CHAPTER 11

INBRED POPULATIONS AND COVARIANCES BETWEEN INBRED RELATIVES

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CHAPTER 11
INBRED POPULATIONS
AND
COVARIANCES BETWEEN INBRED RELATIVES

In Chapter 8, 9, and 10, we dealt entirely with noninbred populations. We
defined the population mean, allelic effects, and different kinds of genetic
variances of such populations in Chapter 8, and the covariances between noninbred
relatives in Chapter 9. Then in Chapter 10, we discussed mating systems that can
be used to generate noninbred relatives and the covariances from which the
different genetic variances can be estimated. We now turn to inbred populations.

An inbred population may be any population for which the average coefficient
of inbreeding is greater than zero. The population may be the kind described in
Chapter 5, where a certain amount of mating occurs between relatives within a
single large population which is otherwise random mating, or that described in
Chapter 6 where inbreeding subdivides the whole population into a large number of
subpopulations, each of which is finite in size and is, within itself, mating at
random or with some avoidance of inbreeding (see Section 6.1). That inbred
populations commonly show inbreeding depression or a decline in the mean of
characters, particularly those related to reproductive capacity or fitness, is
well known. Since inbreeding, in the absence of selection, does not bring about a
change in allelic frequencies, the decline in the mean must be due to the relative
change in genotypic frequencies -- the increase of homozygotes and the decrease of
heterozygotes.
11.1 Mean, genotypic variance, and its partitions: One locus. Assumptions:

First, we consider a single locus with multiple alleles, and define the mean and genotypic variance of any inbred population \(0 < F < 1\) (Wright, 1951, p. 343). The two genes that any random individual in the population carries at any given locus are either not identical by descent with probability of \(1 - F\) or identical by descent with probability \(F\). In the first portion, the population is random mating, and in the second portion the genes are fixed. The genotypic array thereby subdivided into a panmictic portion and a fixed portion is given in (5.9). By replacing each genotype in that expression with its genotypic value (8.2), we obtain

\[
\mu_F = (1 - F) \sum_{i=1}^{m} \sum_{j=1}^{m} p_i p_j G_{ij} + F \sum_{i=1}^{m} p_i^2 G_{ii} \quad \text{(sub. (8.9))}
\]

\[
= (1 - F) \mu_0 + F \mu_1
\]

\[
= \mu_0 + F(\mu_1 - \mu_0)
\]

(11.1)

where \(\mu_0 = \mu = \text{mean of random-mating, noninbred population (8.9)}\),

\(\mu_F = \text{mean of population inbred to the coefficient of inbreeding F}\),

\(\mu_1 = \text{mean of completely inbred population (F = 1), or mean of a very large number of completely inbred lines}\).

Equation (11.1) is one given by Wright (1951, p. 343), and shows that the population mean declines linearly with respect to \(F\) (see (5.30), Figure 5.3). For a large single population with a certain amount of mating occurring between relatives (Chapter 5), one can never have a completely inbred population, because an equilibrium is achieved (5.52). For the other kind of population subdivided into a large number of subpopulations (Chapter 6), the mean of the inbred population refers to the mean of all possible subpopulations or lines of the same size and mating system, or the expected value of any such random line.
Alternatively, we may find the population mean by taking the expectation of the genotypic value under those two different states of identity (Weir and Cockerham, 1977), namely,

\[ \mu_F = E(G_{ij}) = E(G_{ij} \mid A_i \neq A_j)P(A_i \neq A_j) + E(G_{ij} \mid A_i = A_j)P(A_i = A_j) \]

\[ = (\sum_{i=1}^{m} \sum_{j=1}^{m} p_ip_jG_{ij})(1 - F) + (\sum_{i=1}^{m} p_iG_{ii})F \]

\[ = \mu_0(1 - F) + \mu_1F \]

\[ = \mu_0 + F(\mu_1 - \mu_0) \quad (11.2) \]

