

Chapter 5

Diallel Analysis for an Animal Model with Sex-Linked and Maternal Effects Along with Genotype-by-Environment Interaction Effects

Jun Zhu

Purpose

To analyze balanced or unbalanced data of an animal genetic model for estimating components of variance, covariance, heritability, and selection response.

Definitions

Mating Design

A set of inbred lines is sampled from a reference population. Parents are used to produce F_1 crosses. Experiments with parents and their F_1 s are conducted in multiple environments.

Genetic Model

The genetic model for the phenotypic mean (y_{ijks}) of sex s in block k within environment h from the cross between maternal line i and paternal line j is

$$y_{hijks} = \mu + E_h + G_{ijs} + GE_{hijks} + e_{hijks}$$

where μ = population mean, E_h = environment effect, G_{ijs} = genotype effect, GE_{hij_s} = genotype-environment effect, and $e_{hij_s k}$ = residual effect.

The total genotype effect G_{ijs} and genotype \times environment interaction effect GE_{hij_s} can be further partitioned into different components for heterogametic progeny (XY or ZW, $s = 1$) and for homogametic progeny (XX or ZZ, $s = 2$):

$$\begin{aligned} G_{ij1}^{XY} + GE_{ij1}^{XY} &= A_i + A_j + D_{ij} + L_{i1} + M_i + AE_{hi} + AE_{hj} + DE_{hij} + LE_{hi1} + ME_{hi} \\ \text{or } G_{ij1}^{ZW} + GE_{ij1}^{ZW} &= A_i + A_j + D_{ij} + L_{j1} + M_i + AE_{hi} + AE_{hj} + DE_{hij} + LE_{hj1} + ME_{hi} \\ G_{ij2}^{XX/ZZ} + GE_{ij2}^{XX/ZZ} &= A_i + A_j + D_{ij} + \frac{1}{2}L_{i2} + \frac{1}{2}L_{j2} + M_i + AE_{hi} + AE_{hj} + DE_{hij} + \frac{1}{2}LE_{hi2} \\ &\quad + \frac{1}{2}LE_{hj2} + ME_{hi} \end{aligned}$$

where A_i (or A_j) $\sim (0, \sigma_A^2)$ is the additive effect of autosomal genes; D_{ij} $\sim (0, \sigma_D^2)$ is the dominance effect of autosomal genes; L_{i1} (or L_{j1}) and L_{i2} (or L_{j2}) $\sim (0, \sigma_L^2)$ is the additive effect of sex-linked genes; M_i $\sim (0, \sigma_M^2)$ is the maternal effect of dam i ; AE_{hi} (or AE_{hj}) $\sim (0, \sigma_{AE}^2)$ is the additive \times environment interaction effect of autosomal genes; DE_{hij} $\sim (0, \sigma_{DE}^2)$ is the dominance \times environment interaction effect of autosomal genes; L_{i1} (or L_{j1}), L_{i2} (or L_{j2}) $\sim (0, \sigma_{LE}^2)$ is the sex-linked additive \times environment interaction effect; and ME_{hi} $\sim (0, \sigma_M^2)$ is the maternal \times environment interaction effect of dam i .

Analysis

Mixed Linear Model

The phenotypic mean of the genetic model can be expressed by a mixed linear model as

$$\begin{aligned} y &= Xb + U_A e_A + U_D e_D + U_L e_L + U_M e_M + U_{AE} e_{AE} + U_{DE} e_{DE} + U_{LE} e_{LE} \\ &\quad + U_{ME} e_{ME} + e_e \\ &= Xb + \sum_u U_u e_u \end{aligned}$$

with variance-covariance matrix

$$\begin{aligned} \text{var}(y) &= \sigma_A^2 U_A U_A^T + \sigma_D^2 U_D U_D^T + \sigma_L^2 U_L U_L^T + \sigma_M^2 U_M U_M^T + \sigma_{AE}^2 U_{AE} U_{AE}^T \\ &\quad + \sigma_{DE}^2 U_{DE} U_{DE}^T + \sigma_{LE}^2 U_{LE} U_{LE}^T + \sigma_{ME}^2 U_{ME} U_{ME}^T + \sigma_e^2 I \\ &= \sum_{u=1}^9 \sigma_u^2 V_u. \end{aligned}$$

Variance Components

Unbiased estimation of variances can be obtained by REML or MINQUE(1) approaches. When experimental variances are estimated, genetic variance components can be obtained by $V_A = 2\sigma_A^2$, $V_D = \sigma_D^2$, $V_L = \sigma_L^2$, $V_M = \sigma_M^2$, $V_{AE} = 2\sigma_{AE}^2$, $V_{DE} = \sigma_{DE}^2$, $V_{LE} = \sigma_{LE}^2$, $V_M = \sigma_M^2$, $V_e = \sigma_e^2$. The total phenotypic variance is $V_p = V_A + V_D + V_L + V_M + V_{AE} + V_{DE} + V_{LE} + V_{ME} + V_e$.

