

## ANIMAL BREEDING NOTES

### CHAPTER 13

#### GENETIC COVARIANCES BETWEEN INDIVIDUALS

##### Genotypic Variance in a Random Mating Population

The theory of genotypic effects and genotypic variances in a random mating population presented here is based on a development by Kempthorne (1955b).

##### Assumptions

- (a) An arbitrarily large number of loci ( $n$ ).
- (b) An arbitrarily large number of alleles per locus ( $r_i$ ).
- (c) Random segregation and random allocation of alleles (i.e., no linkage) during meiosis.
- (d) Random mating.

Let the total number of alleles in the population be  $T = \sum_{i=1}^n r_i$ .

##### Genotypic mean

Let the ordered genotype of an individual be

$$\frac{A_{1j_{1s}}}{A_{1j_{1d}}}, \frac{A_{2j_{2s}}}{A_{2j_{2d}}}, \dots, \frac{A_{nj_{ns}}}{A_{nj_{nd}}}$$

where

$A_{c j_{cs}}$  = allele  $j$  at locus  $c$  in the sire gamete

$A_{c j_{cd}}$  = allele  $j'$  at locus  $c$  in the dam gamete

If we consider all alleles in a population that can occupy each one of the  $n$  loci an individual

possesses and their frequencies within each locus, then we can construct a **genotypic array**. The genotypic array of the population can be visualized by expanding the following expression:

$$\left( \sum_{j=1}^{r_1} p_{1j} A_{1j} \right)^2 \left( \sum_{j=1}^{r_2} p_{2j} A_{2j} \right)^2 \cdots \left( \sum_{j=1}^{r_n} p_{nj} A_{nj} \right)^2$$

where

$A_{ij}$  = **allele** j at locus i

$p_{ij}$  = frequency of allele  $A_{ij}$

The total effect of each genotype represented in this array will be the sum of: 1) the individual effects of all alleles, 2) the effects of all possible interactions between pairs of alleles, 3) the effects of all possible interactions among 3 alleles, 4) etc. Thus, the total genotypic effect can be thought of as being a **factorial design** problem, where the **total genotypic value of an individual** will be the **sum of a mean (the population mean), 2n main effects (the genetic effects of the 2n alleles in an individual) plus the effects of all possible interactions among these 2n main effects**.

Let the **population mean** be

$$\mu = \left( \sum_{j=1}^{r_1} p_{1j} A_{1j} \right)^2 \left( \sum_{j=1}^{r_2} p_{2j} A_{2j} \right)^2 \cdots \left( \sum_{j=1}^{r_n} p_{nj} A_{nj} \right)^2$$

$$\mu = \prod_{i=1}^n \left( \sum_{j=1}^{r_i} p_{ij} A_{ij} \right)^2$$

where

$A_{ij}$  = **genotypic value** of allele j at locus i

$p_{ij}$  = frequency of allele  $A_{ij}$

Notice that the notation  $A_{ij}$  is being used for **2 purposes**:

- 1) to **identify an allele within a locus** in the genotypic array, and
- 2) to define the **genetic value of an allele** when determining the genotypic value of an animal.

### Genotypic deviations

Let  $u_{cm}$  be the difference between the genetic effect of a specific allele  $m$  in a particular locus  $c$

( $A_{cm}$ ) and the mean of all alleles at this locus ( $\mu_c = \sum_{j=1}^{r_c} p_{cj} A_{cj}$ ), i.e.,

$$u_{cm} = A_{cm} - \sum_{j=1}^{r_c} p_{cj} A_{cj}$$

$$u_{cm} = A_{cm} - \mu_c$$

This intralocus difference ( $u_{cm}$ ) is the **basic deviation** which all genetic effects rely on. Notice that, by the definition of  $u_{cm}$ , the **mean of all intralocus differences is zero**, i.e.,

$$\begin{aligned} \sum_{m=1}^{r_c} p_{cm} u_{cm} &= \sum_{m=1}^{r_c} p_{cm} \left( A_{cm} - \sum_{j=1}^{r_c} p_{cj} A_{cj} \right) \\ &= \sum_{m=1}^{r_c} p_{cm} A_{cm} - \sum_{m=1}^{r_c} p_{cm} \sum_{j=1}^{r_c} p_{cj} A_{cj} \\ &= \mu_c - (1)\mu_c \\ &= 0 \end{aligned}$$

**Consider now the following sets of deviations:**

[1] The deviation of the genotypic value of allele  $cj$  from the mean of all alleles in locus  $c$ , averaged over the values of all possible genotypes at all loci in the population.

$$a_{cm} = \left( A_{cm} - \sum_{j=1}^{r_c} p_{cj} A_{cj} \right) \left( \sum_{j=1}^{r_c} p_{cj} A_{cj} \right) \left( \prod_{\substack{i=1 \\ i \neq c}}^n \left( \sum_{j=1}^{r_i} p_{ij} A_{ij} \right)^2 \right)$$

$$a_{cm} = (A_{cm} - \mu_c) \mu_c \left( \prod_{\substack{i=1 \\ i \neq c}}^n \mu_i^2 \right)$$

$$a_{cm} = (A_{cm} - \mu_c) \mu_c \left( \frac{\mu}{\mu_c^2} \right)$$

$$a_{cm} = \left( \frac{A_{cm}}{\mu_c} \right) \mu - \mu$$

[2] The product of the deviations of two alleles within locus c, cm and cm', from the mean of all alleles in locus c, averaged over the values of all possible genotypes at all loci in the population.

$$a_{cm} a_{cm'} = \left( A_{cm} - \sum_{j=1}^{r_c} p_{cj} A_{cj} \right) \left( A_{cm'} - \sum_{j=1}^{r_c} p_{cj} A_{cj} \right) \left( \prod_{\substack{i=1 \\ i \neq c}}^n \left( \sum_{j=1}^{r_i} p_{ij} A_{ij} \right)^2 \right)$$

$$a_{cm} a_{cm'} = (A_{cm} - \mu_c) (A_{cm'} - \mu_c) \left( \prod_{\substack{i=1 \\ i \neq c}}^n \mu_i^2 \right)$$

$$a_{cm} a_{cm'} = (A_{cm} A_{cm'} - A_{cm} \mu_c - \mu_c A_{cm'} + \mu_c^2) \left( \frac{\mu}{\mu_c^2} \right)$$

$$a_{cm} a_{cm'} = \left( \frac{A_{cm}}{\mu_c} \right) \left( \frac{A_{cm'}}{\mu_c} \right) \mu - \left( \frac{A_{cm}}{\mu_c} \right) \mu - \left( \frac{A_{cm'}}{\mu_c} \right) \mu + \mu$$

[3] The product of the deviation of allele cm located at locus c from the mean of all alleles in locus c times the deviation of allele c'm' located at locus c', averaged over the values of all possible genotypes at all loci in the population.

$$a_{cm} a_{c'm'} = \left( A_{cm} - \sum_{j=1}^{r_c} p_{cj} A_{cj} \right) \left( \sum_{j=1}^{r_c} p_{cj} A_{cj} \right) \left( A_{c'm'} - \sum_{j=1}^{r_{c'}} p_{c'j} A_{c'j} \right) \left( \sum_{j=1}^{r_{c'}} p_{c'j} A_{c'j} \right) \left( \prod_{\substack{i=1 \\ i \neq c \\ i \neq c'}}^n \left( \sum_{j=1}^{r_i} p_{ij} A_{ij} \right)^2 \right)$$

$$a_{cm} a_{c'm'} = (A_{cm} - \mu_c) \mu_c (A_{c'm'} - \mu_{c'}) \mu_{c'} \left( \prod_{\substack{i=1 \\ i \neq c \\ i \neq c'}}^n \mu_i^2 \right)$$

$$a_{cm} a_{c'm'} = (A_{cm} A_{c'm'} - A_{cm} \mu_{c'} - \mu_c A_{c'm'} - \mu_c \mu_{c'}) \mu_c \mu_{c'} \left( \frac{\mu}{\mu_c^2 \mu_{c'}^2} \right)$$

$$a_{cm} a_{c'm'} = \left( \frac{A_{cm}}{\mu_c} \right) \left( \frac{A_{c'm'}}{\mu_{c'}} \right) \mu - \left( \frac{A_{cm}}{\mu_c} \right) \mu - \left( \frac{A_{c'm'}}{\mu_{c'}} \right) \mu + \mu$$

[4] The product of the deviation of allele  $cm$  located at locus  $c$  from the mean of all alleles in locus  $c$  times the deviation of allele  $c'm'$  located at locus  $c'$  times the deviation of allele  $c'w'$  located at locus  $c'$ , averaged over the values of all possible genotypes at all loci in the population.

