## Quantitative characters - solutions to exercises

**1.** a) 
$$Cov(HS) = \frac{1}{4}\sigma_{10}^2 + 0\sigma_{01}^2 + \frac{1}{16}\sigma_{20}^2 + 0\sigma_{11}^2 + 0\sigma_{02}^2$$

b) 
$$Cov(FS) = \frac{1}{2}\sigma_{10}^2 + \frac{1}{4}\sigma_{01}^2 + \frac{1}{4}\sigma_{20}^2 + \frac{1}{8}\sigma_{11}^2 + \frac{1}{16}\sigma_{02}^2$$

c) 
$$\sigma_D^2 = \sigma_{01}^2 \approx 4[Cov(FS) - 2Cov(HS)]$$

Bias due to epistatic effects

2. a) 
$$a_{XY} = (\frac{1}{2})^{2+2}(1+F_A) + (\frac{1}{2})^{2+2}(1+F_B) = \frac{1}{16} + \frac{1}{16} = \frac{1}{8}$$
 
$$d_{XY} = \frac{1}{4}(a_{ED} \times a_{CF} + a_{EF} \times a_{CD}) = \frac{1}{4}(0 \times 0 + 0 \times \frac{1}{2}) = 0$$

b) 
$$\operatorname{Cov}(X,Y) = \sum_{i=0}^{n} \sum_{j=0}^{n} \left(\frac{1}{8}\right)^{i} (0)^{j} \sigma_{ij}^{2}$$

$$1 \leq i + j \leq n$$

When maximum three loci are considered: Cov(X,Y) =

$$= \left(\frac{1}{8}\right)^{1}(0)^{0}\sigma_{10}^{2} + \left(\frac{1}{8}\right)^{0}(0)^{1}\sigma_{01}^{2} + \left(\frac{1}{8}\right)^{2}(0)^{0}\sigma_{20}^{2} + \left(\frac{1}{8}\right)^{1}(0)^{1}\sigma_{11}^{2} + \left(\frac{1}{8}\right)^{0}(0)^{2}\sigma_{02}^{2} + \left(\frac{1}{8}\right)^{3}(0)^{0}\sigma_{30}^{2} + \left(\frac{1}{8}\right)^{2}(0)^{1}\sigma_{21}^{2} + \left(\frac{1}{8}\right)^{1}(0)^{2}\sigma_{12}^{2} + \left(\frac{1}{8}\right)^{0}(0)^{3}\sigma_{03}^{2} + \dots$$

$$= \frac{1}{8}\sigma_{10}^{2} + 0 + \frac{1}{64}\sigma_{20}^{2} + 0 + 0 + \frac{1}{512}\sigma_{30}^{2} + 0 + 0 + 0 + \dots$$

The genetic covariance between cousins is composed only of additive variance and epistatic variance between additive gene effects

3. 
$$a_{XY} = (\frac{1}{2})^{2+2}(1+F_A) + (\frac{1}{2})^{2+2}(1+F_B) + (\frac{1}{2})^{2+2}(1+F_C) + (\frac{1}{2})^{2+2}(1+F_D)$$
  
 $= \frac{1}{16} + \frac{1}{16} + \frac{1}{16} + \frac{1}{16} = \frac{4}{16} + = \frac{1}{4}$ 

$${\rm d_{XY}} \ = \ \frac{1}{4}(a_{FE}\times a_{GH} + a_{FH}\times a_{GE}) \ = \ \frac{1}{4}(\frac{1}{2}\times\frac{1}{2} + 0\times 0) \ = \ \frac{1}{4}\times\frac{1}{4} \ = \ \frac{1}{16}$$

$$Cov (X,Y) = (\frac{1}{4})^{1} (\frac{1}{16})^{0} \sigma_{10}^{2} + (\frac{1}{4})^{0} (\frac{1}{16})^{1} \sigma_{01}^{2} + (\frac{1}{4})^{2} (\frac{1}{16})^{0} \sigma_{20}^{2} + (\frac{1}{4})^{1} (\frac{1}{16})^{1} \sigma_{11}^{2}$$

$$+ (\frac{1}{4})^{0} (\frac{1}{16})^{2} \sigma_{02}^{2}$$

$$= \frac{1}{4} \sigma_{10}^{2} + \frac{1}{16} \sigma_{01}^{2} + \frac{1}{16} \sigma_{20}^{2} + \frac{1}{64} \sigma_{11}^{2} + \frac{1}{256} \sigma_{02}^{2}$$