Covariance Components and Correlation

Unbiased estimation of covariances can be obtained by MINQUE(1) approaches (Zhu, 1997; Zhu and Weir, 1996). When experimental covariances are estimated, genetic covariance components can be obtained by $C_A = 2\sigma_{A/A}$, $C_D = \sigma_{D/D}$, $C_L = \sigma_{L/L}$, $C_M = \sigma_{M/M}$, $C_{AE} = \sigma_{AE/AE}$, $C_{DE} = \sigma_{DE/DE}$, $C_{LE} = \sigma_{LE/LE}$, $C_{ME} = \sigma_{ME/ME}$, $C_e = \sigma_{e/e}$. The total phenotypic covariance is $C_p = C_A + C_D + C_L + C_M + C_{AE} + C_{DE} + C_{LE} + C_{ME} + C_e$. For trait 1 and trait 2, correlation coefficients of genetic components can be estimated by

$$\begin{aligned} r_A &= C_A / \sqrt{V_{A(1)} V_{A(2)}}, \\ r_D &= C_D / \sqrt{V_{D(1)} V_{D(2)}}, \\ r_L &= C_L / \sqrt{V_{L(1)} V_{L(2)}}, \\ r_M &= C_M / \sqrt{V_{M(1)} V_{M(2)}}, \\ r_{AE} &= C_{AE} / \sqrt{V_{AE(1)} V_{AE(2)}}, \\ r_{LE} &= r_{LE} = C_{LE} / \sqrt{V_{LE(1)} V_{LE(2)}}, \\ r_{ME} &= r_{ME} = C_{ME} / \sqrt{V_{ME(1)} V_{ME(2)}}, \text{ and} \\ r_{eE} &= r_e = C_e / \sqrt{V_{e(1)} V_{e(2)}}. \end{aligned}$$

Heritability Components

The total heritability (h^2) can be partitioned into two components ($h^2 = h_G^2 + h_{GE}^2$), where $h_G^2 = V_A / V_P$ is general heritability and $h_{GE}^2 = V_{AE} / V_P$ is interaction heritability (Zhu, 1997).

Selection Response

The total selection response ($R = ih^2 \sqrt{V_P}$) can be partitioned into two components (Zhu, 1997):

$$R = R_G + R_{GE}$$

where $R_G = ih_G^2 \sqrt{V_P}$ is general response and $R_{GE} = ih_{GE}^2 \sqrt{V_P}$ is interaction response.

Originators

Zhu, J. (1997). *Analysis Methods for Genetic Models*. Agricultural Publication House of China, Beijing.

Zhu, J. and Weir, B.S. (1996). Diallel analysis for sex-linked and maternal effects. *Theoretical and Applied Genetics*, 92(1):1-9.

Software Available

Zhu, J. (1997). GENSEX.EXE for constructing animal models, GENVAR1R.EXE or GENVAR1C.EXE for estimating components of variance and heritability, GENCOV1R.EXE or GENCOV1C.EXE for estimating components of covariance and correlation, GENHET1R.EXE or GENHET1C.EXE for predicting genetic effects and components of heterosis. *Analysis Methods for Genetic Models* (pp. 278-285), Agricultural Publication House of China, Beijing (program free of charge). Contact Dr. Jun Zhu, Department of Agronomy, Zhejiang University, Hangzhou, China. E-mail: <jzhu@zju.edu.cn>.

EXAMPLE

Balanced mice data (provided by William R. Atchley, Department of Genetics, North Carolina State University, Raleigh, NC) to be analyzed (Parent = 1, Year = 1, Sex = 1 & 2, Blk = 1):

