)      ||(Z3`*Z2)      ||(Z3`*Z3)+I6#K33);
RHS=(X`*Y)/(Z1`*Y)/(Z2`*Y)/(Z3`*Y);
C=INV(LHS);
BU=C*RHS;
RMSE=(Y`*Y-BU`*RHS)#(1/6);
print BU ;

```

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\hat{d}	Animal	\hat{m}_g	\hat{m}_e
1.5428319	14	0.0801625	-0.559916
-2.359447	1 2	-3.53917	0.2879317
1.7392423	15	2.6088634	0.0115168
-3.527759	3	1.1385914	0.1232801
0.0620136	16	0.0930204	0.2434657
2.5431176	7	-0.381468	-0.106279
-1.269176	4	-1.600374	
2.6021552	8	1.5119326	
-1.644282	5	0.6025173	
-3.191177	9	-0.081604	
3.083619	6	1.1281257	369.48125
-1.288459	10	0.9769888	363.16015
-5.48672	11	-0.818822	374.63341
4.0604681	12	0.3420577	41.482657
1.5487832	13	-0.512458	
-0.190198		0.4203896	

} Year
 ← Sex

46

Paternal Effects

- Paternal Genetic
 - What could these be due to?
 - What is the model for analysis
 - Using the same pedigree, what are the MME?
- Paternal Environmental
 - What could these be due to?
 - What is the model for analysis
 - Using the same pedigree, what are the MME?

47

Paternal Genetic Effects

$$y_{ijkmn} = (HY)_i + S_j + D_k + P_n + e_{ijkmn}$$

↑ Herd Year ↑ Sex ↑ Direct Genetic ↑ Paternal Genetic ↓ Random error

⏟ Fixed Effects ⏟ Random Effects

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Paternal Genetic Effects

$$y = Xb + Z_1d + Z_2p_g + e$$

Direct effect
Paternal Genetic

$$V \begin{bmatrix} d \\ p \\ e \end{bmatrix} = \begin{bmatrix} A\sigma_d^2 & A\sigma_{d,p_g} & 0 \\ A\sigma_{d,p_g} & A\sigma_{p_g}^2 & 0 \\ 0 & 0 & I\sigma_e^2 \end{bmatrix}$$

There is a genetic correlation between the animals direct and paternal genetic effect

The are inherited and determined by additive effects in the father

No environmental correlations

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Pedigree

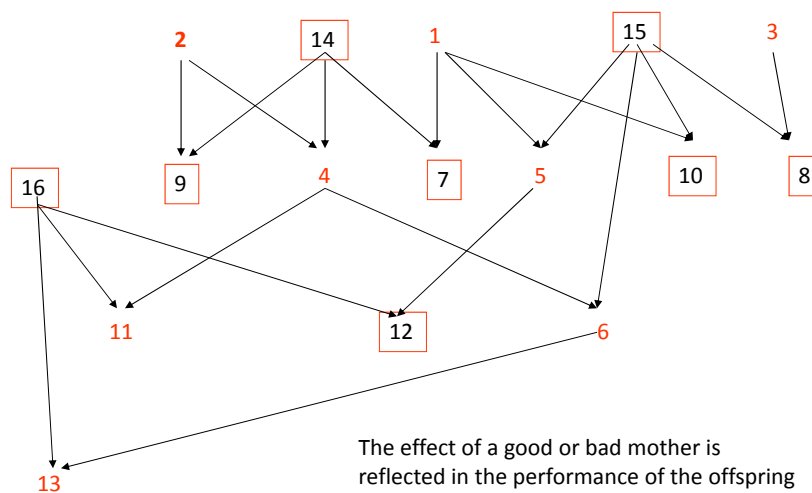
The effect of a good or bad father is reflected in the performance of the offspring

50

Pedigree and Data (same as before)

Animal	Sire	Dam	Year	Sex	Wean Wt
7	14	1	86	M	400
4	14	2	86	F	380
8	15	3	86	M	410
5	15	1	87	F	350
9	14	2	87	M	420
6	15	4	87	F	360
10	15	1	88	M	390
11	16	4	88	F	390
12	16	5	88	M	430
13	16	6	88	F	370

Pedigree



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Year sex
86 87 88 m

$$\mathbf{X} = \begin{bmatrix} 1 & 0 & 0 & 1 \\ 1 & 0 & 0 & 0 \\ 1 & 0 & 0 & 1 \\ 0 & 1 & 0 & 0 \\ 0 & 1 & 0 & 1 \\ 0 & 1 & 0 & 0 \\ 0 & 0 & 1 & 1 \\ 0 & 0 & 1 & 0 \\ 0 & 0 & 1 & 1 \\ 0 & 0 & 1 & 0 \end{bmatrix}$$

$$\mathbf{B} = \begin{bmatrix} b_1 \\ b_2 \\ b_3 \\ b_4 \end{bmatrix}$$

} Herd
 } Year
 ← Sex

$$\mathbf{Y} = \begin{bmatrix} 400 \\ 380 \\ 410 \\ 350 \\ 420 \\ 360 \\ 390 \\ 390 \\ 430 \\ 370 \end{bmatrix}$$

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Question: For Animal Direct Genetic Effect
What values should be placed in this matrix?