which is the same as (11.1). To determine the specific effects in the random-mating population of which the inbreeding depression is a function, we may substitute (8.2) in the second term in (11.2) to obtain

\[ \mu_F = \mu_0(1 - F) + \sum_{i=1}^{m} p_i(\mu + \alpha_i + \alpha_i + \delta_{ii})F \]

\[ = \mu_0(1 - F) + (\mu_0 + \sum_{i} p_i \alpha_i + \sum_{i} p_i \alpha_i + \sum_{i} p_i \delta_{ii})F \quad \text{(sub. (8.7))} \]

\[ = \mu_0(1 - F) + (\mu_0 + 0 + 0 + \sum_{i} p_i \delta_{ii})F \]

\[ = \mu_0(1 - F) + \mu_0F + F \sum_{i} p_i \delta_{ii} \]

\[ = \mu_0 + F \sum_{i=1}^{m} p_i \delta_{ii} \]

\[ = \mu_0 + Fh \quad (11.3) \]

where \( h = \sum_{i=1}^{m} p_i \delta_{ii} = \mu_1 - \mu_0 = \text{total inbreeding depression} \).

That \( h \) is equal to \( \mu_1 - \mu_0 \) can be seen by comparing (11.3) to (11.1) or (11.2).

Thus, the magnitude of the total inbreeding depression is the mean (weighted) of the dominance deviations on the main diagonal or those associated with the homozygotes in the original random-mating population (8.13). More importantly we have expressed the mean of the inbred population entirely in terms of properties of the original reference population.
The genotypic variance is (2.91) (see Box 11.1)

\[ \sigma^2_{G(F)} = \left[ (1 - F) \sum_{i=1}^{m} \sum_{j=1}^{m} p_i p_j g_{ij}^2 + F \sum_{i=1}^{m} p_i^2 g_{ii}^2 \right] - \mu_F^2 \]

\[ = (1 - F)\sigma^2_{G(0)} + F\sigma^2_{G(1)} + F(1 - F)(\mu_1 - \mu_0)^2 \]

(11.4)

where \( \sigma^2_{G(0)} = \sigma^2_G \) is the genotypic variance of a random-mating population (8.29),

\( \sigma^2_{G(F)} \) is the genotypic variance of a population inbred to the coefficient of inbreeding F,

\( \sigma^2_{G(1)} \) is the genotypic variance of a completely inbred population (F = 1), or

genotypic variance among a large number of completely inbred lines.

(This is an equation given by Wright (1951, p. 343) for many loci with no epistasis, but it is incorrect for that multiple-locus situation (see (11.27)). However, it is correct for the single-locus case.)

**Box 11.1**

**Derivation of (11.4)**

We have

\[ \sigma^2_{G(F)} = (1 - F) \sum_{i=1}^{m} \sum_{j=1}^{m} p_i p_j g_{ij}^2 + F \sum_{i=1}^{m} p_i^2 g_{ii}^2 - \mu_F^2 \quad \text{(use (2.91), sub. (11.1))} \]

\[ = (1 - F)(\sigma^2_{G(0)} + \mu_0^2) + F(\sigma^2_{G(1)} + \mu_1^2) - [\mu_0 + F(\mu_1 - \mu_0)]^2 \]

\[ = (1 - F)\sigma^2_{G(0)} + F\sigma^2_{G(1)} + (1 - F)\mu_0^2 + F\mu_1^2 - \mu_0^2 - 2F\mu_0(\mu_1 - \mu_0) - F^2(\mu_1 - \mu_0)^2 \]

\[ = (1 - F)\sigma^2_{G(0)} + F\sigma^2_{G(1)} - F\mu_0^2 + F\mu_1^2 - 2F\mu_0(\mu_1 - \mu_0) - F^2(\mu_1 - \mu_0)^2 \]