$$a_{cm} a_{c'm'} a_{c'w'} = \left( A_{cm} - \sum_{j=1}^{r_c} p_{cj} A_{cj} \right) \left( \sum_{j=1}^{r_c} p_{cj} A_{cj} \right) \left( A_{c'm'} - \sum_{j=1}^{r_{c'}} p_{c'j} A_{c'j} \right) \left( A_{c'w'} - \sum_{j=1}^{r_{c'}} p_{c'j} A_{c'j} \right) \left( \prod_{\substack{i=1 \\ i \neq c \\ i \neq c'}}^n \left( \sum_{j=1}^{r_i} p_{ij} A_{ij} \right)^2 \right)$$

$$a_{cm} a_{c'm'} a_{c'w'} = (A_{cm} - \mu_c) \mu_c (A_{c'm'} - \mu_{c'}) \mu_{c'} (A_{c'w'} - \mu_{c'}) \left( \prod_{\substack{i=1 \\ i \neq c \\ i \neq c'}}^n \mu_i^2 \right)$$

$$a_{cm} a_{c'm'} a_{c'w'} = (A_{cm} \mu_{c'} - \mu_c) (A_{c'm'} A_{c'w'} - A_{c'm'} \mu_{c'} - \mu_{c'} A_{c'w'} + \mu_{c'}^2) \left( \frac{\mu}{\mu_c^2 \mu_{c'}^2} \right)$$

[13-6]

$$\begin{aligned} a_{cm} a_{c'm'} a_{c'w'} &= \left( \frac{A_{cm}}{\mu_c} \right) \left( \frac{A_{c'm'}}{\mu_{c'}} \right) \left( \frac{A_{c'w'}}{\mu_{c'}} \right) \mu - \left( \frac{A_{cm}}{\mu_c} \right) \left( \frac{A_{c'm'}}{\mu_{c'}} \right) \mu - \left( \frac{A_{cm}}{\mu_c} \right) \left( \frac{A_{c'w'}}{\mu_{c'}} \right) \mu \\ &\quad - \left( \frac{A_{c'm'}}{\mu_{c'}} \right) \left( \frac{A_{c'w'}}{\mu_{c'}} \right) \mu + \left( \frac{A_{cm}}{\mu_c} \right) \mu + \left( \frac{A_{c'm'}}{\mu_{c'}} \right) \mu + \left( \frac{A_{c'w'}}{\mu_{c'}} \right) \mu - \mu \end{aligned}$$

[5] The product of the deviation of allele cm located at locus c from the mean of all alleles in locus c times the deviation of allele cw located at locus c times the deviation of allele c'm' located at locus c' times the deviation of allele c'w' located at locus c', averaged over the values of all possible genotypes at all loci in the population.

$$\begin{aligned} a_{cm} a_{cw} a_{c'm'} a_{c'w'} &= \left( A_{cm} - \sum_{j=1}^{r_c} p_{cj} A_{cj} \right) \left( A_{cw} - \sum_{j=1}^{r_c} p_{cj} A_{cj} \right) \left( A_{c'm'} - \sum_{j=1}^{r_{c'}} p_{c'j} A_{c'j} \right) \left( A_{c'w'} - \sum_{j=1}^{r_{c'}} p_{c'j} A_{c'j} \right) \left( \prod_{\substack{i=1 \\ i \neq c \\ i \neq c'}}^n \left( \sum_{j=1}^{r_i} p_{ij} A_{ij} \right)^2 \right) \\ a_{cm} a_{cw} a_{c'm'} a_{c'w'} &= (A_{cm} - \mu_c) (A_{cw} - \mu_c) (A_{c'm'} - \mu_{c'}) (A_{c'w'} - \mu_{c'}) \left( \prod_{\substack{i=1 \\ i \neq c \\ i \neq c'}}^n \mu_i^2 \right) \\ a_{cm} a_{cw} a_{c'm'} a_{c'w'} &= (A_{cm} A_{cw} - A_{cm} \mu_c - \mu_c A_{cw} + \mu_c^2) (A_{c'm'} A_{c'w'} - A_{c'm'} \mu_{c'} - \mu_{c'} A_{c'w'} + \mu_{c'}^2) \left( \frac{\mu}{\mu_c^2 \mu_{c'}^2} \right) \end{aligned}$$

$$\begin{aligned}
a_{cm} a_{cw} a_{c'm'} a_{c'w'} &= \left( \frac{A_{cm}}{\mu_c} \right) \left( \frac{A_{cw}}{\mu_c} \right) \left( \frac{A_{c'm'}}{\mu_{c'}} \right) \left( \frac{A_{c'w'}}{\mu_{c'}} \right) \mu - \left( \frac{A_{cm}}{\mu_c} \right) \left( \frac{A_{cw}}{\mu_c} \right) \left( \frac{A_{c'm'}}{\mu_{c'}} \right) \mu \\
&\quad - \left( \frac{A_{cm}}{\mu_c} \right) \left( \frac{A_{cw}}{\mu_c} \right) \left( \frac{A_{c'w'}}{\mu_{c'}} \right) \mu - \left( \frac{A_{cm}}{\mu_c} \right) \left( \frac{A_{c'm'}}{\mu_{c'}} \right) \left( \frac{A_{c'w'}}{\mu_{c'}} \right) \mu - \left( \frac{A_{cw}}{\mu_c} \right) \left( \frac{A_{c'm'}}{\mu_{c'}} \right) \left( \frac{A_{c'w'}}{\mu_{c'}} \right) \mu \\
&\quad + \left( \frac{A_{cm}}{\mu_c} \right) \left( \frac{A_{cw}}{\mu_c} \right) \mu + \left( \frac{A_{cm}}{\mu_c} \right) \left( \frac{A_{c'm'}}{\mu_{c'}} \right) \mu + \left( \frac{A_{cm}}{\mu_c} \right) \left( \frac{A_{c'w'}}{\mu_{c'}} \right) \mu + \left( \frac{A_{cw}}{\mu_c} \right) \left( \frac{A_{c'm'}}{\mu_{c'}} \right) \mu \\
&\quad + \left( \frac{A_{cw}}{\mu_c} \right) \left( \frac{A_{c'w'}}{\mu_{c'}} \right) \mu + \left( \frac{A_{c'm'}}{\mu_{c'}} \right) \left( \frac{A_{c'w'}}{\mu_{c'}} \right) \mu \\
&\quad - \left( \frac{A_{cm}}{\mu_c} \right) \mu - \left( \frac{A_{cw}}{\mu_c} \right) \mu - \left( \frac{A_{c'm'}}{\mu_{c'}} \right) \mu - \left( \frac{A_{c'w'}}{\mu_{c'}} \right) \mu + \mu
\end{aligned}$$

[6] And so on, until considering all the deviations of individual alleles from their means at all loci, and all possible combinations of products of these allelic deviations within and across loci.

### Genotypic effects

If all deviations due to all single alleles that can occupy the  $2n$  loci of an individual, and all deviations due to products of deviations of two, three, ...,  $2n$  alleles are added, it can be shown that the resulting expression is  $A_{11} A_{12} \dots A_{1r_1} A_{21} A_{22} \dots A_{2r_2} \dots A_{2n1} A_{2n2} \dots A_{2nr_{2n}}$ . However, out of the  $T$  available alleles in the population, only 2 alleles per locus, and only  $2n$  alleles per genotype, are assumed to be randomly sampled to construct the genotype of an animal. **The randomness of the process of generating genotypes stems from the following assumptions: 1)** random segregation and random allocation of alleles during meiosis (heretofore **Mendelian sampling**), which implies that each allele within a gamete is inherited independently of any other, and **2)** random mating, i.e., male and female gametes will join at random to form zygotes.

**Consequently, 1)** the genotype of each animal can be considered to be the result of  $2n$  random occurrences, and **2)** the probability that an individual gets a particular allele at a given locus will be given by the frequency of occurrence of that allele at the specified locus in the population, i.e.,  $(A_{ij}) = p_{ij}$ . **Furthermore, as a consequence of the random process of genotype formation, and because genotypic deviations were defined as functions of intralocus deviations (whose means are zeroes), each one of the genotypic deviations is an occurrence of an independent random variable with mean zero, and variance equal to the sum of the expected values of the square of each possible deviation of this type in the population.** Genetic effects corresponding to the deviations and products of deviations 1 to 5 above are now described.

**[1] Additive genetic effect of an individual (A):** sum of the  $2n$  additive deviations of an animal (i.e., sum of the average genotypic effects of the  $2n$  alleles of an animal).

$$A = \sum_{k=1}^n a_{sk} + \sum_{k=1}^n a_{dk}$$

where

$n$  = number of additive contributions to the genotypic value of an animal coming from the sire and dam gametes

$a_{sk}$  = deviation due to the allele occupying locus  $k$  in the sire gamete (= average genotypic effect of this allele)

$a_{dk}$  = deviation due to the allele occupying locus  $k$  in the female gamete (= average genotypic effect of this allele)

The **expected value of A** is:



$$\begin{aligned}
E[A] &= E\left[\sum_{k=1}^n a_{sk} + \sum_{k=1}^n a_{dk}\right] \\
&= E\left[\sum_{k=1}^n a_{sk}\right] + E\left[\sum_{k=1}^n a_{dk}\right] \\
&= \sum_{k=1}^n E[a_{sk}] + \sum_{k=1}^n E[a_{dk}]
\end{aligned}$$

But,

$$\begin{aligned}
E[a_{sk}] &= E\left[\left(\frac{A_{scm}}{\mu_c}\right)\mu - \mu\right] \\
&= \sum_{m=1}^{r_c} p_{cm} \left(\frac{A_{scm}}{\mu_c}\right)\mu - \sum_{m=1}^{r_c} p_{cm} \mu \\
&= \left(\frac{\mu_c}{\mu_c}\right)\mu - (1)\mu \\
&= 0
\end{aligned}$$

and

$$\begin{aligned}
E[a_{dk}] &= E\left[\left(\frac{A_{dcm}}{\mu_c}\right)\mu - \mu\right] \\
&= \sum_{m=1}^{r_c} p_{cm} \left(\frac{A_{dcm}}{\mu_c}\right)\mu - \sum_{m=1}^{r_c} p_{cm} \mu \\
&= \left(\frac{\mu_c}{\mu_c}\right)\mu - (1)\mu \\
&= 0
\end{aligned}$$