An	Sire	Dam
7	14	1
4	14	2
8	15	3
5	15	1
9	14	2
6	15	4
10	15	1
11	16	4
12	16	5
13	16	6

$$\mathbf{Z}_1 = \begin{bmatrix} 14 & 1 & 2 & 15 & 3 & 16 & 7 & 4 & 8 & 5 & 9 & 6 & 10 & 11 & 12 & 13 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \end{bmatrix}$$

54

Paternal Genetic Effect-identify the fathers of the animal

What values should be placed in this matrix?

An	Sire	Dam
7	14	1
4	14	2
8	15	3
5	15	1
9	14	2
6	15	4
10	15	1
11	16	4
12	16	5
13	16	6

$$\mathbf{Z}_2 = \begin{matrix} & \begin{matrix} 14 & 1 & 2 & 15 & 3 & 16 & 7 & 4 & 8 & 5 & 9 & 6 & 10 & 11 & 12 & 13 \end{matrix} \\ \begin{matrix} 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \end{matrix} \end{matrix}$$

55

MME

$$\begin{bmatrix} \mathbf{X}'\mathbf{X} & \mathbf{X}'\mathbf{Z}_1 & \mathbf{X}'\mathbf{Z}_2 \\ \mathbf{Z}_1'\mathbf{X} & \mathbf{Z}_1'\mathbf{Z}_1 + \mathbf{A}^{-1}\mathbf{k}_{11} & \mathbf{Z}_1'\mathbf{Z}_2 + \mathbf{A}^{-1}\mathbf{k}_{12} \\ \mathbf{Z}_2'\mathbf{X} & \mathbf{Z}_2'\mathbf{Z}_1 + \mathbf{A}^{-1}\mathbf{k}_{21} & \mathbf{Z}_2'\mathbf{Z}_2 + \mathbf{A}^{-1}\mathbf{k}_{22} \end{bmatrix} \begin{bmatrix} \hat{\mathbf{b}} \\ \hat{\mathbf{d}} \\ \hat{\mathbf{p}}_g \end{bmatrix} = \begin{bmatrix} \mathbf{X}'\mathbf{y} \\ \mathbf{Z}_1'\mathbf{y} \\ \mathbf{Z}_2'\mathbf{y} \end{bmatrix}$$

$$\begin{bmatrix} k_{11} & k_{12} \\ k_{21} & k_{22} \end{bmatrix} = \begin{bmatrix} \sigma_d^2 & \sigma_{d,p_g} \\ \sigma_{d,p_g} & \sigma_{p_g}^2 \end{bmatrix}^{-1} \sigma_e^2$$

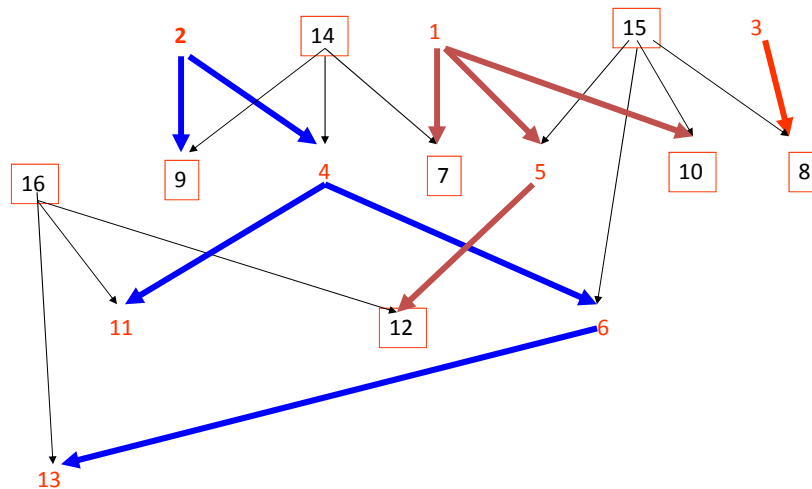
56

Cytoplasmic Effects

Nuclear Environmental Effect
Follows Maternal Lines Only

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Pedigree



58

Model Cytoplasmic Effects

$$y_{ijkmn} = (HY)_i + S_j + D_k + M_n + e_{ijkmn}$$

↑ Herd Year ↑ Sex ↑ Direct Genetic ↑ Cytoplasmic ↑ Random error

⏟ Fixed Effects ⏟ Random Effects

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Cytoplasmic Effects Mixed Model

$$\mathbf{y} = \mathbf{X}\mathbf{b} + \mathbf{Z}_1\mathbf{d} + \mathbf{Z}_2\mathbf{c} + \mathbf{e}$$