\[ = (1 - F)\sigma^2_{G(0)} + F\sigma^2_{G(1)} + F[\mu_1^2 - \mu_0^2 - 2\mu_0(\mu_1 - \mu_0)] - F^2(\mu_1 - \mu_0)^2 \]

\[ = (1 - F)\sigma^2_{G(0)} + F\sigma^2_{G(1)} + F[(\mu_1 + \mu_0)(\mu_1 - \mu_0) - 2\mu_0(\mu_1 - \mu_0)] - F^2(\mu_1 - \mu_0)^2 \]

\[ = (1 - F)\sigma^2_{G(0)} + F\sigma^2_{G(1)} + F(\mu_1 - \mu_0)(\mu_1 + \mu_0 - 2\mu_0) - F^2(\mu_1 - \mu_0)^2 \]
\begin{align*}
= (1 - F)\sigma^2_G(0) + F\sigma^2_G(1) + (F - F^2)(\mu_1 - \mu_0)^2 \\
= (1 - F)\sigma^2_G(0) + F\sigma^2_G(1) + F(1 - F)(\mu_1 - \mu_0)^2
\end{align*}

which is (11.4).

The next thing that we want to do is to partition that total genotypic variance in (11.4) into components which are functions of the effects of the original population. From (2.91) we recall that

\[
\sigma^2_G(F) = \mathbb{E}(G_{ij}(F))^2 - \mu_F^2 
\]

(sub. (8.2))

\[
= \mathbb{E}(\mu_0 + \alpha_i + \beta_j + \delta_{ij})^2 - \mu_F^2
\]

(11.5)

When we square the quantity enclosed in parentheses, we obtain sixteen terms. We desire the expectation of each of them under the two possible states of two-gene identities. To obtain each of their expectation we classify the terms with different expectations as follows (Weir and Cockerham, 1977)

\[
\begin{array}{c|cccc}
\mu_0 & \alpha_i & \beta_j & \delta_{ij} \\
\hline
\mu_0 & 1 & 2 & 2 & 3 \\
\alpha_i & 2 & 4 & 5 & 6 \\
\beta_j & 2 & 5 & 4 & 6 \\
\delta_{ij} & 3 & 6 & 6 & 7 \\
\end{array}
\]

(11.6)

Each of the classes has the following expectation.

Class 1:

\[
\mathbb{E}(\mu_0^2|A_i \neq A_j)P(A_i \neq A_j) + \mathbb{E}(\mu_0^2|A_i = A_j)P(A_i = A_j)
\]

\[
= \mu_0^2(1 - F) + \mu_0^2F
\]

\[
= \mu_0^2
\]

(11.7)

Since \(\mu_0\) is a constant, its expectation is the same under both identity states.

Class 2:
\[ E(\mu_0\alpha_1 | A_1 \neq A_j)P(A_1 \neq A_j) + E(\mu_0\alpha_1 | A_1 = A_j)P(A_1 = A_j) \]

\[ = \left( \sum_{i=1}^{m} p_i \mu_0 \alpha_1 \right)(1 - F) + \left( \sum_{i=1}^{m} p_i \mu_0 \alpha_1 \right)F \]

\[ = (\mu_0 \sum_{i} p_i \alpha_1)(1 - F) + (\mu_0 \sum_{i} p_i \alpha_1)F \quad \text{(sub. (8.7))} \]

\[ = 0 \quad (11.8) \]

The remaining three terms of class 2 have the same expectation.

**Class 3:**

\[ E(\mu_0\delta_{ij} | A_1 \neq A_j)P(A_1 \neq A_j) + E(\mu_0\delta_{ij} | A_1 = A_j)P(A_1 = A_j) \]

\[ = (\mu_0 \sum_{i,j} p_i p_j \delta_{ij})(1 - F) + (\mu_0 \sum_{i,j} p_i \delta_{ij})F \quad \text{(sub. (8.16))} \]

\[ = \mu_0^2 \sum_{i} p_i \delta_{ii} \quad (11.9) \]

The other remaining term has the same expectation.