Thus,

$$E[A] = 0$$

The **variance of A** is:

$$\text{var}(A) = \text{var}\left(\sum_{k=1}^n a_{sk} + \sum_{k=1}^n a_{dk}\right)$$

Because male and female gametes are uncorrelated in a random mating population,

$$\text{var}(A) = \text{var}\left(\sum_{k=1}^n a_{sk}\right) + \text{var}\left(\sum_{k=1}^n a_{dk}\right)$$

$$\begin{aligned} \text{var}(A) &= \sum_{k=1}^n \text{var}(a_{sk}) + 2 \sum_{k=1}^n \sum_{k' > k}^n \text{cov}(a_{sk}, a_{sk'}) \\ &\quad + \sum_{k=1}^n \text{var}(a_{dk}) + 2 \sum_{k=1}^n \sum_{k' > k}^n \text{cov}(a_{dk}, a_{dk'}) \end{aligned}$$

But **loci were assumed to be independent of one another**, thus the **covariance between additive genetic effects between different loci in both male and female gametes is zero**. In algebraic terms,

$$\begin{aligned} \text{cov}(a_{sk}, a_{sk'}) &= E[a_{sk} a_{sk'}] - E[a_{sk}]E[a_{sk'}] \\ &= E[a_{sk} a_{sk'}] - (0)(0) \\ &= E_{k'} E[a_{sk} a_{sk'} | k'] \\ &= E_{k'} \left[ E_k[a_{sk}] a_{sk'} \right] \\ &= E_{k'} [(0) a_{sk'}] \\ &= 0 \end{aligned}$$

Thus,

$$\begin{aligned}
\text{var}(A) &= \sum_{k=1}^n \text{var}(a_{sk}) + \sum_{k=1}^n \text{var}(a_{dk}) \\
&= \sum_{k=1}^n \left( E[a_{sk}^2] - (E[a_{sk}])^2 \right) + \sum_{k=1}^n \left( E[a_{dk}^2] - (E[a_{dk}])^2 \right) \\
&= \sum_{k=1}^n \left( E[a_{sk}^2] - (0)^2 \right) + \sum_{k=1}^n \left( E[a_{dk}^2] - (0)^2 \right) \\
&= \sum_{k=1}^n E[a_{sk}^2] + \sum_{k=1}^n E[a_{dk}^2] \\
&= \sigma_A^2
\end{aligned}$$

**[2] Dominance genetic effect of an individual (D):** sum of the n dominance deviations of an animal.

$$D = \sum_{k=1}^n d_k$$

where

n = number of contributions to the genotypic value of an animal due to intralocus interactions, and

$$d_k = a_{sc} a_{dc}$$

= product of deviations of alleles occupying locus c in the gametes of the sire and the dam.

The **expected value of D** is:

$$\begin{aligned}
E[D] &= E\left[\sum_{k=1}^n d_k\right] \\
&= \sum_{k=1}^n E[d_k]
\end{aligned}$$

But,

$$\begin{aligned}
 E[d_k] &= E\left[\left(\frac{A_{cm}}{\mu_c}\right)\left(\frac{A_{cm'}}{\mu_c}\right)\mu - \left(\frac{A_{cm}}{\mu_c}\right)\mu - \left(\frac{A_{cm'}}{\mu_c}\right)\mu + \mu\right] \\
 &= \sum_{m=1}^{r_c} p_{cm} \sum_{m'=1}^{r_{c'}} p_{cm'} \left[\left(\frac{A_{cm}}{\mu_c}\right)\left(\frac{A_{cm'}}{\mu_c}\right)\mu - \left(\frac{A_{cm}}{\mu_c}\right)\mu - \left(\frac{A_{cm'}}{\mu_c}\right)\mu + \mu\right] \\
 &= \left(\frac{\mu_c}{\mu_c}\right)\left(\frac{\mu_c}{\mu_c}\right)\mu - \left(\frac{\mu_c(1)}{\mu_c}\right)\mu - \left(\frac{(1)\mu_c}{\mu_c}\right)\mu + (1)(1)\mu \\
 &= \mu - \mu - \mu + \mu \\
 &= 0
 \end{aligned}$$

Thus,

$$\begin{aligned}
 E[D] &= \sum_{k=1}^n (0) \\
 &= 0
 \end{aligned}$$

The **variance of D** is:

$$\begin{aligned}
 \text{var}(D) &= \text{var}\left(\sum_{k=1}^n d_k\right) \\
 &= \sum_{k=1}^n \text{var}(d_k) + 2 \sum_{k=1}^n \sum_{k'>k}^n \text{cov}(d_k, d_{k'})
 \end{aligned}$$

By the **assumption of independence among loci**, the **covariance between dominance deviations is zero**, i.e.,

$$\begin{aligned}
\text{cov}(d_k, d_{k'}) &= E[d_k d_{k'}] - E[d_k]E[d_{k'}] \\
&= E[d_k d_{k'}] - (0)(0) \\
&= E_{k'} E_k [d_k d_{k'} | k'] \\
&= \left[ E_k [d_k] d_{k'} \right] \\
&= E_{k'} [(0) d_{k'}] \\
&= 0
\end{aligned}$$

Thus,

$$\begin{aligned}
\text{var}(D) &= \sum_{k=1}^n \text{var}(d_k) \\
&= \sum_{k=1}^n (E[d_k^2] - (E[d_k])^2) \\
\text{var}(D) &= \sum_{k=1}^n (E[d_k^2] - (0)^2) \\
&= \sum_{k=1}^n E[d_k^2] \\
&= \sigma_D^2
\end{aligned}$$

**[3] Additive  $\times$  Additive genetic effect of an individual (AA):** sum of the  $4[n(n-1)/2]$  different additive  $\times$  additive deviations of an animal.

$$AA = \sum_{k=1}^{N_{aa}} aa_k$$

where

$$N_{aa} = 4[n(n-1)/2]$$

= number of contributions to the genotypic value of an animal due to interlocus additive  $\times$  additive interactions.

$$aa_k = a_{cm} a_{c'm'}$$

= product of the deviations of one allele located at locus c and another allele housed at locus c', where both alleles may be from the same gamete (male or female) or from different gametes.

The **expected value of AA** is:

$$\begin{aligned} E[AA] &= E\left[\sum_{k=1}^{N_{aa}} aa_k\right] \\ &= \sum_{k=1}^{N_{aa}} E[aa_k] \end{aligned}$$

But,

$$\begin{aligned} E[aa_k] &= E\left[\left(\frac{A_{cm}}{\mu_c}\right)\left(\frac{A_{c'm'}}{\mu_{c'}}\right)\mu - \left(\frac{A_{cm}}{\mu_c}\right)\mu - \left(\frac{A_{c'm'}}{\mu_{c'}}\right)\mu + \mu\right] \\ &= \sum_{m=1}^{r_c} p_{cm} \sum_{m'=1}^{r_{c'}} p_{c'm'} \left[\left(\frac{A_{cm}}{\mu_c}\right)\left(\frac{A_{c'm'}}{\mu_{c'}}\right)\mu - \left(\frac{A_{cm}}{\mu_c}\right)\mu - \left(\frac{A_{c'm'}}{\mu_{c'}}\right)\mu + \mu\right] \\ &= \left(\frac{\mu_c}{\mu_c}\right)\left(\frac{\mu_{c'}}{\mu_{c'}}\right)\mu - \left(\frac{\mu_c(1)}{\mu_c}\right)\mu - \left(\frac{(1)\mu_{c'}}{\mu_{c'}}\right)\mu + (1)(1)\mu \\ &= \mu - \mu - \mu + \mu \\ &= 0 \end{aligned}$$

Thus,

$$E[AA] = \sum_{k=1}^{N_{aa}} (0)$$

$$= 0$$

The **variance of AA** is:

$$\begin{aligned} \text{var}(AA) &= \text{var}\left(\sum_{k=1}^{N_{aa}} aa_k\right) \\ &= \sum_{k=1}^{N_{aa}} \text{var}(aa_k) + 2 \sum_{k=1}^{N_{aa}} \sum_{k'>k}^{N_{aa}} \text{cov}(aa_k, aa_{k'}) \end{aligned}$$

By the **assumption of independence among loci**, the **covariance between additive  $\times$  additive deviations is zero**, i.e.,

$$\begin{aligned} \text{cov}(aa_k, aa_{k'}) &= E[aa_k aa_{k'}] - E[aa_k]E[aa_{k'}] \\ &= E[aa_k aa_{k'}] - (0)(0) \end{aligned}$$

$$\begin{aligned} \text{cov}(aa_k, aa_{k'}) &= E_{k'} E_k [aa_k aa_{k'} | k'] \\ &= E_{k'} \left[ E_k [aa_k] aa_{k'} \right] \\ &= E_{k'} [(0) aa_{k'}] \\ &= 0 \end{aligned}$$

Thus,

$$\begin{aligned}
\text{var}(AA) &= \sum_{k=1}^{N_{aa}} \text{var}(aa_k) \\
&= \sum_{k=1}^{N_{aa}} \left( E[aa_k^2] - (E[aa_k])^2 \right) \\
&= \sum_{k=1}^{N_{aa}} \left( E[aa_k^2] - (0)^2 \right) \\
&= \sum_{k=1}^{N_{aa}} E[aa_k^2] \\
&= \sigma_{AA}^2
\end{aligned}$$

**[4] Additive × Dominance genetic effect of an individual (AD):** sum of the  $2[n(n - 1)]$  different additive × dominance deviations of an animal.

$$AD = \sum_{k=1}^{N_{ad}} ad_k$$

where

$$N_{ad} = 2[n(n - 1)]$$

= number of contributions to the genotypic value of an animal due to interlocus additive × dominance interactions

$$ad_k = a_{cm} a_{c'm'} a_{c'w'}$$

= product of the deviations of one allele located at locus c times the deviations of the two alleles located at locus c', where the allele at locus c may come from the male or the female gamete, and one of the alleles at locus c' come from the male gamete and another one from the female gamete.