↑ Direct effect ↑ Cytoplasmic

$$V \begin{bmatrix} \mathbf{d} \\ \mathbf{m} \\ \mathbf{e} \end{bmatrix} = \begin{bmatrix} \mathbf{A}\sigma_d^2 & 0 & 0 \\ 0 & \mathbf{I}\sigma_m^2 & 0 \\ 0 & 0 & \mathbf{I}\sigma_e^2 \end{bmatrix}$$

Assumes no cytoplasmic – nuclear gene interaction

60

Year	sex
86 87 88 m	

$$\mathbf{X} = \begin{bmatrix} 1 & 0 & 0 & 1 \\ 1 & 0 & 0 & 0 \\ 1 & 0 & 0 & 1 \\ 0 & 1 & 0 & 0 \\ 0 & 1 & 0 & 1 \\ 0 & 1 & 0 & 0 \\ 0 & 0 & 1 & 1 \\ 0 & 0 & 1 & 0 \\ 0 & 0 & 1 & 1 \\ 0 & 0 & 1 & 0 \end{bmatrix}$$

$$\mathbf{B} = \begin{bmatrix} b_1 \\ b_2 \\ b_3 \\ b_4 \end{bmatrix}$$

}

Herd
Year

←

Sex

$$\mathbf{Y} = \begin{bmatrix} 400 \\ 380 \\ 410 \\ 350 \\ 420 \\ 360 \\ 390 \\ 390 \\ 430 \\ 370 \end{bmatrix}$$

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Direct effect: Animal

An	Sire	Dam
7	14	1
4	14	2
8	15	3
5	15	1
9	14	2
6	15	4
10	15	1
11	16	4
12	16	5
13	16	6

$$\mathbf{Z}_1 = \begin{bmatrix} 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 \end{bmatrix}$$

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Cytoplasmic

Animal 1 was the mother lineage of animals 7, 5, 10, 12

An	Sire	Dam
7	14	1
4	14	2
8	15	3
5	15	1
9	14	2
6	15	4
10	15	1
11	16	4
12	16	5
13	16	6

↓

1 2 3 Maternal Lineages

$$\mathbf{Z}_2 = \begin{bmatrix} 1 & 0 & 0 \\ 0 & 1 & 0 \\ 0 & 0 & 1 \\ 1 & 0 & 0 \\ 0 & 1 & 0 \\ 0 & 1 & 0 \\ 1 & 0 & 0 \\ 0 & 1 & 0 \\ 1 & 0 & 0 \\ 0 & 1 & 0 \\ 1 & 0 & 0 \\ 0 & 1 & 0 \end{bmatrix}$$

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MME

$$\begin{bmatrix} \mathbf{X}'\mathbf{X} & \mathbf{X}'\mathbf{Z}_1 & \mathbf{X}'\mathbf{Z}_2 \\ \mathbf{Z}_1'\mathbf{X} & \mathbf{Z}_1'\mathbf{Z}_1 + \mathbf{A}^{-1}k_{11} & \mathbf{Z}_1'\mathbf{Z}_2 \\ \mathbf{Z}_2'\mathbf{X} & \mathbf{Z}_2'\mathbf{Z}_1 & \mathbf{Z}_2'\mathbf{Z}_2 + \mathbf{I}k_{22} \end{bmatrix} \begin{bmatrix} \hat{\mathbf{b}} \\ \hat{\mathbf{a}} \\ \hat{\mathbf{c}} \end{bmatrix} = \begin{bmatrix} \mathbf{X}'\mathbf{y} \\ \mathbf{Z}_1'\mathbf{y} \\ \mathbf{Z}_2'\mathbf{y} \end{bmatrix}$$