**Class 4:**

\[ E(\alpha_1^2 | A_1 \neq A_j)P(A_1 \neq A_j) + E(\alpha_1^2 | A_1 = A_j)P(A_1 = A_j) \]

\[ = \left( \sum_{i} p_i \alpha_1^2 \right)(1 - F) + \left( \sum_{i} p_i \alpha_1^2 \right)F \]

\[ = \sum_{i} p_i \alpha_1^2 \quad \text{(sub. (8.27))} \]

\[ = \sigma_\alpha^2 \quad (11.10) \]

The other remaining term has the same expectation.

**Class 5:**

\[ E(\alpha_1 \alpha_j | A_1 \neq A_j)P(A_1 \neq A_j) + E(\alpha_1 \alpha_j | A_1 = A_j)P(A_1 = A_j) \]

\[ = \left( \sum_{i,j} p_i p_j \alpha_1 \alpha_j \right)(1 - F) + \left( \sum_{i,j} p_i \alpha_1^2 \right)F \]

\[ = \left( \sum_{i} p_i \alpha_1 \right) \left( \sum_{j} p_j \alpha_j \right)(1 - F) + \left( \sum_{i} p_i \alpha_1^2 \right)F \quad \text{(sub. (8.7) (8.8))} \]

\[ = 0 + 0 + F \sum_{i} p_i \alpha_1^2 \quad \text{(sub. (8.27))} \]

\[ = F \sigma_\alpha^2 \quad (11.11) \]
The other remaining term has the same expectation.

Class 6:

\[
E(\alpha_i \delta_{ij} | A_i \neq A_j)P(A_i \neq A_j) + E(\alpha_i \delta_{ij} | A_i = A_j)P(A_i = A_j)
\]

\[
= (\sum \sum p_i p_j \alpha_i \delta_{ij})(1 - F) + (\sum p_i \alpha_i \delta_{ii})F
\]

\[
= \sum p_i \alpha_i (\sum p_j \delta_{ij})(1 - F) + (\sum p_i \alpha_i \delta_{ii})F \quad \text{(sub. (8.15a))}
\]

\[
= F \sum p_i \alpha_i \delta_{ii}
\]

(11.12)

The remaining three terms have the same expectation.

Class 7:

\[
E(\delta^2_{ij} | A_i \neq A_j)P(A_i \neq A_j) + E(\delta^2_{ij} | A_i = A_j)P(A_i = A_j)
\]

\[
= (\sum \sum p_i p_j \delta^2_{ij})(1 - F) + (\sum p_i \delta^2_{ii})F \quad \text{(sub. (8.28))}
\]

\[
= (1 - F)\sigma^2_D + F \sum p_i \delta^2_{ii} \quad \text{(sub. (8.29))}
\]

\[
= (1 - F)\sigma^2_D + F \sum p_i \delta^2_{ii}
\]

(11.13)

Collecting terms over all classes, multiplying each by the number of terms in each class, and summing them give the expectation of \( G^2_{(F)} \) in (11.5).

Substituting that and (11.3) in (11.5), we have

\[
\sigma^2_G(F) = \mu^2_0 + 2\mu_0 F \sum p_i \delta_{ii} + 2\alpha^2 + 2F\alpha^2 + 4F \sum p_i \alpha_i \delta_{ii}
\]

\[
+ (1 - F)\sigma^2_D + F \sum p_i \delta^2_{ii} - (\mu_0 + F \sum p_i \delta_{ii})^2 \quad \text{(sub. (8.29))}
\]

\[
= (1 + F)\sigma^2_A + (1 - F)\sigma^2_D + 4F \sum p_i \alpha_i \delta_{ii} + F \sum p_i \delta^2_{ii} - F^2(\sum p_i \delta_{ii})^2
\]

(11.14)