The **expected value of AD** is:



$$\begin{aligned}
E[AD] &= E\left[\sum_{k=1}^{N_{ad}} ad_k\right] \\
&= \sum_{k=1}^{N_{ad}} E[ad_k]
\end{aligned}$$

But,

$$\begin{aligned}
E[ad_k] &= E\left[\left(\frac{A_{cm}}{\mu_c}\right)\left(\frac{A_{c'm'}}{\mu_{c'}}\right)\left(\frac{A_{c'w'}}{\mu_{c'}}\right)\mu\right. \\
&\quad - \left(\frac{A_{cm}}{\mu_c}\right)\left(\frac{A_{c'm'}}{\mu_{c'}}\right)\mu - \left(\frac{A_{cm}}{\mu_c}\right)\left(\frac{A_{c'w'}}{\mu_{c'}}\right)\mu - \left(\frac{A_{c'm'}}{\mu_{c'}}\right)\left(\frac{A_{c'w'}}{\mu_{c'}}\right)\mu \\
&\quad \left. + \left(\frac{A_{cm}}{\mu_c}\right)\mu + \left(\frac{A_{c'm'}}{\mu_{c'}}\right)\mu + \left(\frac{A_{c'w'}}{\mu_{c'}}\right)\mu - \mu\right] \\
E[ad_k] &= \sum_{m=1}^{r_c} p_{cm} \sum_{m'=1}^{r_{m'}} p_{c'm'} \sum_{w'=1}^{r_{w'}} p_{c'w'} \left[\left(\frac{A_{cm}}{\mu_c}\right)\left(\frac{A_{c'm'}}{\mu_{c'}}\right)\left(\frac{A_{c'w'}}{\mu_{c'}}\right)\mu\right. \\
&\quad - \left(\frac{A_{cm}}{\mu_c}\right)\left(\frac{A_{c'm'}}{\mu_{c'}}\right)\mu - \left(\frac{A_{cm}}{\mu_c}\right)\left(\frac{A_{c'w'}}{\mu_{c'}}\right)\mu - \left(\frac{A_{c'm'}}{\mu_{c'}}\right)\left(\frac{A_{c'w'}}{\mu_{c'}}\right)\mu \\
&\quad \left. + \left(\frac{A_{cm}}{\mu_c}\right)\mu + \left(\frac{A_{c'm'}}{\mu_{c'}}\right)\mu + \left(\frac{A_{c'w'}}{\mu_{c'}}\right)\mu - \mu\right] \\
E[ad_k] &= \mu - \mu - \mu - \mu + \mu + \mu + \mu - \mu \\
&= 0
\end{aligned}$$

Thus,

$$E[AD] = \sum_{k=1}^{N_{ad}} (0)$$

$$= 0$$

The **variance of AD** is:

$$\begin{aligned} \text{var}(AD) &= \text{var}\left(\sum_{k=1}^{N_{ad}} ad_k\right) \\ &= \sum_{k=1}^{N_{ad}} \text{var}(ad_k) + 2 \sum_{k=1}^{N_{ad}} \sum_{k' > k}^{N_{ad}} \text{cov}(ad_k, ad_{k'}) \end{aligned}$$

By the **assumption of independence among loci**, the **covariance between additive  $\times$  dominance deviations is zero**, i.e.,

$$\begin{aligned} \text{cov}(ad_k, ad_{k'}) &= E[ad_k ad_{k'}] - E[ad_k]E[ad_{k'}] \\ &= E[ad_k ad_{k'}] - (0)(0) \\ \text{cov}(ad_k, ad_{k'}) &= E_{k'} E_k [ad_k ad_{k'} | k'] \\ &= E_{k'} \left[ E_k [ad_k] ad_{k'} \right] \\ &= E_{k'} [(0) ad_{k'}] \\ &= 0 \end{aligned}$$

Thus,

$$\begin{aligned}
\text{var}(AD) &= \sum_{k=1}^{N_{ad}} \text{var}(ad_k) \\
&= \sum_{k=1}^{N_{ad}} \left( E[ad_k^2] - (E[ad_k])^2 \right) \\
&= \sum_{k=1}^{N_{ad}} \left( E[ad_k^2] - (0)^2 \right) \\
&= \sum_{k=1}^{N_{ad}} E[ad_k^2] \\
&= \sigma_{AD}^2
\end{aligned}$$

**[5] Dominance  $\times$  Dominance genetic effect of an individual (DD):** sum of the  $n(n - 1)$  different dominance  $\times$  dominance deviations of an animal.

$$DD = \sum_{k=1}^{N_{dd}} dd_k$$

where

$$\begin{aligned}
N_{dd} &= n(n - 1) \\
&= \text{number of contributions to the genotypic value of an animal due to} \\
&\text{interlocus dominance} \times \text{dominance interactions.} \\
dd_k &= a_{cm} a_{cw} a_{c'm'} a_{c'w'} \\
&= \text{product of the deviations of the two alleles located at locus } c \text{ times the} \\
&\text{deviations of the two alleles located at locus } c', \text{ where one of the alleles at both loci} \\
&c \text{ and } c' \text{ come from the male gamete and another one from the female gamete.}
\end{aligned}$$

The **expected value of DD** is:

$$\begin{aligned}
E[DD] &= E\left[\sum_{k=1}^{N_{dd}} dd_k\right] \\
&= \sum_{k=1}^{N_{dd}} E[dd_k]
\end{aligned}$$

But

$$\begin{aligned}
E[dd_k] &= E\left[\left(\frac{A_{cm}}{\mu_c}\right)\left(\frac{A_{cw}}{\mu_c}\right)\left(\frac{A_{c'm'}}{\mu_{c'}}\right)\left(\frac{A_{c'w'}}{\mu_{c'}}\right)\mu - \left(\frac{A_{cm}}{\mu_c}\right)\left(\frac{A_{cw}}{\mu_c}\right)\left(\frac{A_{c'm'}}{\mu_{c'}}\right)\mu\right. \\
&\quad - \left(\frac{A_{cm}}{\mu_c}\right)\left(\frac{A_{cw}}{\mu_c}\right)\left(\frac{A_{c'w'}}{\mu_{c'}}\right)\mu - \left(\frac{A_{cm}}{\mu_c}\right)\left(\frac{A_{c'm'}}{\mu_{c'}}\right)\left(\frac{A_{c'w'}}{\mu_{c'}}\right)\mu \\
&\quad - \left(\frac{A_{cw}}{\mu_c}\right)\left(\frac{A_{c'm'}}{\mu_{c'}}\right)\left(\frac{A_{c'w'}}{\mu_{c'}}\right)\mu + \left(\frac{A_{cm}}{\mu_c}\right)\left(\frac{A_{cw}}{\mu_c}\right)\mu + \left(\frac{A_{cm}}{\mu_c}\right)\left(\frac{A_{c'm'}}{\mu_{c'}}\right)\mu \\
&\quad + \left(\frac{A_{cm}}{\mu_c}\right)\left(\frac{A_{c'w'}}{\mu_{c'}}\right)\mu + \left(\frac{A_{cw}}{\mu_c}\right)\left(\frac{A_{c'm'}}{\mu_{c'}}\right)\mu + \left(\frac{A_{cw}}{\mu_c}\right)\left(\frac{A_{c'w'}}{\mu_{c'}}\right)\mu + \left(\frac{A_{c'm'}}{\mu_{c'}}\right)\left(\frac{A_{c'w'}}{\mu_{c'}}\right)\mu \\
&\quad \left. - \left(\frac{A_{cm}}{\mu_c}\right)\mu - \left(\frac{A_{cw}}{\mu_c}\right)\mu - \left(\frac{A_{c'm'}}{\mu_{c'}}\right)\mu - \left(\frac{A_{c'w'}}{\mu_{c'}}\right)\mu + \mu\right]
\end{aligned}$$