**4.** a) Parent-Offspring Cov(PO) = 
$$\frac{1}{2}\sigma_{10}^2 + \frac{1}{4}\sigma_{20}^2$$

c) 
$$\sigma_{10}^{2} \quad \sigma_{01}^{2} \quad \sigma_{20}^{2} \quad \sigma_{11}^{2} \quad \sigma_{02}^{2}$$

$$2 \times \text{Cov(OP)} \qquad 1 \qquad \frac{1}{2}$$

$$2 \times \text{Cov(FS)} \qquad 1 \quad \frac{1}{2} \quad \frac{1}{2} \quad \frac{1}{4} \quad \frac{1}{8}$$

$$4 \times Cov(HS) \qquad \qquad 1 \qquad \qquad \frac{1}{2}$$

- \* Cov(OP) and Cov(HS) only give bias due to epistatic (add. x add.) gene effects. This bias is smaller for Cov(HS) compared to Cov(OP).
- \* Cov(FS) gives biased estimates of  $\sigma_A^2$  due to influence of dominance effects and also all types of epistatic effects.

The estimates of  $\sigma_{10}^2$  calculated from the genetic covariance between half sibs contains the least bias as regards non-additive components.

5. a) 
$$Y_{ij}=\mu+s_i+e_{ij}$$
 
$$E(S_i)=0 \qquad E(S_i^2)=\sigma_S^2$$
 
$$E(e_{ij})=0 \qquad E(e_{ij}^2)=\sigma_e^2$$

Source of var.	d.f.	SS <sup>1</sup>	MS	E(MS)
Between sires	4	С-В	4299	$\sigma_e^2 + 8 \sigma_S^2$
Within sires	35	A-C	2334	$\sigma_e^{\scriptscriptstyle 2}$
Total	39	A-B		

1) 
$$A = \sum_{i} \sum_{j} Y_{ij}^{2} = 18773473$$
  
 $B = (\sum_{i} Y_{ij})^{2} / N = (27331)^{2} / 40 = 18674589$   
 $C = \sum_{i} (\sum_{j} Y_{ij})^{2} / n_{i} = \frac{(5720)^{2}}{8} = + \dots + \frac{(5466)^{2}}{8} = 18691786$ 

c) 
$$\sigma_e^2 = 2334$$
  $\sigma_s^2 = \frac{4299 - 2334}{8} = 246$   $\sigma_A^2 = 4 \sigma_s^2 = 4 \times 246 = 984$   $\sigma_P^2 = \sigma_s^2 + \sigma_e^2 = 2334 + 246 = 2580$ 

d) The genetic covariance (HS) has the following composition:

$$\frac{1}{4}\sigma_{10}^2 + \frac{1}{16}\sigma_{20}^2 + \frac{1}{64}\sigma_{30}^2 + \dots$$

- Interaction between non-allelic genes, i.e.  $\sigma_{20}^2,~\sigma_{30}^2$  give some bias as an overstimation of  $\sigma_A^2$  .
- Interaction between non-allelic genes (dominance), i.e.  $\sigma_{01}^2$ , is not included in Cov(HS) and thus do not affect the estimate of  $\sigma_A^2$ .

e) 
$$h^2 = \frac{\sigma_A^2}{\sigma_P^2} = \frac{984}{2580} = 0.38$$

6.

Source of var.	d.f.	SS <sup>1</sup>	MS	E(MS)
Between sires	39	5000	128.20	$\sigma_e^2 + 88\sigma_s^2$
Within sires	3480	46800	13.45	$\sigma_{m{e}}^{\scriptscriptstyle 2}$
Total	3519	51800		

a) 
$$n = \frac{3520}{40} = 88$$
  
 $\sigma_e^2 = 13.45;$   $\sigma_s^2 = \frac{128.20 - 13.45}{88} = 1.30$   
 $\sigma_A^2 = \frac{1}{a_{HS}} \times \sigma_s^2 = \frac{1}{0.28} \times 1.30 = 4.64$   
 $\sigma_P^2 = \sigma_s^2 + \sigma_e^2 = 1.30 + 13.34 = 14.75$ 

b) Yes. The trait is sex limited and the covariance sire-offspring can not be used. The covariance dam-offspring is not so good since the environmental covariance dam-daughter is usually ≠ 0.