Year	Fem	Male	Cross	Rep	Sex	35BW	35TL
1	1	1	0	1	1	20.23	79.78
1	1	1	0	1	2	17.71	78.93
1	1	2	1	1	1	22.01	84.79
1	1	2	1	1	2	19.44	82.87
1	1	3	1	1	1	22.48	93.66
1	1	3	1	1	2	18.34	88.74
1	1	4	1	1	1	22.80	85.48
1	1	4	1	1	2	20.41	85.09
1	1	5	1	1	1	22.57	82.83
1	1	5	1	1	2	19.25	81.83
1	1	6	1	1	1	25.11	86.36
1	1	6	1	1	2	21.79	84.54
1	1	7	1	1	1	22.67	89.44
1	1	7	1	1	2	19.80	87.06
1	2	1	1	1	1	22.91	88.60
1	2	1	1	1	2	19.14	86.39
1	2	2	0	1	1	20.94	83.13
1	2	2	0	1	2	18.50	82.40
1	2	3	1	1	1	22.09	91.83
1	2	3	1	1	2	18.28	88.57
1	2	4	1	1	1	22.37	81.91
1	2	4	1	1	2	20.30	82.42
1	2	5	1	1	1	23.61	86.13
1	2	5	1	1	2	20.16	83.73
1	2	6	1	1	1	26.45	88.73
1	2	6	1	1	2	22.01	86.77
1	2	7	1	1	1	22.86	87.86
1	2	7	1	1	2	19.85	86.45
1	3	1	1	1	1	23.73	85.75
1	3	1	1	1	2	19.86	84.80
1	3	2	1	1	1	24.18	84.48
1	3	2	1	1	2	19.75	82.55
1	3	3	0	1	1	23.72	87.41
1	3	3	0	1	2	19.09	84.93
1	3	4	1	1	1	25.36	87.27
1	3	4	1	1	2	20.00	85.20
1	3	5	1	1	1	21.98	79.03
1	3	5	1	1	2	18.77	77.21
1	3	6	1	1	1	26.48	85.66
1	3	6	1	1	2	21.85	83.52
1	3	7	1	1	1	24.99	86.89
1	3	7	1	1	2	20.41	85.06
1	4	1	1	1	1	23.33	84.48
1	4	1	1	1	2	20.77	83.14
1	4	2	1	1	1	23.18	81.61
1	4	2	1	1	2	19.47	79.41
1	4	3	1	1	1	22.50	88.10
1	4	3	1	1	2	18.90	84.24

1	4	4	0	1	1	24.24	85.97
1	4	4	0	1	2	20.91	84.16
1	4	5	1	1	1	23.22	83.22
1	4	5	1	1	2	19.33	82.19
1	4	6	1	1	1	24.01	83.07
1	4	6	1	1	2	20.62	81.25
1	4	7	1	1	1	24.86	86.73
1	4	7	1	1	2	20.70	85.19
1	5	1	1	1	1	22.07	87.14
1	5	1	1	1	2	19.37	87.90
1	5	2	1	1	1	21.05	82.04
1	5	2	1	1	2	18.78	82.88
1	5	3	1	1	1	21.32	84.22
1	5	3	1	1	2	18.19	82.25
1	5	4	1	1	1	23.31	90.07
1	5	4	1	1	2	20.18	89.91
1	5	5	0	1	1	23.79	84.50
1	5	5	0	1	2	20.48	84.69
1	5	6	1	1	1	24.48	87.04
1	5	6	1	1	2	21.15	87.06
1	5	7	1	1	1	21.41	81.79
1	5	7	1	1	2	19.18	82.03
1	6	1	1	1	1	22.28	87.39
1	6	1	1	1	2	18.81	85.55
1	6	2	1	1	1	18.86	75.66
1	6	2	1	1	2	15.75	74.44
1	6	3	1	1	1	21.68	87.52
1	6	3	1	1	2	16.24	83.10
1	6	4	1	1	1	23.01	85.38
1	6	4	1	1	2	18.64	85.04
1	6	5	1	1	1	22.97	84.62
1	6	5	1	1	2	18.69	82.70
1	6	6	0	1	1	25.60	84.43
1	6	6	0	1	2	20.88	83.36
1	6	7	1	1	1	22.91	84.57
1	6	7	1	1	2	18.81	82.43
1	7	1	1	1	1	22.59	91.29
1	7	1	1	1	2	17.91	88.00
1	7	2	1	1	1	22.48	86.97
1	7	2	1	1	2	17.50	83.04
1	7	3	1	1	1	21.71	86.41
1	7	3	1	1	2	17.54	83.27
1	7	4	1	1	1	24.23	92.60
1	7	4	1	1	2	19.88	89.00
1	7	5	1	1	1	23.79	86.83
1	7	5	1	1	2	18.93	84.83
1	7	6	1	1	1	25.07	89.44
1	7	6	1	1	2	20.21	87.38
1	7	7	0	1	1	24.31	90.48
1	7	7	0	1	2	19.81	86.65