By adding and subtracting the same quantity to the right side of (11.14), we partition the genotypic variance of the inbred population into five basic quadratic components, each defined in terms of parameters or effects of the original, noninbred population (Cockerham, 1983), namely,
\[
\sigma_{G(F)}^2 = (1 + F)\sigma_A^2 + (1 - F)\sigma_D^2 + 4F \sum_i p_i \alpha_i \delta_{ii} + F \sum_i p_i \delta_{ii}^2
\]

\[
\text{subtract and add}
\]

\[- F(\sum_i p_i \delta_{ii})^2 + F(\sum_i p_i \delta_{ii})^2 - F^2(\sum_i p_i \delta_{ii})^2
\]

\[
= (1 + F)\sigma_A^2 + (1 - F)\sigma_D^2 + 4F \sum_i p_i \alpha_i \delta_{ii} + F \left[ \sum_i p_i \delta_{ii}^2 - (\sum_i p_i \delta_{ii})^2 \right]
\]

\[+ F(1 - F)(\sum_i p_i \delta_{ii})^2
\]

\[
= (1 + F)\sigma_A^2 + (1 - F)\sigma_D^2 + 4F \text{Cov}(\alpha_i, \delta_{ii}) + F\sigma_{\delta_{ii}}^2 + F(1 - F)h^2 \tag{11.15}
\]

where \( \sigma_A^2 \) = additive variance of original, noninbred, reference population (8.29) (8.27),

\( \sigma_D^2 \) = dominance variance of original, noninbred, reference population (8.29) (8.28),

\[\text{Cov}(\alpha_i, \delta_{ii}) = \sum_i p_i \alpha_i \delta_{ii} - (\sum_i p_i \alpha_i)(\sum_i p_i \delta_{ii}) = \sum_i p_i \alpha_i \delta_{ii} - 0(\sum_i p_i \delta_{ii})\]

= covariance between additive and homozygous dominance effects,

\[\sigma_{\delta_{ii}}^2 = \sum_i p_i \delta_{ii}^2 - (\sum_i p_i \delta_{ii})^2 = \sum_i p_i \delta_{ii}^2 - h^2\]

= variance of homozygous dominance effects,

\[h = \sum_i p_i \delta_{ii} - \mu_1 - \mu_0 = \text{total inbreeding depression} \tag{11.3}\]

Later we will find these five quadratic components useful in expressing the covariance of inbred relatives.

Setting \( F = 0 \) in (11.14) gives the genotypic variance of the noninbred population (8.29)

\[\sigma_{G(0)}^2 = \sigma_A^2 + \sigma_D^2 \tag{11.16}\]

and setting \( F = 1 \) gives the variance of the completely inbred population

\[\sigma_{G(1)}^2 = 2\sigma_A^2 + 4 \sum_i p_i \alpha_i \delta_{ii} + \sum_i p_i \delta_{ii}^2 - (\sum_i p_i \delta_{ii})^2
\]

\[= 2\sigma_A^2 + 4 \sum_i p_i \alpha_i \delta_{ii} + \sigma_{\delta_{ii}}^2 \tag{11.17}\]
That (11.17) is correct can be shown in an alternative way, i.e.,

\[ E(G_{i1}^2) = \mu_1^2 = \sum_i p_i (\mu_0 + \alpha_i + \alpha_{i1} + \delta_{i1})^2 - (\mu_0 + \sum_i p_i \delta_{i1})^2 \]

\[ = \sum_i p_i (\mu_0^2 + \alpha_i^2 + \alpha_{i1}^2 + \delta_{i1}^2 + 4\mu_0\alpha_i + 2\mu_0\delta_{i1} + 2\alpha_i^2 + 4\alpha_{i1}\delta_{i1}) \]

\[ - \mu_0^2 - 2\mu_0 \sum_i p_i \delta_{i1} - (\sum_i p_i \delta_{i1})^2 \]

