THE TWO-LOCUS INBREEDING FUNCTION

by

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ERRATA

THE TWO LOCUS INBREEDING FUNCTION

Weir and Cockerham

Page iv: Omit 4.3.10

Page vi: Omit 4.6

Page 7, line 11: Narain (1965)

Page 10, line 6: $X_{10} = \text{Prob}(a = a', b \neq b')$

Page 18, line 1: $+ \frac{1-\lambda^2}{4} \theta_{\text{ED}}$

Page 24: Omit section 4.3.10

Page 25: Omit Table 4.6

Page 25, equation (4.3.13): $\frac{1}{2} \wedge \theta_{\text{HG}}$

Page 25, equation (4.3.14): $\frac{1}{4} \vee \theta_{\text{HG}}$

Page 28, line 17: replace "function" by "coefficient"

Page 28, line 24: replace t by t-1

Page 28, line 25: replace t-1 by t

Page 41, line 9: add "The offspring of U and V is generation 0."

Page 42, line 14: $\alpha^{t+2}$

Page 42, line 18: (generation 0)

Page 43, line 2: Omit $F'$

Page 43, line 9: Omit $F_{\infty}$

Page 43, line 10: $F^0$

Page 43, line 12: $F'$
ERRATA (continued)

Page 43, line 16: $F^2$
Page 44, line 14: (6.2.1)
Page 44, line 15: $\frac{1+\lambda}{4} F_{00}^{t+1}$
Page 45, line 5: $F^0$
Page 49: Generation 2, $\lambda = 1.0$: 0.2500
Page 49, Generation 3, $\lambda = 0.8$: 0.2800
Page 54, line 4: $2^8_{AA'}$, $A^\prime A^\prime$
Page 54, line 5: $5_{AA'}$, $A''A''$
Page 56, line 13: $N_{BA}$, $D_{YZ}$
Page 58, line 13: $a_B^b_B$, $a_C^b_C$
Page 63, line 4: $P_{B_1} = 6P_{B_1} - 12P_{B_2} + 6P_{B_4} - 2P_{B_6}$
Page 66, last equation is (7.4.16)
Page 67, line 2: (7.4.16)
Page 83, line 9: $Z_B$, $B'B''$
Page 84, element (1, 4): $(1-\lambda^2)(N-1)/2N$
Page 84: element (4, 5): $(1-\lambda)(N-1)/8N$, element (8, 1): $l/8N(N-1)$, element (8, 2):
$1/8N(N-1)$
Page 93, line 3: insert $f_1$, before $Z_f$, $m_f$
Page 94, line 4: first divisor is 2.
Page 94, line 7: Omit $P_t(\delta_{mm'}, mm'' + \delta_{m'm}, m''m)$
ERRATA (continued)

Page 99, element (5, 3): \( \frac{(P_1-P_2)}{2} + \frac{(1+\lambda)(1+2P_2-3P_1)}{8} \)

Page 99, element (5, 4): \( P_1 + \frac{(1+\lambda)(1+2P_2-3P_1)}{4} \), element (5, 6):
\[ \frac{(1-\lambda)(1+P_2-2P_1)}{8} \]

Page 99, element (6, 9): \( \frac{Q_4}{8} \), element (8, 4): \( \frac{2P_1-P_2}{4} \), element (8, 8):
\[ \frac{(2+P_2-3P_1)}{4} \]

Page 99, element (8, 9): \( \frac{(1-3P_1+2P_2)}{8} \), element (9, 1): \( \frac{P_6}{12} + \frac{P_4}{4} \)

Page 99, element (9, 6): \( \frac{(1+3P_4-4P_2)}{4} - \frac{(P_6+P_7)}{12} \)

Page 100, line 5: \( T_1^{t+1} = T_1^t + \frac{T_2^t}{2} \), \( T_2^{t+1} = T_1^t + \frac{(1-P_1)T_2^t}{2} \)

Page 127, generation 7, \( \tau_{NLL} = 0.0192 \)

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1. INTRODUCTION

A consequence of all forms of inbreeding is that all homologous loci of the inbred individual tend to have identical genes. Such genes will not only be identical in nature ("identical in state"), but also will be "identical by descent" through having originated from a single ancestral gene. This work is concerned with determining the probability that two linked autosomal loci of a disomic individual carry genes identical by descent. Such probability statements will be considered relative to some base population where there was no identity by descent.