1. Run GENSEX.EXE to create mating design matrix files and AD+L+M model data. Before running this program, create a data file (MICEDATA.TXT) for your analysis with six design columns fol-

- lowed by trait columns. The six design columns are (1) environment, (2) maternal, (3) paternal, (4) generation, (5) replication, and (6) sex. There is a limitation (<100 traits) for the number of trait columns. An example of the data file is provided with the name MICEDATA.TXT.
2. Run programs for variance and covariance analyses. Standard errors of estimates are calculated by the jackknife procedures. If you have multiple blocks for your experiments, you can use GENVAR1R.EXE or GENCOV1R.EXE for jackknifing over blocks. Otherwise you can use GENVAR1C.EXE or GENCOV1C.EXE for jackknifing over cell means.
 3. Run GENVAR1R.EXE or GENVAR1C.EXE for estimating variance components and predicting genetic effects before estimating covariance and correlation. These two programs will allow you to choose the parental type (inbred or outbred) and the prediction methods (LUP or AUP). You also need to input coefficients (1, 0, or -1) for conducting linear contrasts for genetic effects of parents.
 4. After finishing variance analysis, run GENCOV1R.EXE or GENCOV1C.EXE to estimate covariance components and coefficients of correlation among all analyzed traits.
 5. Results will automatically be stored in text files for later use or printing.

Output 1 for Variance Analysis

Traits = , 2
 Variance components = , 5
 Degree of freedom = , 48
 File name is micedata.VAR
 Date and Time for Analysis: Sat Jun 24 20:03:15 2000

Variance Components Estimated by MINQUE(1) with GENVAR1R.EXE.
 Jackknifing Over Block Conducted for Estimating S.E.
 Predicting Genetic Effects by Adjusted Unbiased Prediction (AUP) Method.

NS = Not significant; S+ = Significant at 0.10 level.
 S* = Significant at 0.05 level; S** = Significant at 0.01 level.

Linear Contrasts:
 +<1> +<2> +<3> +<4> -<5> -<6> -<7>

Diallel Analysis of Trait, 35BW, for Public Users.

Var Comp	Estimate	S. E.	P-value	
(1): Additive Var	4.05678	0.914491	2.67e-005	S**
(2): Dominance Var	0.447741	0.114861	0.00015	S**
(3): Sex-linked Var	4.82177	0.332787	2.87e-017	S**

(4): Maternal Var	3.16826	0.912454	0.000551	S**
(5): Residual Var	0.979275	0.309302	0.00134	S**
(6): Var (Pheno.)	13.4738	1.91195	3.11e-009	S**

Proportion of Var(G)/Var(T)Estimate	S. E.	P-value	
(1): Additive Var/Vp	0.301086	0.0251507	2.53e-016 S**
(2): Dominance Var/Vp	0.0332304	0.011576	0.00304 S**
(3): Sex-linked Var/Vp	0.357862	0.032024	2.98e-015 S**
(4): Maternal Var/Vp	0.235142	0.0202444	7.84e-016 S**
(5): Residual Var/Vp	0.0726798	0.0271762	0.0051 S**

Heritability	Estimate	S. E.	P-value	
(6): Heritability(N)	0.301086	0.0251507	2.53e-016	S**
(7): Heritability(B)	0.334316	0.0236245	3.21e-017	S**

Genetic Predictor, S. E. , P-value

(1): Random Effect is Additive Effects				
A1	-1.163629	0.383414	0.00388	S**
A2	-1.622929	0.534681	0.00387	S**
A3	-1.099644	0.273847	0.000208	S**
A4	0.535614	0.274989	0.0573	S+
A5	0.188242	0.412984	0.651	NS
A6	2.638442	0.623674	0.000104	S**
A7	0.517437	0.316664	0.109	NS
Linear Contrast	-6.21749	1.79317	0.00112	S**