\[ = 4\sum_i p_i \alpha_i^2 + \sum_i p_i \delta_{i1}^2 + 0 + 4 \sum_i p_i \alpha_i \delta_{i1} - (\sum_i p_i \delta_{i1})^2 \text{ (sub. (8.27))} \]

\[ = 4\sigma_a^2 + 4 \sum_i p_i \alpha_i \delta_{i1} + \sum_i p_i \delta_{i1}^2 - (\sum_i p_i \delta_{i1})^2 \text{ (sub. (8.29) (11.15))} \]

\[ = 2\sigma_a^2 + 4 \sum_i p_i \alpha_i \delta_{i1} + \sigma_{\delta_{i1}}^2 \]

(11.18)

The genotypic variance of the inbred population (11.14) can also be shown to be equal to (11.4), as given by Wright, namely,

\[ \sigma^2_{G(F)} = (1 + F)\sigma^2_A + (1 - F)\sigma^2_D + 4F \sum_i p_i \alpha_i \delta_{i1}^2 + F \sum_i p_i \delta_{i1}^2 - F^2 (\sum_i p_i \delta_{i1})^2 \]

subtracted and added

\[ = \sigma_A^2 - 2F \sigma_A^2 + \sigma_D^2 + \sigma_A^2 + (1 - F)\sigma_D^2 + 4F \sum_i p_i \alpha_i \delta_{i1} + F \sum_i p_i \delta_{i1} \]

\[ - F(\sum_i p_i \delta_{i1})^2 + F(\sum_i p_i \delta_{i1})^2 - F^2 (\sum_i p_i \delta_{i1})^2 \]

\[ = (1 - F)\sigma_A^2 + (1 - F)\sigma_D^2 + F \left[ 2\sigma_A^2 + 4 \sum_i p_i \alpha_i \delta_{i1} + \sum_i p_i \delta_{i1}^2 - (\sum_i p_i \delta_{i1})^2 \right] \]

\[ + F(1 - F) (\sum_i p_i \delta_{i1})^2 \text{ (sub. (11.16) (11.17) (11.3))} \]

\[ = (1 - F)\sigma^2_{G(0)} + F \sigma^2_{G(1)} + F(1 - F)(\mu_1 - \mu_0)^2 \]

(11.19)

For only two alleles, the mean of the inbred population (11.3) becomes

\[ \mu_F = \mu_0 + F \sum_{i=1}^2 p_i \delta_{i1} \]

\[ = \mu_0 + F(p_1 \delta_{11} + p_2 \delta_{22}) \text{ (sub. (8.48))} \]

\[ = \mu_0 + F([-p_1 p_2(2G_{12} - G_{11} - G_{22})] + [-p_1 p_2(2G_{12} - G_{11} + G_{22})]) \]

\[ = \mu_0 - Fp_1 p_2(p_2 + p_1)(2G_{12} - G_{11} - G_{22}) \]

\[ = \mu_0 - Fp_1 p_2(2G_{12} - G_{11} - G_{22}) \]

(11.20)
In terms of Falconer's notation (8.31) (8.101), substituting 2d for \((2G_{12} - G_{11} - G_{22})\), and \(p_1 = p\) and \(p_2 = q\), we have

\[
\mu_F = \mu_0 - Fpq(2d) = \mu_0 - 2Fpqd
\]

(11.21)

where \(2pqd = \mu_1 - \mu_0\) = total inbreeding depression.

Only if \(d = 0\), i.e., the genotypic value of the heterozygote lies exactly between the two homozygotes, no decline in the population mean occurs with inbreeding. On the other hand, if \(d \neq 0\), then a change in the mean occurs. If \(d\) is positive, then a decline in the population mean occurs, i.e., the decline is toward the value of the genotype of the "recessive" allele, or toward one or both homozygotes if overdominance exists. The change in the population mean is always opposite to the sign of \(d\). The change for any given locus is greatest when \(pq\) is a maximum, namely, when \(p = q = 1/2\). Any locus with alleles at intermediate frequencies therefore contributes more to a change of the mean than other loci with high or low allelic frequencies, if the loci happen to have the same \(d\) value.