For an individual a two locus inbreeding function will be defined. This will be a vector valued function with four components which measure the probability that both, the first, the second, or neither of the two loci respectively carry genes identical by descent. The first component, corresponding to an individual with double identity, will be termed the two locus inbreeding coefficient and the fourth component, corresponding to an individual with double non-identity, will be termed the two locus panmictic function. This terminology is a natural extension of that for the one locus case.

While similar two locus inbreeding functions have been discussed before (Haldane, 1947; Schnell, 1961; Shikata, 1962), no correct method has been given for their determination in all generations of systems other than self mating. The difficulty arises because linkage between loci prevents genes from each locus being transmitted independently.
This work shows that recurrence formulae can be found when the
inbreeding function is regarded as a special case of a more general
measure. Instead of insisting that the two genes at each locus are in
one individual, the general measure is defined for any two genes at
each of two loci. As with the inbreeding function it is a vector func-
tion with four components giving the probabilities that both, the
first, the second or neither of the two loci carry genes identical by
descent. Three broad classes of this measure arise according to wheth-
er the four genes are carried on two, three or four gametes. These
three will be called digametic, trigametic or quadrigametic measures
respectively. For two uniting gametes then, the digametic measure is
just the inbreeding function. For two gametes from two parents, the
digametic measure is called the coancestry function.

For the general pedigree (Figure 1.1) general transition equations
for the three types of measure will be derived. When any specific
inbreeding system is to be analyzed each of the three types must be
further subdivided into special cases according to whether the corre-
sponding gametes came from separate or common individuals. The method
is also applied to finite populations when there is random pairing of
gametes.

For all systems studied, transition equations linking values be-
tween the measures in successive generations are given. The equations
for the fourth ("panmictic") component of the measures are usually
written in matrix form, and the characteristic equation of this transi-
tion matrix employed to give a recurrence formula for the two locus
panmictic coefficient. Tables of values of the dominant root of the
transition matrix and graphs showing values of the two locus inbreeding coefficient for various linkage values will be given.

Effects such as selection, mutation or interference are assumed to be absent, but no restriction will be made on the number of alleles for a locus.

Figure 1.1 The general pedigree
2. REVIEW OF LITERATURE

The effects of inbreeding on one locus have been studied extensively by many authors. Calculation of the one locus inbreeding coefficient has been by three methods. Wright (1921) used the concept of correlation between uniting gametes and gave a general formula, Wright (1922), which gives the value of the inbreeding coefficient for any individual in terms of those of ancestors common to both of its parents. Malécot (1948) used probability arguments to derive the probability that two genes at a locus were identical by descent. Fisher (1949) unified the method of using a generation matrix of mating types. Kempthorne (1957) has evaluated these approaches. The methods of Malécot were extended by Cockerham (1967) to include pedigrees of groups.

The study of two loci, when the loci may be linked, has not progressed as far. Early approaches almost always specified an initial array of zygotes, calculated the gametic array formed by these zygotes and then, according to the mating scheme being studied, calculated the zygotic array in the next generation. The first paper was by Jennings (1917) and showed such calculations for random mating, selfing, sib mating and some forms of assortative mating. The unwieldy nature of the method is indicated by the fact that sib mating required 55 "family types". Only for selfing could Jennings display the zygotic array after n generations. Robbins (1918) extended this work for random and self mating. Haldane and Waddington (1931) attempted to complete the work of Jennings by setting up transition equations for mating types. They were able to give the equilibrium frequency of crossover zygotes
for sib mating (100 mating types) and successive parent-offspring mating (20 mating types). They estimated it would take 10,000 mating types to treat double first cousin mating, and the method could not be applied to dioecious systems with unequal numbers of males and females.

Bennett (1954a) just considered those mating types that gave offspring heterozygous at both loci. He listed the dominant roots of the appropriate generation matrix for sib mating (9 mating types) and successive parent-offspring mating (8 mating types). His object was to determine the fraction of map length expected to be heterogeneous after a given amount of inbreeding. While all the papers listed thus far have considered only two alleles per locus, Bennett (1954b) used the zygote-gamete-zygote approach to study random mating for an arbitrary number of alleles at an arbitrary number of loci.