$$\begin{aligned}
E[dd_k] &= \sum_{m=1}^{r_c} p_{cm} \sum_{w=1}^{r_c} p_{cw} \sum_{m'=1}^{r_{c'}} p_{c'm'} \sum_{w'=1}^{r_{c'}} p_{c'w'} \left[ \left( \frac{A_{cm}}{\mu_c} \right) \left( \frac{A_{cw}}{\mu_c} \right) \left( \frac{A_{c'm'}}{\mu_{c'}} \right) \left( \frac{A_{c'w'}}{\mu_{c'}} \right) \mu \right. \\
&\quad - \left( \frac{A_{cm}}{\mu_c} \right) \left( \frac{A_{cw}}{\mu_c} \right) \left( \frac{A_{c'm'}}{\mu_{c'}} \right) \mu - \left( \frac{A_{cm}}{\mu_c} \right) \left( \frac{A_{cw}}{\mu_c} \right) \left( \frac{A_{c'w'}}{\mu_{c'}} \right) \mu - \left( \frac{A_{cm}}{\mu_c} \right) \left( \frac{A_{c'm'}}{\mu_{c'}} \right) \left( \frac{A_{c'w'}}{\mu_{c'}} \right) \mu \\
&\quad - \left( \frac{A_{cw}}{\mu_c} \right) \left( \frac{A_{c'm'}}{\mu_{c'}} \right) \left( \frac{A_{c'w'}}{\mu_{c'}} \right) \mu + \left( \frac{A_{cm}}{\mu_c} \right) \left( \frac{A_{cw}}{\mu_c} \right) \mu + \left( \frac{A_{cm}}{\mu_c} \right) \left( \frac{A_{c'm'}}{\mu_{c'}} \right) \mu \\
&\quad + \left( \frac{A_{cm}}{\mu_c} \right) \left( \frac{A_{c'w'}}{\mu_{c'}} \right) \mu + \left( \frac{A_{cw}}{\mu_c} \right) \left( \frac{A_{c'm'}}{\mu_{c'}} \right) \mu + \left( \frac{A_{cw}}{\mu_c} \right) \left( \frac{A_{c'w'}}{\mu_{c'}} \right) \mu + \left( \frac{A_{c'm'}}{\mu_{c'}} \right) \left( \frac{A_{c'w'}}{\mu_{c'}} \right) \mu \\
&\quad \left. - \left( \frac{A_{cm}}{\mu_c} \right) \mu - \left( \frac{A_{cw}}{\mu_c} \right) \mu - \left( \frac{A_{c'm'}}{\mu_{c'}} \right) \mu - \left( \frac{A_{c'w'}}{\mu_{c'}} \right) \mu + \mu \right]
\end{aligned}$$

$$\begin{aligned}
E[dd_k] &= \mu - \mu - \mu - \mu - \mu + \mu + \mu + \mu + \mu + \mu + \mu + \mu - \mu - \mu - \mu - \mu + \mu \\
&= 0
\end{aligned}$$

Thus,

$$\begin{aligned}
E[DD] &= \sum_{k=1}^{N_{dd}} (0) \\
&= 0
\end{aligned}$$

The **variance of DD** is:

$$\begin{aligned}
\text{var}(DD) &= \text{var} \left( \sum_{k=1}^{N_{dd}} dd_k \right) \\
&= \sum_{k=1}^{N_{dd}} \text{var}(dd_k) + 2 \sum_{k=1}^{N_{dd}} \sum_{k' > k}^{N_{dd}} \text{cov}(dd_k, dd_{k'})
\end{aligned}$$

By the **assumption of independence among loci**, the **covariance between dominance**  $\times$

**dominance deviations is zero, i.e.,**

$$\begin{aligned}
 \text{cov}(dd_k, dd_{k'}) &= E[dd_k dd_{k'}] - E[dd_k]E[dd_{k'}] \\
 &= E[dd_k dd_{k'}] - (0)(0) \\
 &= E_{k'} E_k [dd_k dd_{k'} | k'] \\
 &= E_{k'} \left[ E_k [dd_k] dd_{k'} \right] \\
 &= E_{k'} [(0) dd_{k'}] \\
 &= 0
 \end{aligned}$$

Thus,

$$\begin{aligned}
 \text{var}(DD) &= \sum_{k=1}^{N_{dd}} \text{var}(dd_k) \\
 &= \sum_{k=1}^{N_{dd}} \left( E[dd_k^2] - (E[dd_k])^2 \right) \\
 &= \sum_{k=1}^{N_{dd}} \left( E[dd_k^2] - (0)^2 \right) \\
 &= \sum_{k=1}^{N_{dd}} E[dd_k^2] \\
 &= \sigma_{DD}^2
 \end{aligned}$$

**[6] Additive × additive × additive, additive × additive × dominance, additive × dominance × dominance, dominance × dominance × dominance, additive × additive × additive × additive, etc.** All other interaction effects will:

(a) be equal to the sum of their respective individual deviations within an individual,

- (b) have expectation equal to zero,
- (c) variance equal to the sum of the squares of their individual deviations, and
- (d) be uncorrelated to all other genetic effects.

**The total number of deviations contributing to the genotype of an animal is  $(2^{2n} - 1)$ , where the 1 corresponds to the mean of the population.**

### Genotypic value of an individual

The **genotypic value of an individual (G)** is equal to the sum of the genotypic mean plus all  $(2^{2n} - 1)$  genotypic effects.

$$\begin{aligned}
 G &= \mu + \left( \sum_{k=1}^n a_{sk} + \sum_{k=1}^n a_{dk} \right) + \sum_{k=1}^{N_d} d_k + \sum_{k=1}^{N_{aa}} aa_k + \sum_{k=1}^{N_{ad}} ad_k + \sum_{k=1}^{N_{dd}} dd_k + \dots \\
 &= \mu + A + D + AA + AD + DD + \dots
 \end{aligned}$$

The **expected value of G** is:

$$\begin{aligned}
 E[G] &= \mu + 0 + 0 + 0 + 0 + 0 + \dots \\
 &= \mu
 \end{aligned}$$

The **variance of G** is:

$$\begin{aligned}
 \text{var}(G) &= \left( \sum_{k=1}^n E[a_{sk}^2] + \sum_{k=1}^n E[a_{dk}^2] \right) + \sum_{k=1}^{N_d} E[d_k^2] + \sum_{k=1}^{N_{aa}} E[aa_k^2] + \sum_{k=1}^{N_{ad}} E[ad_k^2] + \sum_{k=1}^{N_{dd}} E[dd_k^2] + \dots \\
 &= \sigma_A^2 + \sigma_D^2 + \sigma_{AA}^2 + \sigma_{AD}^2 + \sigma_{DD}^2 + \dots \\
 &= \sigma_G^2
 \end{aligned}$$

[13-24]

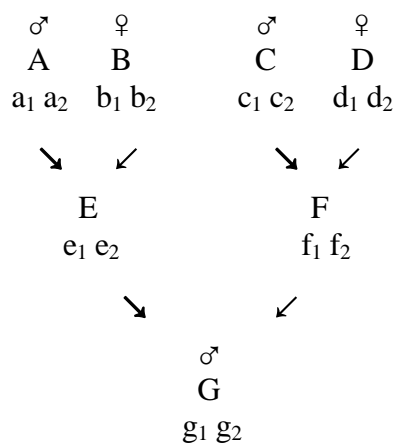
A better notation from a computational viewpoint is to use two subscripts instead of letters. The first subscript indicates the number of additive genetic effects, and the second one the number of dominance genetic effects. For example,  $\sigma_{10}^2 = \sigma_A^2$ ,  $\sigma_{01}^2 = \sigma_D^2$ ,  $\sigma_{02}^2 = \sigma_{AA}^2$ ,  $\sigma_{11}^2 = \sigma_{AD}^2$ ,  $\sigma_{02}^2 = \sigma_{DD}^2$ , etc. Thus, the **variance of G** is:

$$\begin{aligned}\sigma_G^2 &= \sigma_{10}^2 + \sigma_{01}^2 + \sigma_{20}^2 + \sigma_{11}^2 + \sigma_{02}^2 + \dots \\ &= \sum_{i=0}^n \sum_{\substack{j=0 \\ j+i>1}}^n \sigma_{ij}^2\end{aligned}$$

Thus, **the variance of the genotypic value of an individual is the sum of the expected values of the square of  $(2^{2n} - 1)$  deviations.**

## Genetic Relationships Among Individuals

[1] **Coefficient of coancestry (Malécot's coefficient de parenté):** probability that a random allele at a random locus in one individual is identical by descent to a random allele taken from the same random locus in another individual. For example, consider the following pedigree:





$$r_{EF} = \frac{1}{4} [ P(e_1 = f_1) + P(e_1 = f_2) + P(e_2 = f_1) + P(e_2 = f_2) ]$$

It can be shown (Falconer, 1981, pg. 81) that

$$r_{EF} = \frac{1}{4} [ r_{AC} + r_{AD} + r_{BC} + r_{BD} ]$$

Also, the **coefficient of coancestry of an individual with itself**, e.g., the probability that two gametes taken at random from individual G carry identical alleles is:

$$r_{GG} = \frac{1}{4} [ P(g_1 = g_1) + P(g_1 = g_2) + P(g_2 = g_1) + P(g_2 = g_2) ]$$

$$r_{GG} = \frac{1}{4} [ 1 + F_G + F_G + 1 ]$$

$$r_{GG} = \frac{1}{2} (1 + F_G)$$

where

$F_G$  = coefficient of inbreeding of individual G.