11.2. Mean, genotypic variance, and its partitions: Two or more loci with no epistasis. Assumptions:

With no epistasis, the loci contribute additively. Hence, we can sum over all loci. Thus, the population mean from (11.1) is (We insert a \(k\) subscript in all formulas in the previous section to denote the \(k\)th locus.)

\[
\mu_F = \sum_{k=1}^{n} \mu_{Fk} = \sum_k \left[ \mu_{0k} + F(\mu_{1k} - \mu_{0k}) \right]
\]

\[
= \sum_k \mu_{0k} + F(\sum_k \mu_{1k} - \sum_k \mu_{0k})
\]

\[
= \mu_0 + F(\mu_1 - \mu_0)
\]

(11.22)

From (11.3), the population mean is
\[ \mu_F = \sum_{k=1}^{n} \mu_{Fk} = \sum_{k=1}^{n} \left[ \mu_{0k} + F \Sigma_{k=1}^{n} \Sigma_{i=1}^{m} p_{ki} \delta_{k_i k_i} \right] \]  

(11.23)

where \( p_{ki} \) = frequency of ith allele at the kth locus,
\( \delta_{k_i k_i} \) = dominance effect of the homozygote of the ith allele at the kth locus in the original, random-mating population,
\( \sum_{k=1}^{n} \sum_{i=1}^{m} p_{ki} \delta_{k_i k_i} = \sum_{k=1}^{m} h_k = \mu_1 - \mu_0 \) = total inbreeding depression over n loci.

To be able to express the total genotypic variance for n loci as simply the sum of those at each of the n loci, we must assume linkage equilibrium in the original noninbred population, as we did for noninbred populations (8.98). However, to maintain genotypic equilibrium and thereby independence of genotypic effects between loci (to avoid covariances between effects at different loci) during the inbreeding process, we must also assume no linkage between loci (see Section 7.2.7, part 3, Genotypic disequilibrium). Thus, with these assumptions we have from (11.15)

\[ \sigma_{G(F)}^2 = \sum_{k=1}^{n} \left[ (1 + F) \sigma_{Ak}^2 + (1 - F) \sigma_{Dk}^2 + 4F \text{Cov}(\alpha_{k_i}, \delta_{k_i k_i}) + F \sigma_{\delta_{k_i k_i}}^2 + F(1 - F)h_k^2 \right] \]

\[ = (1 + F) \sum_{k=1}^{n} \sigma_{Ak}^2 + (1 - F) \sum_{k=1}^{n} \sigma_{Dk}^2 + 4F \sum_{k=1}^{n} \text{Cov}(\alpha_{k_i}, \delta_{k_i k_i}) + F \sum_{k=1}^{n} \sigma_{\delta_{k_i k_i}}^2 + F(1 - F) \sum_{k=1}^{n} h_k^2 \]

\[ = (1 + F) \sigma_A^2 + (1 - F) \sigma_D^2 + 4FD_1 + FD_2 + F(1 - F)\bar{H} \]  

(11.24)

where \( \sigma_A^2 = \sum_{k=1}^{n} \sigma_{Ak}^2 \)  
(= \sum_{k=1}^{n} \left( 2 \Sigma_{i} p_{ki} \sigma_{ki}^2 \right) \)
(sub. (8.27)-(8.29))

\( \sigma_D^2 = \sum_{k=1}^{n} \sigma_{Dk}^2 \)
(= \sum_{k=1}^{n} \left( \Sigma_{i} p_{ki} p_{kj} \delta_{ki kj} \right) \)
(sub. (8.28)-(8.29))