Quite different methods have also been used. Wright (1933) by using path coefficients obtained the results of Haldane and Waddington with much less effort, and could also analyze the dioecious systems. For each system his result was the equilibrium frequency of crossover zygotes. Geiringer (1944) proved that, for random mating and an arbitrary number of alleles at any number of loci, the limiting gametic distribution was the product of the appropriate marginal gene distributions, unless linkage was complete. Kimura (1963) worked with just three probabilities. For any two nonallelic genes he considered the probabilities that they were on one chromosome, or two chromosomes in the same or different individuals. He derived expressions for equilibrium crossover frequencies.
Mixtures of self and random mating have received a lot of attention. Bennett and Binet (1956) and Chai (1964a) used a zygote-gamete-zygote approach. Kimura (1958) gave equilibrium frequencies of double homozygotes and single and double heterozygotes. Other papers by Chai and Narain are mentioned below.

The techniques discussed in all of the above papers were only able to describe some aspect of the equilibrium population, or else specify one generation in terms of the immediately preceding (non-inbred) one for any system other than self mating. The first paper to extend the concept of inbreeding function to two loci, and give properties of generations between initial and final was by Haldane (1947). He defined a function giving the probability that two loci carried genes identical by descent. Restricting himself to two alleles per locus he gave this probability for the first generation of inbreeding for half first cousins, full sibs and double half first cousins. He also gave a formula, analogous to that of Wright for one locus, for his function for an offspring of two individuals related by a single chain of m links through a single common outbred ancestor. The requirement of an outbred ancestor precluded its general use.

A general inbreeding function for any number of alleles at any number of loci was defined by Schnell (1961)—it gave the probability that a certain set of loci carried genes identical by descent. As with Haldane though, he could give its value only for the first generation of inbreeding. Both Haldane and Schnell said that, in the absence of linkage, the n-locus inbreeding coefficient must be the n-th power of the one locus coefficient. This is only true for regular inbreeding
pedigrees of individuals where all matings are specified, and does not hold for pedigrees of finite groups where matings are at random.

Shikata (1962) defined a function very similar to that of Schnell and gave recurrence formulae for it for several systems. These formulae were correct for self mating, but not for other systems such as sib mating and parent-offspring mating (Shikata, 1965a), which he acknowledged (Shikata, 1965b).

Rajagopalan (1958) used what was essentially one component of the measure of Schnell and Shikata and gave its value for self mating. Ghai (1964b) extended this work for a mixture of self and random mating for the case of zero linkage. Narain (1963) used the function of Schnell to give a completely general analysis of selfing (arbitrary numbers of alleles and loci), and a mixture of self and random mating (Narain, 1966).

A new class of measures was defined by Cockerham and Weir (1968), which included the measure used by Schnell and Shikata. For an arbitrary number of alleles at two loci they found the probability that two loci carried genes identical by descent for any generation of a sib mating scheme, and any degree of linkage.

---

1Cockerham, C. Clark, and B. S. Weir. 1968. Sib mating with two linked loci. Department of Experimental Statistics, North Carolina State University at Raleigh, North Carolina. (Submitted to Genetics for publication.)
3. ONE LOCUS MEASURES

The one locus case will be reviewed briefly to introduce the concept of general measure which forms the basis of the two locus work. For any two distinct genes a, a' at a locus a general measure $\mathbf{X}(a, a')$ is defined as:

$$
\mathbf{X}(a, a') = \begin{bmatrix}
X_1(a, a') \\
X_0(a, a')
\end{bmatrix} = \begin{bmatrix}
\text{Prob}(a = a') \\
\text{Prob}(a \neq a')
\end{bmatrix}
$$  \hspace{1cm} (3.1)

where the identity sign $\equiv$ means identity by descent. Thus $\mathbf{X}(a, a')$ is a vector with two components, the sum of which is unity. Note that there has been no restriction on the number of possible alleles for either locus.

Now a, a' will necessarily be carried on distinct gametes between generations, but two cases of the digametic measure will be distinguished according to whether or not the two gametes unite. These two cases are given special symbols:

$$
F_A = \mathbf{X}(a, a' : a \equiv A, a' \equiv A) 
$$  \hspace{1cm} (3.2)

$$
\Theta_{BC} = \mathbf{X}(a, a' : a \in B, a' \in C).
$$  \hspace{1cm} (3.3)

Equation (3.2) expresses the fact that a, a' are on gametes that unite to form individual A, while (3.3) states that a, a' are on gametes formed by individuals B, C respectively.
The usual terminology for these measures is:

\[ F_{1A} : \text{ the inbreeding coefficient of } A, \]
\[ F_{0A} : \text{ the panmictic coefficient of } A, \]
\[ \theta_{1BC} : \text{ the coefficient of parentage (coancestry) of } B \text{ and } C. \]