The **coefficient of coancestry between individuals of different generations**, e.g.,  $r_{EC}$ , is equal to:

$$r_{EC} = \frac{1}{2} [ r_{AC} + r_{BC} ]$$

[2] **Additive relationship between two individuals:** probability that **the two alleles at a random locus** are identical by descent in two individuals. This is a measure of the fraction of genes which are identical by descent in two individuals. The additive relationship between individuals E and F is:

$$a_{EF} = \frac{1}{2} [ P(e_1 = f_1) + P(e_1 = f_2) ] + \frac{1}{2} [ P(e_2 = f_1) + P(e_2 = f_2) ]$$

$$a_{EF} = \frac{1}{2} [ P(e_1 = f_1) + P(e_1 = f_2) + P(e_2 = f_1) + P(e_2 = f_2) ]$$

$$\Rightarrow a_{EF} = 2r_{EF}$$

The **relationship of an animal with itself** (e.g., G) is:

$$a_{GG} = \frac{1}{2} [ P(g_1 = g_1) + P(g_1 = g_2) ] + \frac{1}{2} [ P(g_2 = g_1) + P(g_2 = g_2) ]$$

$$a_{GG} = \frac{1}{2} [ 1 + F_G ] + \frac{1}{2} [ F_G + 1 ]$$

$$a_{GG} = 1 + F_G$$

$$\Rightarrow a_{GG} = 2r_{GG}$$

The relationship of an animal with itself is also called the **coefficient of inbreeding** of an individual, and it is defined as the probability that the two alleles at a random locus in individual X are identical by descent, i.e.,

$$P(X_i = X_j) = \sum [ (1/2)^{n_1+n_2+1} (1 + F_A) ]$$

$$\equiv F_X$$

where

$F_X$  = coefficient of inbreeding of animal X,

$1/2$  = probability of transmission of an allele across 1 generation,

$n_1$  = number of generations between the sire of X and a common ancestor A,

$n_2$  = number of generations between the dam of X and a common ancestor A, and

$F_A$  = coefficient of inbreeding of common ancestor A.

In terms of the coefficient of coancestry:

$$F_X = r_{SD}$$

where

S = sire of X, and

D = dam of X.

### Sewall Wright's coefficient of relationship

$$R_{XY} = \frac{a_{XY}}{[a_{XX} a_{YY}]^{1/2}}$$

**Remark:** In a noninbred population  $a_{XX} = a_{YY} = 1$ , thus,  $R_{XY} = a_{XY}$ .

[3] **Dominance relationship between two individuals:** probability that **both alleles at a random locus** in two individuals are identical by descent. For instance, the dominance relationship between E and F is:

$$d_{EF} = P(e_1 = f_1 \text{ and } e_2 = f_2) + P(e_2 = f_1 \text{ and } e_1 = f_2)$$

$$d_{EF} = P(e_1 = f_1) P(e_2 = f_2) + P(e_2 = f_1) P(e_1 = f_2)$$

$$d_{EF} = r_{AC}r_{BD} + r_{AD}r_{BC}$$

$$\Rightarrow d_{EF} = \frac{1}{4} (a_{AC}a_{BD} + a_{AD}a_{BC})$$

**Remark:** The **dominance relationship of an animal with itself** is:

$$d_{GG} = P(e_1 = e_1) P(e_2 = e_2) + P(e_1 = e_2) P(e_2 = e_1)$$

$$d_{GG} = (1)(1) + (r_{AB})(r_{AB})$$

$$\Rightarrow d_{GG} = 1 + (r_{AB})^2$$

$$\Rightarrow d_{GG} = 1 + (F_G)^2$$

$$\Rightarrow d_{GG} = 1 + \frac{1}{4} (a_{AB})^2$$

[4] **Additive  $\times$  additive relationship between two individuals:** probability that **individual alleles at two random loci** in two individuals are identical by descent. Because of the assumption that loci segregate independently, the additive  $\times$  additive relationship between two individuals is equal to the square of the additive relationship between two individuals. For instance, the additive  $\times$  additive relationship between E and F is:

$$aa_{EF} = (a_{EF})^2$$

$$aa_{EF} = (2r_{EF})^2$$

[5] **Additive  $\times$  dominance relationship between two individuals:** probability that **individual alleles at one random locus**, and **both alleles at another random locus** in two individuals are

identical by descent. Because loci are assumed to segregate independently, the additive  $\times$  dominance relationship between two individuals is equal to the product of the additive relationship times the dominance relationship between two individuals. For instance, the additive  $\times$  dominance relationship between E and F is:

$$\begin{aligned} ad_{EF} &= (a_{EF}) (d_{EF}) \\ \Rightarrow ad_{EF} &= (2r_{EF}) (r_{AC}r_{BD} + r_{AD}r_{BC}) \\ \Rightarrow ad_{EF} &= (a_{EF}) [1/4 (a_{AC}a_{BD} + a_{AD}a_{BC})] \end{aligned}$$

[6] **Dominance  $\times$  dominance relationship between two individuals:** probability that **both alleles at two random loci** in two individuals are identical by descent. Because loci are assumed to segregate independently, the dominance  $\times$  dominance relationship between two individuals is equal to the square of the dominance relationship between two individuals. For instance, the dominance  $\times$  dominance relationship between E and F is:

$$\begin{aligned} dd_{EF} &= (d_{EF})^2 \\ dd_{EF} &= (r_{AC}r_{BD} + r_{AD}r_{BC})^2 \\ \Rightarrow dd_{EF} &= [1/4 (a_{AC}a_{BD} + a_{AD}a_{BC})]^2 \end{aligned}$$

[7] **Relationships due to higher order interactions between two individuals are functions of (i.e., products of) additive and dominance relationships.**

For example, the **additive  $\times$  additive  $\times$  additive relationship between E and F** is:

$$\begin{aligned} aaa_{EF} &= (2r_{EF})^3 \\ \Rightarrow aaa_{EF} &= (a_{EF})^3 \end{aligned}$$

and the **additive  $\times$  additive  $\times$  dominance relationship between E and F** is:

$$aad_{EF} = (2r_{EF})^2 (r_{AC}r_{BD} + r_{AD}r_{BC})$$

$$\Rightarrow aad_{EF} = (a_{EF})^2 [1/4 (a_{AC}a_{BD} + a_{AD}a_{BC})]$$

### Genetic Covariances Among Related Individuals (n loci and $r_i$ alleles per locus)

These covariances can be found by conditioning them on a **random variable X whose outcomes include all types of genotypic effects**. All the outcomes of random variable X are defined to occur **by descent**, i.e., all probabilities **require** equality (i.e., identity) by inheritance from a common ancestor. Thus, the possibility of two alleles being equal by chance (i.e., alike in state) is **not** one of these outcomes. Various outcomes and their probabilities are defined in a Table below. The animals used in this Table are E (with parents A and B) and F (with parents C and D). The first subscript of each allele (i,j,k) denotes a random locus, and the second subscript (1,2) is random allele 1 or 2 within random locus i,j, or k.

Outcome x	Meaning of outcome x	$P(X = x)$	$P(X = x)$
1	$[(e_{i1} = f_{i1}) \text{ or } (e_{i1} = f_{i2})]$ $\text{or } [(e_{i2} = f_{i1}) \text{ or } (e_{i2} = f_{i2})]$ by descent	$a_{EF}$	$a_{EF}$
2	$[(e_{i1} = f_{i1}) \text{ and } (e_{i2} = f_{i2})]$ $\text{or } [(e_{i1} = f_{i2}) \text{ and } (e_{i2} = f_{i1})]$ by descent	$1/4 (a_{AC}a_{BD} + a_{AD}a_{BC})$	$d_{EF}$
3	$[(e_{i1} = f_{i1}) \text{ or } (e_{i1} = f_{i2})]$ $\text{or } [(e_{i2} = f_{i1}) \text{ or } (e_{i2} = f_{i2})]$ and $[(e_{j1} = f_{j1}) \text{ or } (e_{j1} = f_{j2})]$ $\text{or } [(e_{j2} = f_{j1}) \text{ or } (e_{j2} = f_{j2})]$ by descent	$(a_{EF})(a_{EF})$	$(a_{EF})^2$