$$\begin{bmatrix} k_{11} & k_{12} \\ k_{21} & k_{22} \end{bmatrix} = \begin{bmatrix} \sigma_d^2 & 0 \\ 0 & \sigma_c^2 \end{bmatrix}^{-1} \sigma_e^2 \quad \mathbf{I} = \begin{bmatrix} 1 & 0 & 0 \\ 0 & 1 & 0 \\ 0 & 0 & 0 \end{bmatrix}$$

$$\begin{bmatrix} k_{11} & k_{12} \\ k_{21} & k_{22} \end{bmatrix} = \begin{bmatrix} 2000 & 0 \\ 0 & 1200 \end{bmatrix}^{-1} 6500 = \begin{bmatrix} 3.25 & 0 \\ 0 & 5.42 \end{bmatrix}$$

64


```

proc iml;
start main;
y={400,
380,
410,
350,
420,
360,
390,
390,
430,
370};
X={1001,
1000,
1001,
0100,
0101,
0100,
0011,
0010,
0011,
0010};
Z1={0 0 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 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 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 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 0 1};
Z2={ 1 0 0,
0 1 0,
0 0 1,
1 0 0,
0 1 0,
0 0 0,
1 0 0,
0 0 0,
0 0 0,
0 0 0};
I={100,
010,
001};

```

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```

Ainv={2.5 .5 1 0 0 0 -1 -1 0 0 -1 0 0 0 0,
.5 2.5 0 1 0 0 -1 0 0 -1 0 0 -1 0 0,
1 0 2 0 0 0 0 -1 0 0 -1 0 0 0 0,
0 1 0 3 .5 0 0 .5 -1 -1 0 -1 -1 0 0,
0 0 0 .5 1.5 0 0 0 -1 0 0 0 0 0 0,
0 0 0 0 2.5 0 .5 0 .5 0 .5 0 -1 -1 -1,
-1 -1 0 0 0 2 0 0 0 0 0 0 0 0 0,
-1 0 -1 .5 0 .5 0 3 0 0 0 -1 0 -1 0,
0 0 0 -1 -1 0 0 0 2 0 0 0 0 0 0,
0 -1 0 -1 0 .5 0 0 0 2.5 0 0 0 0 -1,
-1 0 -1 0 0 0 0 0 0 0 2 0 0 0 0,
0 0 0 -1 0 .5 0 -1 0 0 2.5 0 0 0 -1,
0 -1 0 -1 0 0 0 0 0 0 0 2 0 0 0,
0 0 0 0 0 -1 0 -1 0 0 0 0 2 0 0,
0 0 0 0 0 -1 0 0 0 -1 0 0 0 2 0,
0 0 0 0 0 -1 0 0 0 0 0 -1 0 0 2};

```

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```

P={2000 0,
   0 1200};

K=inv(P)#6500;

LHS=((X`*X)|(X`*Z1)|(X`*Z2))
//((Z1`*X)|(Z1`*Z1+AINV#K[1,1])|(Z1`*Z2))
//((Z2`*X)|(Z2`*Z1)|(Z2`*Z2+#K[2,2]));

RHS=(X`*Y)/(Z1`*Y)/(Z2`*Y);
C=INV(LHS);
BU=C*RHS;
RMSE=(Y`*Y-BU`*RHS)#(1/6);
print BU RMSE;
finish main;run;quit;

```

“BLUP cytoplasmic Genetic.sas”

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B		\hat{a}	Animal	\hat{c}	Animal
368.15	}	1.55	14	-2.81	1
361.75		-3.45	1 1	2.73	2 3
373.55		2.53	2 15	0.08	3
42.94	←	-3.40	3		
		0.06	16		