In the general pedigree (Figure 1.1), the inbreeding coefficient of \( A \) is just the coancestry of its parents:

\[ F_{1A} = \theta_{1BC} \quad (3.4) \]

so that

\[ F_{-A} = \theta_{-BC}. \]

There is no need in the one locus case to consider both components of the measures in analyzing any system. The recurrence equations for systems of mating are most simply written in terms of the panmictic coefficient, while the inbreeding coefficient is the simplest component to calculate from specific pedigrees.
4. TWO LOCUS MEASURES

4.1 Definitions

The general measure must now take account of genes at two loci. For any two distinct genes \(a, a'\) at one locus (the \(a\)-locus), and any two distinct genes \(b, b'\) at another locus (the \(b\)-locus), a general measure \(X(ab, a'b')\) is defined as:

\[
X(ab, a'b') = \begin{bmatrix}
X_{11}(ab, a'b') & \text{Prob}(a \equiv a', b \equiv b') \\
X_{10}(ab, a'b') & \text{Prob}(a \equiv b', b \neq b') \\
X_{01}(ab, a'b') & \text{Prob}(a \neq a', b \equiv b') \\
X_{00}(ab, a'b') & \text{Prob}(a \neq a', b \neq b')
\end{bmatrix}
\]

(4.1.1)

Once again there has been no restriction on the number of possible alleles for each locus. There is no ordering intended between the two pairs of genes, so that:

\[
X(ab, a'b') = X(a'b', ab)
\]

Other relations will be indicated below for the special cases.

Now the four genes in the argument of \(X\) may be carried on two, three, or four gametes. In the digametic case, once again, a distinction will be made for the case when the two gametes unite. There are thus four symbols, two digametic, one trigametic and one quadrigametic, to be defined:

\[
F_A = X(ab, a'b': ab \not\equiv A, a'b' \not\equiv A)
\]

(4.1.2)
\[ \Theta_{BC} = \chi(ab, a'b': ab\epsilon B, a'b'\epsilon C), \tag{4.1.3} \]

\[ \gamma_{B, DE} = \chi(ab, a'b': ab\epsilon B, a'D, b'\epsilon E), \tag{4.1.4} \]

\[ \delta_{BC, DE} = \chi(ab, a'b': a\epsilon B, b\epsilon C, a'D, b'\epsilon E). \tag{4.1.5} \]

\( F_A \) is the inbreeding function of A and \( \Theta_{BC} \) the coancestry function of B and C. The symbols used have the same meaning as for the one locus case. For example, equation (4.1.4) states that \( a, b \) are on one gamete from B, \( a' \) is on a gamete from individual D and \( b' \) is on a gamete from individual E.

Just as in the one locus case, from Figure 1.1,

\[ F_A = \Theta_{BC}. \tag{4.1.6} \]

The four components of each measure may be arranged in two by two tables as in Table 4.1 and marginal totals taken. These marginal totals will always be one locus measures. This relation between one and two locus measures may be expressed as:

\[ \chi(a, a') = \begin{bmatrix} X_{11}(ab, a'b') + X_{10}(ab, a'b') \\ X_{01}(ab, a'b') + X_{00}(ab, a'b') \end{bmatrix} = \begin{bmatrix} X_{1.}(ab, a'b') \\ X_{.1}(ab, a'b') \end{bmatrix} \tag{4.1.7} \]

and

\[ \chi(b, b') = \begin{bmatrix} X_{.1}(ab, a'b') \\ X_{0.}(ab, a'b') \end{bmatrix} \tag{4.1.8} \]
Table 4.1 Marginal totals of measures