Outcome x	Meaning of outcome x	$P(X = x)$	$P(X = x)$
4	$[(e_{i1} = f_{i1}) \text{ or } (e_{i1} = f_{i2})]$ or $[(e_{i2} = f_{i1}) \text{ or } (e_{i2} = f_{i2})]$ and $[(e_{j1} = f_{j1}) \text{ and } (e_{j2} = f_{j2})]$ or $[(e_{j1} = f_{j2}) \text{ and } (e_{j2} = f_{j1})]$ by descent	$(a_{EF}) [1/4 (a_{AC}a_{BD} + a_{AD}a_{BC})]$	$(a_{EF})(d_{EF})$
5	$[(e_{i1} = f_{i1}) \text{ and } (e_{i2} = f_{i2})]$ or $[(e_{i1} = f_{i2}) \text{ and } (e_{i2} = f_{i1})]$ and $[(e_{j1} = f_{j1}) \text{ and } (e_{j2} = f_{j2})]$ or $[(e_{j1} = f_{j2}) \text{ and } (e_{j2} = f_{j1})]$ by descent	$[1/4 (a_{AC}a_{BD} + a_{AD}a_{BC})]$ $[1/4 (a_{AC}a_{BD} + a_{AD}a_{BC})]$	$(d_{EF})^2$
6	$[(e_{i1} = f_{i1}) \text{ or } (e_{i1} = f_{i2})]$ or $[(e_{i2} = f_{i1}) \text{ or } (e_{i2} = f_{i2})]$ and $[(e_{j1} = f_{j1}) \text{ or } (e_{j1} = f_{j2})]$ or $[(e_{j2} = f_{j1}) \text{ or } (e_{j2} = f_{j2})]$ and $[(e_{k1} = f_{k1}) \text{ or } (e_{k1} = f_{k2})]$ or $[(e_{k2} = f_{k1}) \text{ or } (e_{k2} = f_{k2})]$ by descent	$(a_{EF})(a_{EF})(a_{EF})$	$(a_{EF})^3$
7	$[(e_{i1} = f_{i1}) \text{ or } (e_{i1} = f_{i2})]$ or $[(e_{i2} = f_{i1}) \text{ or } (e_{i2} = f_{i2})]$ and $[(e_{j1} = f_{j1}) \text{ or } (e_{j1} = f_{j2})]$ or $[(e_{j2} = f_{j1}) \text{ or } (e_{j2} = f_{j2})]$ and $[(e_{k1} = f_{k1}) \text{ and } (e_{k2} = f_{k2})]$ or $[(e_{k1} = f_{k2}) \text{ and } (e_{k2} = f_{k1})]$ by descent	$(a_{EF})(a_{EF})$ $[1/4(a_{AC}a_{BD} + a_{AD}a_{BC})]$	$(a_{EF})^2(d_{EF})$

Outcome x	Meaning of outcome x	$P(X = x)$	$P(X = x)$
8	$[(e_{i1} = f_{i1}) \text{ or } (e_{i1} = f_{i2})]$ or $[(e_{i2} = f_{i1}) \text{ or } (e_{i2} = f_{i2})]$ and $[(e_{j1} = f_{j1}) \text{ and } (e_{j2} = f_{j2})]$ or $[(e_{j1} = f_{j2}) \text{ and } (e_{j2} = f_{j1})]$ and $[(e_{k1} = f_{k1}) \text{ and } (e_{k2} = f_{k2})]$ or $[(e_{k1} = f_{k2}) \text{ and } (e_{k2} = f_{k1})]$ by descent	$(a_{EF}) [1/4 (a_{AC}a_{BD} + a_{AD}a_{BC})]$ $[1/4 (a_{AC}a_{BD} + a_{AD}a_{BC})]$	$(a_{EF})(d_{EF})^2$
9	$[(e_{i1} = f_{i1}) \text{ and } (e_{i2} = f_{i2})]$ or $[(e_{i1} = f_{i2}) \text{ and } (e_{i2} = f_{i1})]$ and $[(e_{j1} = f_{j1}) \text{ and } (e_{j2} = f_{j2})]$ or $[(e_{j1} = f_{j2}) \text{ and } (e_{j2} = f_{j1})]$ and $[(e_{k1} = f_{k1}) \text{ and } (e_{k2} = f_{k2})]$ or $[(e_{k1} = f_{k2}) \text{ and } (e_{k2} = f_{k1})]$ by descent	$[1/4 (a_{AC}a_{BD} + a_{AD}a_{BC})]$ $[1/4 (a_{AC}a_{BD} + a_{AD}a_{BC})]$ $[1/4 (a_{AC}a_{BD} + a_{AD}a_{BC})]$	$(d_{EF})^3$

Let the genotypes of individuals E and F be  $G_E$  and  $G_F$ , where

$$G_E = \mu + A_E + D_E + AA_E + AD_E + DD_E + \dots$$

$$= \mu + \sum_{k=1}^{2n} a_{Ek} + \sum_{k=1}^{N_d} d_{Ek} + \sum_{k=1}^{N_{aa}} aa_{Ek} + \sum_{k=1}^{N_{ad}} ad_{Ek} + \sum_{k=1}^{N_{dd}} dd_{Ek} + \dots$$

and

$$G_F = \mu + A_F + D_F + AA_F + AD_F + DD_F + \dots$$

$$= \mu + \sum_{k=1}^{2n} a_{Fk} + \sum_{k=1}^{N_d} d_{Fk} + \sum_{k=1}^{N_{aa}} aa_{Fk} + \sum_{k=1}^{N_{ad}} ad_{Fk} + \sum_{k=1}^{N_{dd}} dd_{Fk} + \dots$$

The **covariance between  $G_E$  and  $G_F$**  is:

$$\begin{aligned} \text{cov}(G_E, G_F) &= \text{cov}(A_E, A_F) + \text{cov}(D_E, D_F) + \text{cov}(AA_E, AA_F) \\ &\quad + \text{cov}(AD_E, AD_F) + \text{cov}(DD_E, DD_F) + \dots \end{aligned}$$

which is equal to

$$\begin{aligned} \text{cov}(G_E, G_F) &= \text{cov}\left(\sum_{k=1}^{2n} a_{Ek}, \sum_{k=1}^{2n} a_{Fk}\right) + \text{cov}\left(\sum_{k=1}^{N_d} d_{Ek}, \sum_{k=1}^{N_d} d_{Fk}\right) + \text{cov}\left(\sum_{k=1}^{N_{aa}} aa_{Ek}, \sum_{k=1}^{N_{aa}} aa_{Fk}\right) \\ &\quad + \text{cov}\left(\sum_{k=1}^{N_{ad}} ad_{Ek}, \sum_{k=1}^{N_{ad}} ad_{Fk}\right) + \text{cov}\left(\sum_{k=1}^{N_{dd}} dd_{Ek}, \sum_{k=1}^{N_{dd}} dd_{Fk}\right) + \dots \end{aligned}$$

by **independence among the various genotypic effects**. Furthermore, **because loci are assumed to segregate independently**,

$$\begin{aligned} \text{cov}(G_E, G_F) &= \sum_{k=1}^{2n} \text{cov}(a_{Ek}, a_{Fk}) + \sum_{k=1}^{N_d} \text{cov}(d_{Ek}, d_{Fk}) + \sum_{k=1}^{N_{aa}} \text{cov}(aa_{Ek}, aa_{Fk}) \\ &\quad + \sum_{k=1}^{N_{ad}} \text{cov}(ad_{Ek}, ad_{Fk}) + \sum_{k=1}^{N_{dd}} \text{cov}(dd_{Ek}, dd_{Fk}) + \dots \end{aligned}$$

**Conditioning each covariance on random variable  $X$**  yields:

$$\begin{aligned} \text{cov}(a_{Ek}, a_{Fk}) &= E[\text{cov}(a_{Ek}, a_{Fk} \mid X = x_1)] + \text{cov}(E[a_{Ek} \mid X = x_1], E[a_{Fk} \mid X = x_1]) \\ &= a_{EFk} \sigma_{A_k}^2 + 0 \\ &= a_{EFk} \sigma_{A_k}^2 \\ \text{cov}(d_{Ek}, d_{Fk}) &= E[\text{cov}(d_{Ek}, d_{Fk} \mid X = x_2)] + \text{cov}(E[d_{Ek} \mid X = x_2], E[d_{Fk} \mid X = x_2]) \\ &= d_{EFk} \sigma_{D_k}^2 + 0 \\ &= d_{EFk} \sigma_{D_k}^2 \end{aligned}$$



[13-33]

$$\text{cov}(\text{aa}_{\text{Ek}}, \text{aa}_{\text{Fk}}) = \text{E}[\text{cov}(\text{aa}_{\text{Ek}}, \text{aa}_{\text{Fk}} \mid \text{X} = \text{x}_3)] + \text{cov}(\text{E}[\text{aa}_{\text{Ek}} \mid \text{X} = \text{x}_3], \text{E}[\text{aa}_{\text{Fk}} \mid \text{X} = \text{x}_3])$$

$$= \text{aa}_{\text{EFk}} \sigma_{\text{AAk}}^2 + 0$$

$$= \text{aa}_{\text{EFk}} \sigma_{\text{AAk}}^2$$

$$\text{cov}(\text{ad}_{\text{Ek}}, \text{ad}_{\text{Fk}}) = \text{E}[\text{cov}(\text{ad}_{\text{Ek}}, \text{ad}_{\text{Fk}} \mid \text{X} = \text{x}_4)] + \text{cov}(\text{E}[\text{ad}_{\text{Ek}} \mid \text{X} = \text{x}_4], \text{E}[\text{ad}_{\text{Fk}} \mid \text{X} = \text{x}_4])$$

$$= \text{ad}_{\text{EFk}} \sigma_{\text{ADk}}^2 + 0$$

$$= \text{ad}_{\text{EFk}} \sigma_{\text{ADk}}^2$$

$$\text{cov}(\text{dd}_{\text{Ek}}, \text{dd}_{\text{Fk}}) = \text{E}[\text{cov}(\text{dd}_{\text{Ek}}, \text{dd}_{\text{Fk}} \mid \text{X} = \text{x}_5)] + \text{cov}(\text{E}[\text{dd}_{\text{Ek}} \mid \text{X} = \text{x}_5], \text{E}[\text{dd}_{\text{Fk}} \mid \text{X} = \text{x}_5])$$

$$= \text{dd}_{\text{EFk}} \sigma_{\text{DDk}}^2 + 0$$

$$= \text{dd}_{\text{EFk}} \sigma_{\text{DDk}}^2$$

Thus,

$$\begin{aligned} \text{cov}(\text{G}_\text{E}, \text{G}_\text{F}) &= \sum_{k=1}^{2n} \text{a}_{\text{EFk}} \sigma_{\text{A}_k}^2 + \sum_{k=1}^{N_d} \text{d}_{\text{EFk}} \sigma_{\text{D}_k}^2 + \sum_{k=1}^{N_{\text{aa}}} \text{aa}_{\text{EFk}} \sigma_{\text{AA}_k}^2 \\ &\quad + \sum_{k=1}^{N_{\text{ad}}} \text{ad}_{\text{EFk}} \sigma_{\text{AD}_k}^2 + \sum_{k=1}^{N_{\text{dd}}} \text{dd}_{\text{EFk}} \sigma_{\text{DD}_k}^2 + \dots \end{aligned}$$