		2.70	7		
		-1.92	4		
		3.17	8		
		-1.60	5		
		-3.20	9		
		3.44	6		
		-1.10	10		
		6.12	11		
		4.37	12		
		1.95	13		
		-0.14			

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What to do with the estimates in a breeding program

- Selection Index
 - Give a weight to each effect and combine in an index

$$I_i = w_1 \hat{a}_i + w_2 \hat{c}_i$$

Weights are dependent on the economic impact of each trait on overall profits.

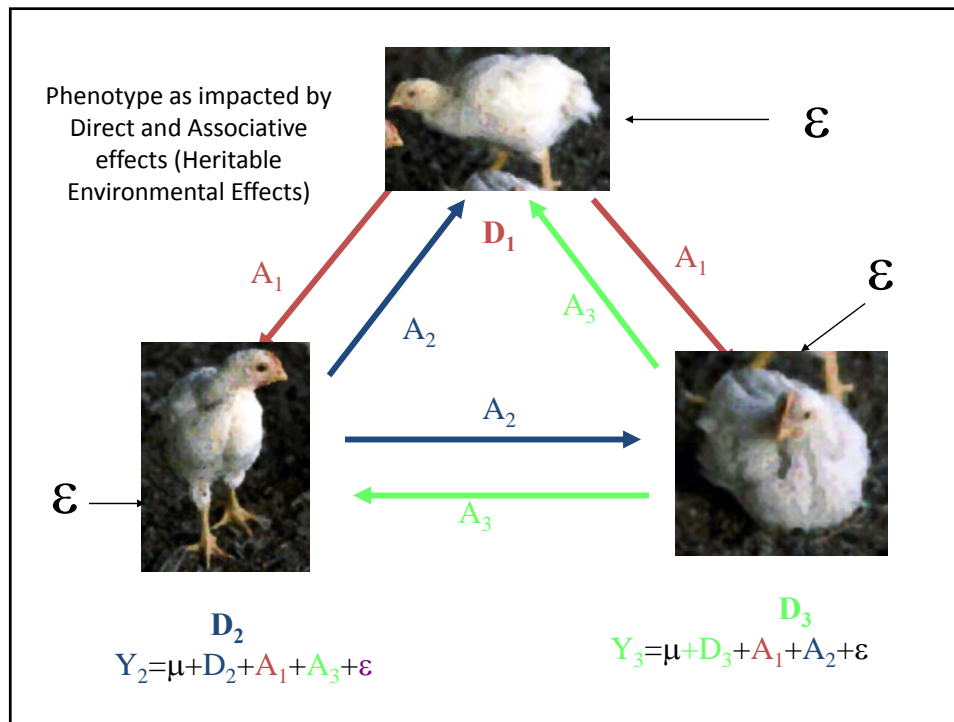
Economic impact of cytoplasmic effect changes with the time horizon. Over a large number of generation could be a very substantial effect

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Social Effects Interacting Genotypes

Animals





Mixed Model Equations

$$Y = X\beta + Z_d\mu_d + Z_a\mu_a + \epsilon$$

Muir and Schinckel (2002)

$$Y = X\beta + Z_d\mu_d + Z_a\mu_a + \epsilon$$

Include correlated residual in R matrix

$$Y = X\beta + Z_d\mu_d + Z_a\mu_a + Z_c\mu_c + e$$

Random effect for shared group

Bijma, P., Muir, W. M., Ellen, E. D., Wolf, J. B., & Van Arendonk, J. A. M. 2007

Variances

$$\mathbf{K} = \begin{bmatrix} k_1 & k_2 \\ k_2 & k_3 \end{bmatrix} = \sigma_\varepsilon^2 \begin{bmatrix} \sigma_D^2 & \sigma_{ad} \\ \sigma_{ad} & \sigma_a^2 \end{bmatrix}^{-1}$$

 σ_d^2

Additive Direct Effects

 σ_a^2

Additive Associate Effects

 σ_{ad}

Covariance Between Additive Direct and Additive Associative Effects

 σ_E^2

Environmental

 σ_c^2

Between Group

 σ_e^2

Within Group

MME with random effect for shared environmental effect

$$\begin{bmatrix} \mathbf{X}'\mathbf{X} & \mathbf{X}'\mathbf{Z}_D & \mathbf{X}'\mathbf{Z}_A & \mathbf{X}'\mathbf{Z}_c \\ \mathbf{Z}_D'\mathbf{X} & \mathbf{Z}_D'\mathbf{Z}_D + \mathbf{A}^{-1}\mathbf{k}_{11} & \mathbf{Z}_D'\mathbf{Z}_A + \mathbf{A}^{-1}\mathbf{k}_{12} & \mathbf{Z}_D'\mathbf{Z}_c \\ \mathbf{Z}_A'\mathbf{X} & \mathbf{Z}_A'\mathbf{Z}_D + \mathbf{A}^{-1}\mathbf{k}_{21} & \mathbf{Z}_A'\mathbf{Z}_A + \mathbf{A}^{-1}\mathbf{k}_{22} & \mathbf{Z}_A'\mathbf{Z}_c \\ \mathbf{Z}_c'\mathbf{X} & \mathbf{Z}_c'\mathbf{Z}_D & \mathbf{Z}_c'\mathbf{Z}_A & \mathbf{Z}_c'\mathbf{Z}_c + \mathbf{I}k_{33} \end{bmatrix} \begin{bmatrix} \hat{\mathbf{b}} \\ \boldsymbol{\mu}_d \\ \boldsymbol{\mu}_a^g \\ \boldsymbol{\mu}_a^e \end{bmatrix} = \begin{bmatrix} \mathbf{X}'\mathbf{y} \\ \mathbf{Z}_D'\mathbf{y} \\ \mathbf{Z}_A'\mathbf{y} \\ \mathbf{Z}_c'\mathbf{y} \end{bmatrix}$$

$$\mathbf{K} = \begin{bmatrix} k_1 & k_2 \\ k_2 & k_3 \end{bmatrix} = \sigma_\varepsilon^2 \begin{bmatrix} \sigma_D^2 & \sigma_{ad} \\ \sigma_{ad} & \sigma_a^2 \end{bmatrix}^{-1}$$

$$k_{33} = \sigma_e^2 / \sigma_c^2$$

MME with correlated residuals

$$\begin{bmatrix} X'R^{-1}X & X'R^{-1}Z_d & X'R^{-1}Z_a \\ Z_dR^{-1}X' & Z_dR^{-1}Z_d + s_1A^{-1} & Z_dR^{-1}Z_a + s_2A^{-1} \\ Z_aR^{-1}X' & Z_aR^{-1}Z_d + s_2A^{-1} & Z_aR^{-1}Z_a + s_3A^{-1} \end{bmatrix} \begin{bmatrix} \beta \\ \mu_d \\ \mu_a \end{bmatrix} = \begin{bmatrix} X'R^{-1}X \\ X'R^{-1}Z_d \\ X'R^{-1}Z_a \end{bmatrix}$$

$$\mathbf{R} = (\sigma_c^2 + \sigma_e^2) \begin{bmatrix} 1 & \rho & \rho & \cdots & 0 & 0 & 0 \\ \rho & 1 & \rho & \cdots & 0 & 0 & 0 \\ \rho & \rho & 1 & \cdots & 0 & 0 & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots & \vdots \\ 0 & 0 & 0 & \cdots & 1 & \rho & \rho \\ 0 & 0 & 0 & \cdots & \rho & 1 & \rho \\ 0 & 0 & 0 & \cdots & \rho & \rho & 1 \end{bmatrix} \quad \begin{bmatrix} s_1 & s_2 \\ s_2 & s_3 \end{bmatrix} = \begin{bmatrix} \sigma_d^2 & \sigma_{ad} \\ \sigma_{ad} & \sigma_a^2 \end{bmatrix}^{-1}$$

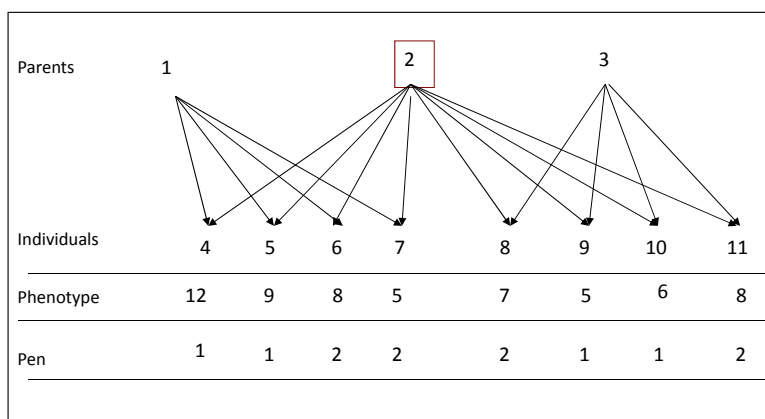
$\rho =$ intra-class environmental correlation

$$\rho = \frac{\sigma_c^2}{\sigma_c^2 + \sigma_e^2}$$

Note if $\rho < 0$, then then

$$\sigma_c^2 < 0$$

Example



Associative Genetic Matrix

					Animal										
Sir	Da	Anim	Pen	Y	1	2	3	4	5	6	7	8	9	10	11
2	1	4	1	12	0	0	0	0	1	0	0	0	1	1	0
2	1	5	1	9	0	0	0	1	0	0	0	0	1	1	0
2	1	6	2	8	0	0	0	0	0	0	1	1	0	0	1
2	1	7	2	5	0	0	0	0	0	1	0	1	0	0	1
2	3	8	2	7	0	0	0	0	0	1	1	0	0	0	1
2	3	9	1	5	0	0	0	1	1	0	0	0	0	1	0
2	3	10	1	6	0	0	0	1	1	0	0	0	1	0	0
2	3	11	2	8	0	0	0	0	0	1	1	1	0	0	0

$Z_a =$

↑