<table>
<thead>
<tr>
<th>$X_{11}(ab, a'b')$</th>
<th>$X_{10}(ab, a'b')$</th>
<th>$X_1(a, a')$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$X_{01}(ab, a'b')$</td>
<td>$X_{00}(ab, a'b')$</td>
<td>$X_0(a, a')$</td>
</tr>
<tr>
<td>$X_1(b, b')$</td>
<td>$X_0(b, b')$</td>
<td>1</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>$F_{11}A$</th>
<th>$F_{10}A$</th>
<th>$F_{1.A}$</th>
<th>$\theta_{11 BC}$</th>
<th>$\theta_{10 BC}$</th>
<th>$\theta_{1.BC}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$F_{01}A$</td>
<td>$F_{00}A$</td>
<td>$F_{0.A}$</td>
<td>$\theta_{01 BC}$</td>
<td>$\theta_{00 BC}$</td>
<td>$\theta_{0.BC}$</td>
</tr>
<tr>
<td>$F_{.1}A$</td>
<td>$F_{.0}A$</td>
<td>1</td>
<td>$\theta_{1.BC}$</td>
<td>$\theta_{0.BC}$</td>
<td>1</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>$\gamma_{11B}, DE$</th>
<th>$\gamma_{10B}, DE$</th>
<th>$\theta_{1.BD}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\gamma_{01B}, DE$</td>
<td>$\gamma_{00B}, DE$</td>
<td>$\theta_{0.BD}$</td>
</tr>
<tr>
<td>$\theta_{1BE}$</td>
<td>$\theta_{0BE}$</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$\theta_{1CE}$</td>
</tr>
</tbody>
</table>
The sum of the four components of $X(ab, a'b')$, which may be written as $X(ab, a'b')$, is equal to unity. One further convention is necessary to distinguish between the two loci. For individual $A$, for example, $F_{1A}$ and $F_{0A}$ are the inbreeding and panmictic coefficients for the a-locus, while $F_{1A}$ and $F_{0A}$ are those for the b-locus.

As mentioned above, certain relations hold among the measures because of the lack of order between the two pairs of genes. These relations are:

$$\theta_{BC} = \theta_{CB}$$

$$\bar{\gamma}_{DE, B} = \bar{\gamma}_{B, DE}$$

$$\delta_{BC, DE} = \delta_{DE, BC} = \delta_{BE, DC} = \delta_{DC, BE}$$

There will also be need for the following averages:

$$\bar{\gamma}_{B, DE} = (\bar{\gamma}_{B, DE} + \bar{\gamma}_{B, ED})/2$$

$$\delta_{BC, DE} = (\delta_{BC, DE} + \delta_{BC, ED})/2$$

$$\delta_{BC, DE} = (\delta_{BC, DE} + \delta_{CB, DE})/2$$

The linkage parameter $\lambda$ is defined so that the gametic array produced by an individual with genotype $ab / a'b'$ is:

$$\left(\frac{1+\lambda}{4} ab, \frac{1+\lambda}{4} a'b', \frac{1-\lambda}{4} ab', \frac{1-\lambda}{4} a'b\right)$$

Hence $\lambda = 1$ corresponds to the one locus case, for the two loci are completely linked and $a$ and $b$ are transmitted as one gene. Independent transmission of $a$ and $b$ occurs when $\lambda = 0$. Often a measure $X$ will be
written as $X(\lambda)$ to emphasize that it is indeed a function of the linkage parameter.

### 4.2 General Expansions

The general expansions of the measures will be derived for the general pedigree in Figure 1.1. As an abbreviation, $X(ab\epsilon B, a'b'\epsilon C)$ will replace $X(ab, a'b': ab\epsilon B, a'b'\epsilon C)$ for example.

#### 4.2.1 $\theta_{BC}$

From Figure 1.1 it can be seen that the gamete $a'b'$ from individual $C$ is a parental type from either $G$ or $H$ with probability $(1+\lambda)/4$ in each case, or a recombinant type with $a'$ from $G$ and $b'$ from $H$ or vice versa, each with probability $(1-\lambda)/4$. The following expansion is thus possible:

$$X(ab\epsilon B, a'b'\epsilon C) = \frac{1+\lambda}{4} X(ab\epsilon B, a'b'\epsilon G) + \frac{1+\lambda}{4} X(ab\epsilon B, a'b'\epsilon H)$$

$$+ \frac{1-\lambda}{4} X(ab\epsilon B, a'\epsilon C, b'\epsilon H) + \frac{1-\lambda}{4} X(ab\epsilon B, a'\epsilon H, b'\epsilon G),$$

$$\therefore \theta_{BC} = \frac{(1+\lambda)}{4} (\theta_{BG} + \theta_{BH}) + \frac{(1-\lambda)}{2} \chi_{B, CH}. \tag{4.2.1}$$