c) 
$$\hat{h}^2 = \frac{\sigma_A^2}{\sigma_B^2} = \frac{4.64}{14.75} = 0.31$$

7. a) 
$$Y_{ijk} = \mu + s_i + d_{ij} + v_K + e_{ijk}$$

$$E(s_i) = 0 E(s_i^2) = \sigma_s^2$$

$$E(d_{ij}) = 0 E(d_y^2) = \sigma_d^2$$

$$E(e_{ijk}) = 0 E(e_{ijk}^2) = \sigma_e^2$$

b)

Source of var.	d.f.	SS	MS	EMS
Between sires	137	184.9	1.35	$\sigma_e^2 + 2\sigma_d^2 + 6\sigma_s^2$
Between sows	276	223.5	0.81	$\sigma_e^2 + 2\sigma_d^2$
Within weights	1	9.4	9.40	$\sigma_e^2 + K \kappa^2$
Residual	413	251.9	0.61	$\sigma_e^2$
Total	827	669.7		

c) 
$$\sigma_e^2 = 0.61$$
  $\sigma_s^2 = \frac{1.35 - 0.81}{6} = 0.09$   $\sigma_d^2 = \frac{0.81 - 0.61}{2} = 0.10$ 

d) 
$$\sigma_A^2 = 4\sigma_S^2 = 4 \times 0.09 = 0.36$$

 $\sigma_s^2$  does not give any bias due to dominance or maternal effects and smaller bias due to epistatic effects compared to  $\sigma_d^2$ .

e) 
$$\sigma_p^2 = \sigma_s^2 + \sigma_d^2 + \sigma_e^2 = 0.09 + 0.10 + 0.61 = 0.80$$

f) 
$$h^2 = \frac{\sigma_A^2}{\sigma_B^2} = \frac{0.36}{0.80} = 0.45$$

g) 
$$\hat{r}_g = \frac{\sigma_{\tilde{s}\tilde{s}}}{\sqrt{\sigma_s^2 \times \sigma_{\tilde{s}}^2}} = \frac{0.06}{\sqrt{0.09 \times 0.40}} = 0.32$$

$$\hat{r}_{p} = \frac{\sigma_{s\tilde{s}} + \sigma_{d\tilde{d}} + \sigma_{e\tilde{e}}}{\sqrt{(\sigma_{s}^{2} + \sigma_{d}^{2} + \sigma_{e}^{2})(\sigma_{\tilde{s}}^{2} + \sigma_{\tilde{d}}^{2} + \sigma_{\tilde{e}}^{2})}} = \frac{0.65}{\sqrt{0.8 \times 2.1}} = 0.50$$

8. a) Weight gain: 
$$\sigma_e^2 = 0.0110; \quad \sigma_s^2 = \frac{0.0187 - 0.0110}{17} = 0.00045$$

Height at withers: 
$$\sigma_e^2 = 1258.5$$
;  $\sigma_s^2 = \frac{3097.2 - 1258.5}{17} = 108.159$ 

Covariance comp.: 
$$\sigma_{e\tilde{e}} = 1.1746$$
;  $\sigma_{s\tilde{s}} = \frac{3.1978 - 1.1746}{17} = 0.119$ 

b) 
$$\sigma_A^2 = 4\sigma_S^2 = 4 \times 0.00045 = 0.0018$$
  $\sigma_{\tilde{A}}^2 = 4\sigma_{\tilde{S}}^2 = 4 \times 108.159 = 432.636$   $\sigma_{A\tilde{A}}^2 = 4\sigma_{S\tilde{S}}^2 = 4 \times 0.119 = 0.476$ 

c) 
$$\sigma_{E\tilde{E}} = \sigma_{e\tilde{e}} - 3\sigma_{s\tilde{s}} = 1.1746 - 3 \times 0.119 = 0.8176$$

$$\sigma_{P\tilde{P}} = \sigma_{\tilde{S}\tilde{S}} + \sigma_{\tilde{P}\tilde{P}} = 0.119 + 1.1746 = 1.2936$$

d) 
$$0.476 + 0.8176 = 1.2936$$
 :  $\sigma_{P\tilde{P}} = \sigma_{A\tilde{A}} + \sigma_{E\tilde{E}}$ 

e) 
$$\hat{r}_g = \frac{\sigma_{A\tilde{A}}^2}{\sqrt{\sigma_A^2 \times \sigma_{\tilde{A}}^2}} = \frac{0.476}{\sqrt{0.0018 \times 432.636}} = 0.54$$