 Who was in the same pen as animal 4

Genetic Parameters

$$\sigma_\varepsilon^2 \begin{bmatrix} \sigma_d^2 & \sigma_{ad}^2 \\ \sigma_d^2 & \sigma_a^2 \end{bmatrix} = 60 \begin{bmatrix} 30 & -4 \\ -4 & 10 \end{bmatrix}$$

$$\sigma_c^2 = 6$$

```

proc iml;
start main;
y={12, 9, 8, 5, 7, 5, 6, 8};
X={1, 1, 1, 1, 1, 1, 1, 1};
A={1 0 0 .5 .5 .5 .5 0 0 0 0,
   0 1 0 .5 .5 .5 .5 .5 .5 .5,
   0 0 1 0 0 0 0 .5 .5 .5 .5,
   .5 .5 0 1 .5 .5 .5 .25 .25 .25 .25,
   .5 .5 0 .5 1 .5 .5 .25 .25 .25 .25,
   .5 .5 0 .5 .5 1 .5 .25 .25 .25 .25,
   0 .5 .5 .25 .25 .25 .25 1 .5 .5 .5,
   0 .5 .5 .25 .25 .25 .25 .5 1 .5 .5,
   0 .5 .5 .25 .25 .25 .25 .5 .5 1 .5,
   0 .5 .5 .25 .25 .25 .25 .5 .5 .5 1};
Za={000100000000,
    000010000000,
    000001000000,
    000000100000,
    000000010000,
    000000001000,
    000000000100,
    000000000010,
    000000000001};
Zb={000010000110,
    000100000110,
    000000011001,
    000000101001,
    000000110001,
    000110000010,
    000110000100,
    000000111000};
Zc={1 0,
    1 0,
    0 1,
    0 1,
    0 1,
    1 0,
    1 0,
    0 1};

```

```

I2=I(2); *IDENTITY MATRIX;
P={30 -4,
   -4 10};
K=inv(P)#60;
K33=(60/6);

LHS=((X`*X) || (X`*Z1) || (X`*Z2) || (X`*Z3))
     ///((Z1`*X) || (Z1`*Z1+AINV#K[1,1]) || (Z1`*Z2+AINV#K[1,2]) || (Z1`*Z3))
     ///((Z2`*X) || (Z2`*Z1+AINV#K[2,1]) || (Z2`*Z2+AINV#K[2,2]) || (Z2`*Z3))
     ///((Z3`*X) || (Z3`*Z1) || (Z3`*Z2) || (Z3`*Z3)+I2#K33);

RHS=(X`*Y)/(Z1`*Y)/(Z2`*Y)/(Z3`*Y);
C=INV(LHS);
BU=C*RHS;
RMSE=(Y`*Y-BU`*RHS)#(1/6);
print BU ;
finish main;
run;
quit;

```

See BLUP Competition.sas

Estimates

$$\hat{\mathbf{u}} = 7.5$$

Individual	Direct Genetics (D_i)	Associative Genetics (A^g)	Cage Effect
1	0.515152	-0.21212	0.090909
2	-2.40E-15	3.37E-15	-0.09091
3	-0.51515	0.212121	
4	1.027597	-0.35985	
5	0.420455	-0.10985	
6	0.352273	-0.20833	
7	-0.25487	0.041667	
8	-0.21807	0.026515	
9	-0.75704	0.375	
10	-0.55465	0.291667	
11	-0.01569	-0.05682	

Note animal with best direct effect has worst associative effect

Index Selection

$$I = b_1 \hat{\mu}_d + b_2 \hat{\mu}_a$$