#### 4.2.2 $\chi_{B, CH}$

Here the gamete $ab$ is replaced by its values in the previous generation:

$$X(ab\epsilon B, a'\epsilon G, b'\epsilon H) = \frac{1+\lambda}{4} X(ab\epsilon D, a'\epsilon G, b'\epsilon H) + \frac{1+\lambda}{4} X(ab\epsilon E, a'\epsilon G, b'\epsilon H)$$

$$+ \frac{1-\lambda}{4} X(ab\epsilon D, b\epsilon E, a'\epsilon G, b'\epsilon H) + \frac{1-\lambda}{4} X(ab\epsilon E, b\epsilon D, a'\epsilon G, b'\epsilon H)$$
\[ \gamma_{B, GH} = \frac{(1 + \lambda)}{4} (\gamma_{D, GH} + \gamma_{E, GH}) + \frac{(1 - \lambda)}{2} \delta_{DE, GH}. \]

A similar equation for \( \gamma_{B, HG} \) leads to:

\[ \gamma_{B, GH} = \frac{(1 + \lambda)}{4} (\gamma_{D, GH} + \gamma_{E, GH}) + \frac{(1 - \lambda)}{2} \delta_{DE, GH} \]  \hspace{1cm} (4.2.2)

Combining equations (4.2.1) and (4.2.2) leads to the complete expansion of \( \triangle_{BC} \):

\[ \triangle_{BC} = \left( \frac{1 + \lambda}{4} \right)^2 (\phi_{DG} + \phi_{DH} + \phi_{EG} + \phi_{EH}) + \frac{1 - \lambda^2}{8} (\gamma_{D, GH} + \gamma_{E, GH} + \gamma_{G, DE} + \gamma_{H, DE}) + \frac{(1 - \lambda)^2}{4} \delta_{DE, GH}. \]  \hspace{1cm} (4.2.3)

4.2.3 \hspace{1cm} \delta_{DE, GH}

Each of the four genes are now on separate gametes, so each has probability of one half of coming from one of two individuals.

\[ X(a\epsilon D, b\epsilon E, a'\epsilon G, b'\epsilon H) = \frac{1}{2} X(a\epsilon K, b\epsilon E, a'\epsilon G, b'\epsilon H) \]

\[ + \frac{1}{2} X(a\epsilon L, b\epsilon E, a'\epsilon G, b'\epsilon H); \]

\[ \delta_{DE, GH} = \frac{1}{2} (\delta_{KE, GH} + \delta_{LE, GH}). \]  \hspace{1cm} (4.2.4)

Proceeding in this fashion leads to:

\[ \delta_{DE, GH} = \frac{1}{4} (\delta_{KM, GH} + \delta_{KN, GH} + \delta_{LM, GH} + \delta_{LN, GH}). \]  \hspace{1cm} (4.2.5)

The parents of \( G \) and \( H \) may also be brought in. This method of treating one gene at a time may also be used to complete the expansion of \( \gamma_{B, GH} \).
\[ \gamma_B, \gamma_H = \frac{1 + \lambda}{4} \left( \gamma_D, \gamma_H + \gamma_H, \gamma_D + \gamma_E, \gamma_H + \gamma_E, \gamma_H \right) \]
\[ + \frac{1 - \lambda}{4} \left( \delta_{DE}, \gamma_H + \delta_{DE}, \gamma_H \right). \]

(4.2.6)

Similarly the parents of \( \text{H} \) may be brought in.

Note that digametic functions expand back to digametic, trigametic, and quadrigametic functions, that trigametic functions expand back to trigametic and quadrigametic functions, and that quadrigametic functions expand only to quadrigametic functions.

### 4.3 Special Expansions

The original definition of \( X \) specified that the genes \( a, a' \) and \( b, b' \) should be distinct. No restrictions were placed on the individuals used as subscripts for \( \Theta, \gamma, \) and \( \delta \). Whenever such a subscript does appear more than once (indicating that more than one gamete per parent is being considered) special expansions are required since the \( a \) and \( b \) genes may no longer be distinct. Such non-distinct genes (or copies of the same gene) are automatically identical by descent.

#### 4.3.1 \( \Theta_{BB} \)

The two gametes being considered, \( ab \) and \( a'b' \), each from individual \( B \), are replaced by their respective gametic arrays. These arrays are identical here and equal to

\[ \left( \frac{1 + \lambda}{4} a_E b_E, \frac{1 + \lambda}{4} a_D b_D, \frac{1 - \lambda}{4} a_E b_D, \frac{1 - \lambda}{4} a_D b_E \right), \]

where subscripts indicate which parent the corresponding gene comes from. These arrays are arranged as headings in a two-way table.
(Table 4.2), and the probabilities that the two gametes carry genes identical by descent are put into the body of the table.