(2): Random Effect is Dominance Effects

D1*1	-1.575254	1.171944	0.185	NS
D2*2	-0.823010	0.741883	0.273	NS
D3*3	0.161857	0.293363	0.584	NS
D4*4	0.306696	0.310885	0.329	NS
D5*5	1.089396	0.790779	0.175	NS
D6*6	1.449270	1.100055	0.194	NS
D7*7	0.697693	0.513080	0.18	NS
D1*2	0.719177	0.566455	0.21	NS
D1*3	0.433285	0.376514	0.256	NS
D1*4	0.532937	0.514004	0.305	NS
D1*5	0.105613	0.398419	0.792	NS
D1*6	0.617389	0.608657	0.316	NS
D1*7	-0.008952	0.420072	0.983	NS
D2*3	0.292272	0.710588	0.683	NS
D2*4	0.047317	0.659437	0.943	NS
D2*5	0.062535	0.567660	0.913	NS
D2*6	-0.378167	2.358942	0.873	NS
D2*7	-0.164429	0.355381	0.646	NS
D3*4	-0.129561	0.270304	0.634	NS
D3*5	-1.016032	0.950404	0.29	NS
D3*6	-0.268319	0.703458	0.705	NS
D3*7	-0.256718	0.609336	0.675	NS
D4*5	-0.370931	0.502767	0.464	NS
D4*6	-0.697666	0.733653	0.346	NS
D4*7	0.261144	0.349548	0.459	NS
D5*6	-0.182574	0.462678	0.695	NS
D5*7	-0.609768	0.793060	0.446	NS
D6*7	-0.298528	0.437983	0.499	NS
Heterosis <Delta>	-0.738068	1.8011	0.684	NS

(3): Random Effect is Sex-linked Effects

L1 for Sex1	1.619670	0.268733	2.28e-007	S**
L2 for Sex1	1.950941	0.409804	1.81e-005	S**
L3 for Sex1	2.545023	0.396915	5.87e-008	S**
L4 for Sex1	1.998426	0.326978	1.69e-007	S**
L5 for Sex1	1.194290	0.283566	0.000111	S**
L6 for Sex1	2.173739	0.465039	2.42e-005	S**
L7 for Sex1	3.040606	0.367137	8.28e-011	S**
L1 for Sex2	-1.468479	0.283005	4.22e-006	S**
L2 for Sex2	-1.416539	0.315276	4.42e-005	S**
L3 for Sex2	-2.789509	0.420796	2.73e-008	S**
L4 for Sex2	-1.799656	0.408109	5.82e-005	S**
L5 for Sex2	-2.015034	0.390778	4.72e-006	S**
L6 for Sex2	-2.912965	0.350283	7.36e-011	S**
L7 for Sex2	-2.124706	0.288782	2.09e-009	S**
Linear Contrast	4.99948	0.147414	5.87e-017	S**

(4): Random Effect is Maternal Effects

M1	0.532529	0.235722	0.0285	S*
M2	1.445810	0.744384	0.058	S+
M3	1.947175	0.459670	0.000102	S**
M4	0.036886	0.341978	0.915	NS
M5	0.198565	0.396981	0.619	NS
M6	-3.214121	0.790225	0.000176	S**
M7	-0.950092	0.338411	0.0072	S**
Linear Contrast	5.89251	1.83518	0.00236	S**

Fixed Effect <1>, 21.2871

Results of Tail Length are not presented.

Time Used (Hour) = 0.001389

Output 2 for Covariance Analysis

Traits =, 2

Covariance components =, 5

Degree of freedom =, 48

File name is micedata.COV

Date and Time for Analysis: Sat Jun 24 20:03:33 2000

Covariance Components Estimated by MINQUE(1) with GENCOV1C.EXE.
Jackknifing Over Cell Mean Conducted for Estimating S.E.

NS = Not significant; S+ = Significant at 0.10 level.

S* = Significant at 0.05 level; S** = Significant at 0.01 level.

Covariances and Correlations Between, 35BW, , &, 35TL, for Public Users.:

Covariances	Estimates	S.E.	P-value	
Additive Cov	1.2739	1.40446	0.369	NS
Dominance Cov	-0.279037	0.886415	0.754	NS
Sex-linked Cov	2.07233	0.465324	5.04e-005	S**
Maternal Cov	0.848917	1.69412	0.619	NS

Residual Cov	1.76704	0.698536	0.0148	S*
Cov <1=Genotypic>				
Cov <2=Phenotypic>	Estimates	S.E.	P-value	
Cov 2	5.68315	2.84705	0.0516	S+
Cov 1	3.91611	2.85586	0.177	NS
Correlation	Estimates	S.E.	P-value	
Additive Cor	0.190211	0.07873	0.0195	S*
Dominance Cor	-0.169791	0.0696301	0.0185	S*
Sex-linked Cor	0.589663	0.0588193	2.33e-013	S**
Maternal Cor	0.138456	0.0704558	0.0552	S+
Residual Cor	0.664416	0.0763856	1.98e-011	S**
Cor <1=Genotypic>				
Cor <2=Phenotypic>	Estimates	S.E.	P-value	
Cor 2	0.248755	0.0830793	0.00434	S**
Cor 1	0.197347	0.0879154	0.0294	S*

Results of Tail Length are not presented.

Time Used (Hour) = 0.000556