Because the Estimates have already been regressed based on genetic parameters and information from relatives, a base index simply adds contribution to the pen mean

$$I = \hat{\mu}_d + (n-1)\hat{A}^g$$

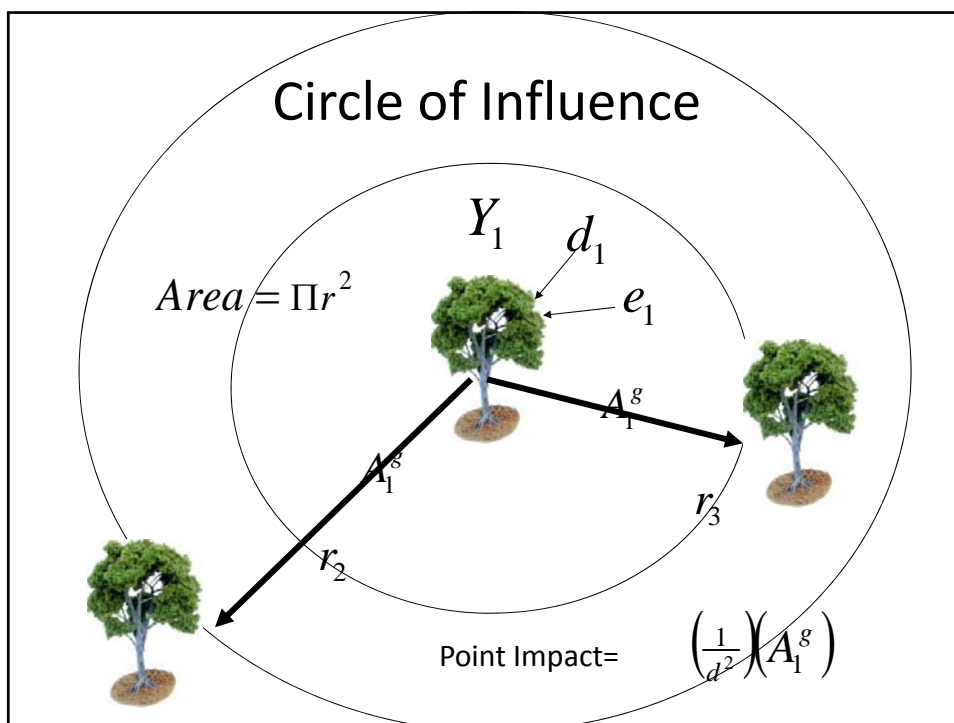
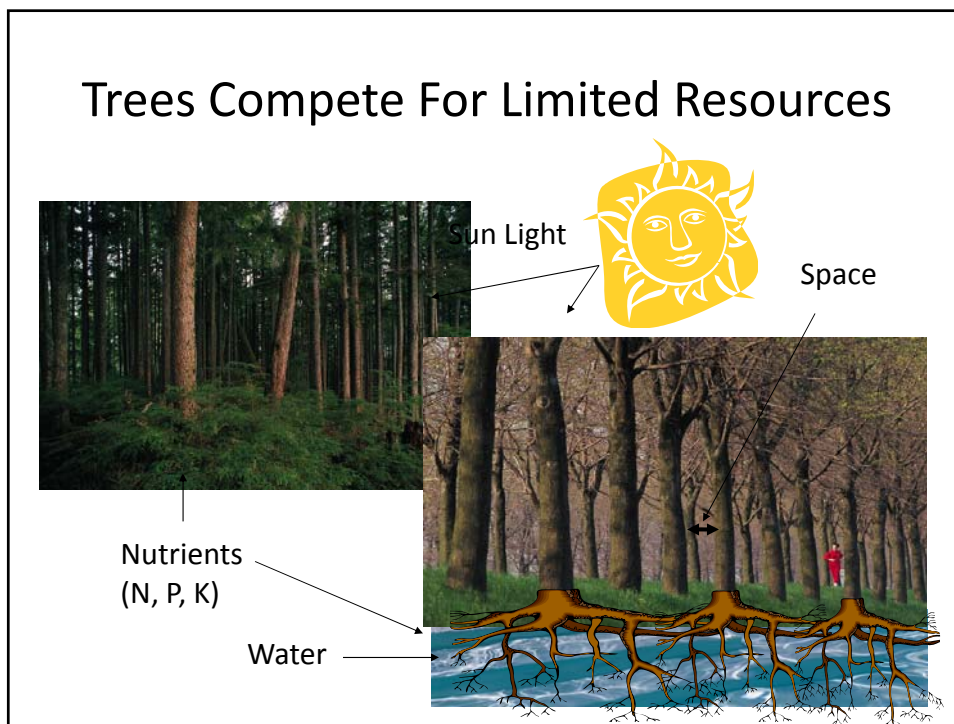
Index

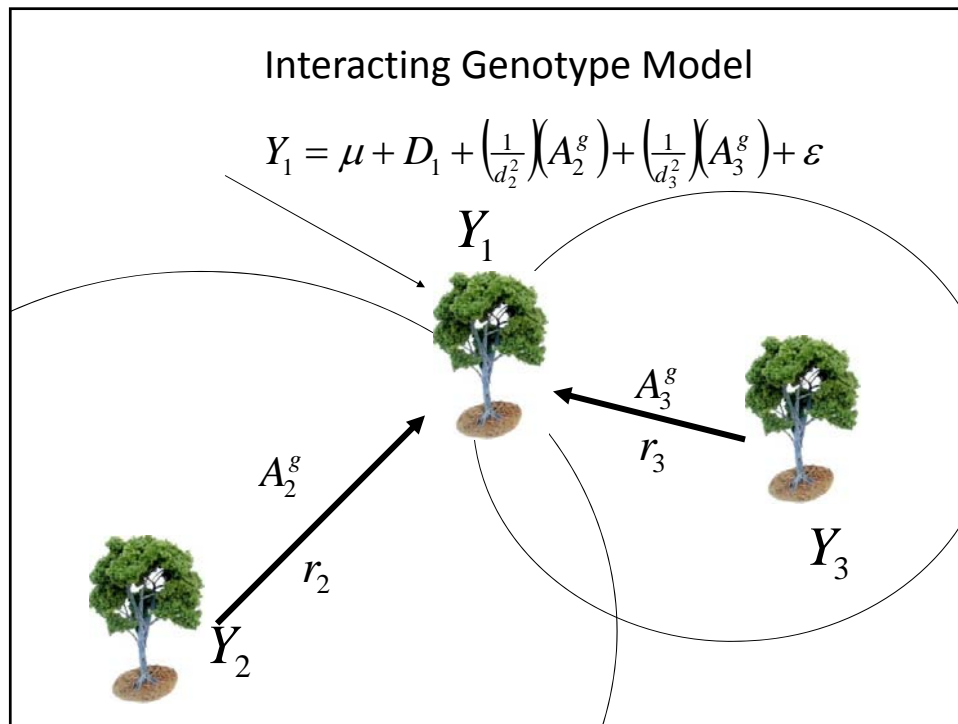
Individual	Direct Genetics (D_i)	Associative Genetics (A_g)	Index	
1	0.464	-0.191	-0.109	
2	0.000	0.000	0	
3	-0.464	0.191	0.109	
4	0.935	-0.327	-0.046	
5	0.368	-0.094	0.086	
6	0.328	-0.192	-0.248	← Worst
7	-0.238	0.040	-0.118	
8	-0.201	0.025	-0.126	
9	-0.721	0.409	0.506	← Best
10	-0.459	0.191	0.114	
11	-0.012	-0.052	-0.168	

Competitive Effects in Tree Breeding Programs Competition by Distance



Trees Compete For Limited Resources





Estimation

- Problem
 - Twice As Many Unknowns than Equations
 - For Each Individual Must Estimate Both

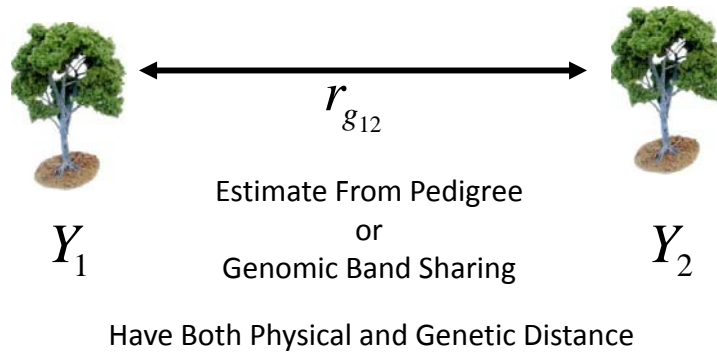
$$D_i \quad A_i$$

From a Series of Equations of the Form

$$Y_1 = \mu + D_1 + \left(\frac{1}{d_2}\right)(A_2^g) + \left(\frac{1}{d_3}\right)(A_3^g) + \varepsilon$$

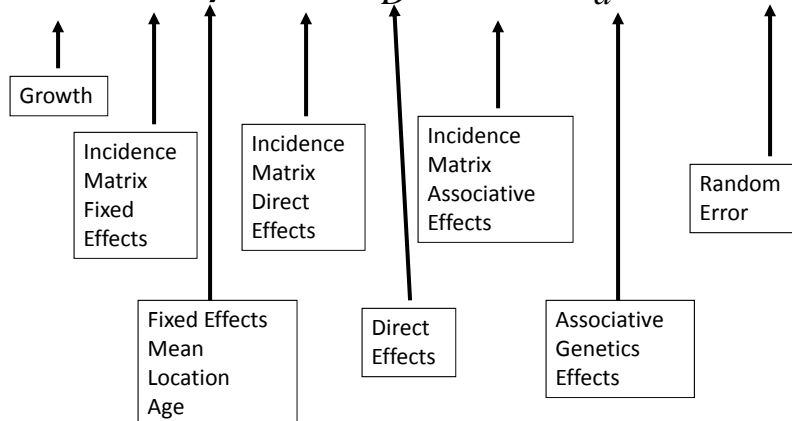
Solution

Genetic Relationships Between Individuals
Can be Used to Augment Equations and
Find Solutions



Mixed Model Equations

$$Y = X\beta + Z_D D + Z_a a + \varepsilon$$



Associative Effects Incidence Matrix

$$\mathbf{Z}_{A^g} = \begin{bmatrix} 0 & \frac{1}{d_2^2} & \frac{1}{d_3^2} \\ \frac{1}{d_2^2} & 0 & \frac{1}{d_4^2} \\ \frac{1}{d_3^2} & \frac{1}{d_4^2} & 0 \end{bmatrix}$$

Maximum Likelihood Solutions

$$\begin{bmatrix} X'R^1X & X'R^1Z_d & X'R^1Z_a \\ Z_d'R^1X & Z_d'R^1Z_d + s_1A^{-1} & Z_d'R^1Z_a + s_2A^{-1} \\ Z_a'R^1X & Z_a'R^1Z_d + s_2A^{-1} & Z_a'R^1Z_a + s_3A^{-1} \end{bmatrix} \begin{bmatrix} \beta \\ \mu_d \\ \mu_a \end{bmatrix} = \begin{bmatrix} X'R^1X \\ X'R^1Z_d \\ X'R^1Z_a \end{bmatrix}$$

\mathbf{A}^{-1} Inverse of Additive Relationship Matrix

$$\begin{bmatrix} s_1 & s_2 \\ s_2 & s_3 \end{bmatrix} = \begin{bmatrix} \sigma_d^2 & \sigma_{ad} \\ \sigma_{ad} & \sigma_a^2 \end{bmatrix}^{-1}$$