 $\hat{r}$  can also be calculated directly from the statistical components according to:

$$\hat{r}_g = \frac{\sigma_{s\tilde{s}}}{\sqrt{\sigma_s^2 \times \sigma_{\tilde{s}}^2}} = \frac{0.119}{\sqrt{0.00045 \times 108.159}} = 0.54$$

Conclusions: When we select for weight gain we will also get a correlated increase in height at withers or vice versa. The correlation is high enough for an indirect selection.

$$\hat{r}_p = \frac{\sigma_{P\tilde{P}}}{\sqrt{\sigma_P^2 \times \sigma_{\tilde{p}}^2}} = \frac{\sigma_{s\tilde{s}} + \sigma_{e\tilde{e}}}{\sqrt{(\sigma_s^2 + \sigma_e^2)(\sigma_{\tilde{s}}^2 + \sigma_{\tilde{e}}^2)}} = \frac{0.119 + 1.1746}{\sqrt{(0.00045 + 0.0110)(108.159 + 1258.5)}} = 0.33$$

g) 
$$\hat{r}_e = \frac{\sigma_{e\tilde{e}}}{\sqrt{\sigma_e^2 \times \sigma_{\tilde{e}}}}$$

$$\sigma_{e\tilde{e}} = 0.8176$$

$$\sigma_E^2 = \sigma_e^2 - 3\sigma_s^2 = 0.0110 - 3 \times 0.00045 = 0.00965$$

$$\sigma_{\tilde{E}}^2 = \sigma_{\tilde{e}}^2 - 3\sigma_{\tilde{s}}^2 = 1258.5 - 3 \times 108.159 = 934.023$$

$$\hat{r}_e = \frac{0.8176}{\sqrt{0.00965 \times 934.023}} = 0.27$$

9. a) 
$$\sigma_{P_1P_2} = \sigma_{G_1G_2} + \sigma_{G_1E_2} + \sigma_{G_2E_1} + \sigma_{E_1E_2}$$

$$\sigma_{G_1G_2} = Cov(XY) = \frac{1}{4}\sigma_{10}^2 + \underbrace{\frac{1}{16}\sigma_{20}^2}_{16} + \underbrace{\frac{1}{64}\sigma_{30}^2}_{16} + \underbrace{\frac{1$$

Variance due to epistatic effects,  $\sigma_I^2$ 

b) 
$$\sigma_{G_1E_2}$$
  $\sigma_{G_2E_1}$   $\sigma_{E_1E_2}$  and  $\sigma_I^2$ 

- 10. Quantitative traits are influenced both by a number of genes and by environment. They can be described by  $\mu$  and  $\sigma^2$  but gene frequencies and genotypes can not be estimated. The estimated biological variances covariances are used for:
  - \* Calculation of genetic parameters ⇒ description of the traits.
  - \* Breeding values: Calculations of selection index and BLUP assumes known values of

$$\sigma_A^2$$
,  $\sigma_P^2$  (or quotas),  $\sigma_{A\tilde{A}}$  and  $\sigma_{P\tilde{P}}$ .

\* Prediction of genetic gain and changes in correlated traits assumes known values of

$$\sigma_A^2$$
 and  $\sigma_{A ilde{A}}$  .

- 11. \*  $\sigma_A^2$  constitutes the major part of the genetic variance for most of the traits.
  - \*  $\sigma_A^2$  is that part of the genetic variance which is utilized in selection. Individuals submit genes and not genotypes to their offspring.
- 12. \* The traits are measured at the same time and on the same type of animals.
  - \* Also sex limited and carcass traits can be measured
  - \* Effects of  $\sigma_M^2 + \sigma_C^2$  are omitted for paternal halfsibs, but often occur for example between mothers and daughters.
  - \* Large materials of sibs are available in field data
  - \* Half sibs give less epistatic bias than parent-offspring