\( D_1 = \sum_{k=1}^{n} \text{Cov}(\alpha_{k_i}, \delta_{k_i k_i}) \)
(= \sum_{k=1}^{n} \left( \Sigma_{i} p_{ki} \alpha_{ki} \delta_{ki k_i} \right) \)
(sub. (11.15))

\( D_2 = \sum_{k=1}^{n} \sigma_{\delta_{k_i k_i}}^2 \)
(= \sum_{k=1}^{n} \left( \Sigma_{i} p_{ki} \delta_{ki k_i} \right) \)
(sub. (11.15))

\( \bar{H} = \sum_{k=1}^{n} h_k^2 \)
(= \sum_{k=1}^{n} \left( \Sigma_{i} p_{ki} \delta_{ki k_i} \right)^2 \)
(sub. (11.15))

and
\( \sigma^2_A \) = total additive variance of original, noninbred, reference population,

\( \sigma^2_D \) = total dominance variance of original, noninbred, reference population,

\( D_1 \) = total covariance between additive and homozygous dominance effects over all loci,

\( D_2 \) = total variance of homozygous dominance effects over all loci,

\( \bar{H} \) = sum of the squares of the inbreeding depression due to each locus individually,

\[ \bar{H} = \sum_k h_k = \sum_k \left( \sum_i p_{ki} \delta_{ki} k_i k_i \right) = \text{total inbreeding depression over n loci}. \]

For completeness sake, we may now sum the other form of the genotypic variance (11.19) over n loci. First, we obtain

\[
\sigma^2_G(F) = \sum_k \sigma^2_{G(F)k} = \sum_k \left( (1 - F) \sigma^2_{G(0)k} + F \sigma^2_{G(1)k} + F(1 - F)(\mu_{1k} - \mu_{0k})^2 \right)
\]

\[ = (1 - F) \sum_k \sigma^2_{G(0)k} + F \sum_k \sigma^2_{G(1)k} + F(1 - F) \sum_k (\mu_{1k} - \mu_{0k})^2 \] (sub. (11.3))

\[ = (1 - F) \sigma^2_{G(0)} + F \sigma^2_{G(1)} + F(1 - F) \sum_k h_k^2 \] (11.25)

where \( h_k = \mu_{1k} - \mu_{0k} \) = inbreeding depression due to kth locus.

Then we obtain the variance of \( h \), using (2.91), as follows (see Section 3.3.5 for similar manipulation)

\[
\sigma_h^2 = E(h^2) - [E(h)]^2
\]

\[ = \sum_{k=1}^{n} h_k^2 - \left( \sum_{k=1}^{n} h_k \right)^2 \]

\[ \approx \frac{\sum_{k=1}^{n} h_k^2}{n} \approx \frac{(\sum h_k)^2}{n} \] (sub. (11.23))

\[
\sum_k h_k^2 = n \sigma_h^2 + \frac{(\mu_1 - \mu_0)^2}{n} \] (11.26)
where $\sigma_h^2 = \text{variance of inbreeding depression of individual loci},$

$$\mu_1 - \mu_0 = \sum \sigma_{k} = \sum (\mu_{1k} - \mu_{0k}) = \text{total inbreeding depression due to n loci.}$$

Substituting (11.26) in (11.25), we obtain

$$\sigma_{G(F)}^2 = (1 - F)\sigma_{G(0)}^2 + F\sigma_{G(1)}^2 + F(1 - F)\left[ n\sigma_h^2 + \frac{(\mu_1 - \mu_0)^2}{n} \right]$$  \hspace{1cm} (11.27)

This differs from the formula given by Wright (1951, p. 343) for no epistasis. He gives the multilocus formula as being of the same form as that for the single locus (11.4). If $\sigma_h^2 = 0$, the quantity inside the brackets becomes $(\mu_1 - \mu_0)^2/n$.

My writing efforts during my sabbatical leave, June to December, 1983, ended here. Much more needs to be written to complete this chapter.

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