But,

$$\text{a}_{\text{EF}_k} = \text{a}_{\text{EF}_{k'}} = \text{a}_{\text{EF}} \quad \text{for all } k, k' \text{ combinations}$$

$$\text{d}_{\text{EF}_k} = \text{d}_{\text{EF}_{k'}} = \text{d}_{\text{EF}} \quad \text{for all } k, k' \text{ combinations}$$

$$\text{aa}_{\text{EF}_k} = \text{aa}_{\text{EF}_{k'}} = \text{aa}_{\text{EF}} \quad \text{for all } k, k' \text{ combinations}$$

$$\text{ad}_{\text{EF}_k} = \text{ad}_{\text{EF}_{k'}} = \text{ad}_{\text{EF}} \quad \text{for all } k, k' \text{ combinations}$$

$$\text{dd}_{\text{EF}_k} = \text{dd}_{\text{EF}_{k'}} = \text{dd}_{\text{EF}} \quad \text{for all } k, k' \text{ combinations}$$

etc., thus,

$$\begin{aligned} \text{cov}(G_E, G_F) &= \sum_{k=1}^{2n} a_{EF} \sigma_{A_k}^2 + \sum_{k=1}^{N_d} d_{EF} \sigma_{D_k}^2 + \sum_{k=1}^{N_{aa}} aa_{EF} \sigma_{AA_k}^2 \\ &\quad + \sum_{k=1}^{N_{ad}} ad_{EF} \sigma_{AD_k}^2 + \sum_{k=1}^{N_{dd}} dd_{EF} \sigma_{DD_k}^2 + \dots \end{aligned}$$

$$\begin{aligned} \text{cov}(G_E, G_F) &= a_{EF} \sum_{k=1}^{2n} \sigma_{A_k}^2 + d_{EF} \sum_{k=1}^{N_d} \sigma_{D_k}^2 + aa_{EF} \sum_{k=1}^{N_{aa}} \sigma_{AA_k}^2 \\ &\quad + ad_{EF} \sum_{k=1}^{N_{ad}} \sigma_{AD_k}^2 + dd_{EF} \sum_{k=1}^{N_{dd}} \sigma_{DD_k}^2 + \dots \end{aligned}$$

$$\begin{aligned} \text{cov}(G_E, G_F) &= a_{EF} \sigma_A^2 + d_{EF} \sigma_D^2 + aa_{EF} \sigma_{AA}^2 \\ &\quad + ad_{EF} \sigma_{AD}^2 + dd_{EF} \sigma_{DD}^2 + \dots \end{aligned}$$

In terms of the **two-subscript notation**,

$$\begin{aligned} \text{cov}(G_E, G_F) &= a_{EF} \sigma_{10}^2 + d_{EF} \sigma_{01}^2 + aa_{EF} \sigma_{20}^2 \\ &\quad + ad_{EF} \sigma_{11}^2 + dd_{EF} \sigma_{02}^2 + \dots \\ &= a_{EF} \sigma_{10}^2 + d_{EF} \sigma_{01}^2 + (a_{EF})^2 \sigma_{20}^2 \\ &\quad + (a_{EF})(d_{EF}) \sigma_{11}^2 + (d_{EF})^2 \sigma_{02}^2 + \dots \\ &= \sum_{i=0}^n \sum_{\substack{j=0 \\ j+i>1}}^n (a_{EF})^i (d_{EF})^j \sigma_{ij}^2 \end{aligned}$$

Finally, the **covariance matrix of a vector of genotypic values**, i.e.,  $\text{cov}(g, g')$ , is a function of matrices of additive and dominance relationships, and Hadamard products of elements of these matrices, times their appropriate variances.

$$\begin{aligned}
\text{cov}(g, g') &= A \sigma_{10}^2 + D \sigma_{01}^2 + A \# A \sigma_{20}^2 \\
&\quad + A \# D \sigma_{11}^2 + D \# D \sigma_{02}^2 + \dots \\
&= \left\{ \sum_{i=0}^n \sum_{\substack{j=0 \\ j+i>1}}^n (a_{EF})^i (d_{EF})^j \sigma_{ij}^2 \right\}
\end{aligned}$$

where

$g$  = vector of animal genotypic values,

$A$  = matrix of additive genetic relationships,

$D$  = matrix of dominance relationships, and

$\#$  = Hadamard product (Searle, 1982, pg. 49).

## References

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## APPENDIX

### Tabular Method to compute additive relationships

The tabular method is based on the fact that the additive relationship between two individuals is equal to the average of the relationships of one of them and the parents of the other one, e.g.,

$$a_{EF} = \frac{1}{2}[a_{EC} + a_{ED}],$$

or, in terms of coefficients of coancestry,

$$r_{EF} = \frac{1}{2}[r_{EC} + r_{ED}]$$

**Proof:** See Van Vleck (1974).

### Steps of the Tabular Method

- (1) Include all animals in the pedigree in order of birth date, oldest first.
- (2) Write the sequential numbers of the animals in order of birth on the side and on top of the table.
- (3) Write the sequential numbers of the known parents across the top, above their progeny.
- (4) Put a 1 on the diagonal cells of the table. Add the coefficient of inbreeding to the diagonal cells of the animals in the base generation. Also, enter the relationships among base animals if known, otherwise, set these off diagonal cells to zero.
- (5) Compute the coefficient of inbreeding of the first animal with two known parents.
- (6) Compute all the offdiagonal entries of the row in (5), by adding  $\frac{1}{2}$  times the entry corresponding to parent 1 plus  $\frac{1}{2}$  times the entry corresponding to parent 2, in the same row.
- (7) Write the row values in the corresponding column entries.
- (8) Repeat steps (5), (6) and (7) until the last animal.

**Numerical example****Additive relationships**

Animal	$\begin{smallmatrix} - & - \\ A \end{smallmatrix}$	$\begin{smallmatrix} - & - \\ B \end{smallmatrix}$	$\begin{smallmatrix} - & - \\ E \end{smallmatrix}$	$\begin{smallmatrix} A & B \\ C \end{smallmatrix}$	$\begin{smallmatrix} A & B \\ D \end{smallmatrix}$	$\begin{smallmatrix} C & D \\ X \end{smallmatrix}$	$\begin{smallmatrix} D & E \\ V \end{smallmatrix}$
A	1	0	0	$\frac{1}{2}$	$\frac{1}{2}$	$\frac{1}{2}$	$\frac{1}{4}$
B	0	1	0	$\frac{1}{2}$	$\frac{1}{2}$	$\frac{1}{2}$	$\frac{1}{4}$
E	0	0	1	0	0	0	$\frac{1}{2}$
C	$\frac{1}{2}$	$\frac{1}{2}$	0	1	$\frac{1}{2}$	$\frac{3}{4}$	$\frac{1}{4}$
D	$\frac{1}{2}$	$\frac{1}{2}$	0	$\frac{1}{2}$	1	$\frac{3}{4}$	$\frac{1}{2}$
X	$\frac{1}{2}$	$\frac{1}{2}$	0	$\frac{3}{4}$	$\frac{3}{4}$	$1 + \frac{1}{4}$	$\frac{3}{8}$
V	$\frac{1}{4}$	$\frac{1}{4}$	$\frac{1}{2}$	$\frac{1}{4}$	$\frac{1}{2}$	$\frac{3}{8}$	1

**Dominance relationships**

$$d_{CD} = \frac{1}{4}(a_{AA}a_{BB} + a_{AB}a_{BA})$$

$$= \frac{1}{4}(1 * 1 + 0 * 0)$$

$$= \frac{1}{4}$$

$$d_{CX} = \frac{1}{4}(a_{AC}a_{BD} + a_{AD}a_{BC})$$

$$= \frac{1}{4}[(\frac{1}{2})(\frac{1}{2}) + (\frac{1}{2})(\frac{1}{2})]$$

$$= \frac{1}{2}$$

$$d_{CV} = \frac{1}{4}(a_{AD}a_{BE} + a_{AE}a_{BD})$$

$$= \frac{1}{4}[(\frac{1}{2})(0) + (0)(\frac{1}{2})]$$

$$= 0$$

$$d_{XV} = \frac{1}{4}(a_{CD}a_{DE} + a_{CE}a_{DD})$$

$$= \frac{1}{4}[(\frac{1}{2})(0) + (0)(1)]$$

$$= 0$$