It should be noted that this approach could have been used to derive the previous expansions. While it would have provided the same results, it has the disadvantage of being cumbersome, for it gives only one component of the measure at one time.

Table 4.2 Expansion of $\Theta_{11BB}$

<table>
<thead>
<tr>
<th>$\Theta_{11BB}$</th>
<th>$\frac{1 + \lambda}{4}$</th>
<th>$\frac{1 + \lambda}{4}$</th>
<th>$\frac{1 - \lambda}{4}$</th>
<th>$\frac{1 - \lambda}{4}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$a_E b_E$</td>
<td>$a_D b_D$</td>
<td>$a_E b_D$</td>
<td>$a_D b_E$</td>
<td></td>
</tr>
<tr>
<td>$\frac{1 + \lambda}{4} a_E b_E$</td>
<td>1</td>
<td>$\Theta_{11ED}$</td>
<td>$\Theta_{1ED}$</td>
<td>$\Theta_{1.ED}$</td>
</tr>
<tr>
<td>$\frac{1 + \lambda}{4} a_D b_D$</td>
<td>$\Theta_{11ED}$</td>
<td>1</td>
<td>$\Theta_{1.ED}$</td>
<td>$\Theta_{1.ED}$</td>
</tr>
<tr>
<td>$a' b'$</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$\frac{1 - \lambda}{4} a_E b_D$</td>
<td>$\Theta_{1.ED}$</td>
<td>$\Theta_{1.ED}$</td>
<td>1</td>
<td>$\Theta_{11ED}$</td>
</tr>
<tr>
<td>$\frac{1 - \lambda}{4} a_D b_E$</td>
<td>$\Theta_{1.ED}$</td>
<td>$\Theta_{1.ED}$</td>
<td>$\Theta_{11ED}$</td>
<td>1</td>
</tr>
</tbody>
</table>
\[ \theta_{11BB} = \frac{1 + \lambda^2}{4} + \frac{1 + \lambda^2}{4} \theta_{11ED} + \frac{1 - \lambda^2}{4} \theta_{1.ED} + \frac{1 - \lambda^2}{4} \theta_{1ED} \]

\[ = \frac{1 + \lambda^2}{4} (\theta_{11ED} + \theta_{10ED} + \theta_{01ED} + \theta_{00ED}) + \frac{1 + \lambda^2}{4} \theta_{11ED} \]

\[ + \frac{1 - \lambda^2}{4} (\theta_{11ED} + \theta_{10ED}) + \frac{1 - \lambda^2}{4} (\theta_{11ED} + \theta_{01ED}) \]

\[ = \theta_{11ED} + \frac{1}{2} \theta_{10ED} + \frac{1}{2} \theta_{01ED} + \frac{1 + \lambda^2}{4} \theta_{00ED} . \]

Applying the same procedure for the other three components of $\theta_{BB}$ leads to the following equation.

\[
\begin{pmatrix}
1 & \frac{1}{2} & \frac{1}{2} & \frac{1 + \lambda^2}{4} \\
0 & \frac{1}{2} & 0 & \frac{1 - \lambda^2}{4} \\
0 & 0 & \frac{1}{2} & \frac{1 - \lambda^2}{4} \\
0 & 0 & 0 & \frac{1 + \lambda^2}{4}
\end{pmatrix}
\]

\[= \theta_{BB} \cdot \theta_{ED} \]

\[= \theta_{F_B} . \quad (4.3.1)\]

### 4.3.2 $\gamma_{B, BB}$

The two-way table for $\gamma_{B, BB}$ is the same as that for $\theta_{BB}$ except that the frequencies for the gametic array for $a'b'$ are all equal to $\frac{1}{4}$. Since $a'$, $b'$ are on separate gametes, linkage cannot affect these
frequencies. The expansion, then, is obtained directly from (4.3.1) by removing $\lambda$.

$$\chi_{B, BB} = \Pi F_B ,$$  
(4.3.2)

$$
\begin{bmatrix}
1 & \frac{1}{2} & \frac{1}{2} & \frac{1}{4} \\
0 & \frac{1}{2} & 0 & \frac{1}{4} \\
0 & 0 & \frac{1}{2} & \frac{1}{4} \\
0 & 0 & 0 & \frac{1}{4}
\end{bmatrix}
$$

where $\Pi =$

4.3.3 $\delta_{BB, BB}$

Linkage does not affect the gametic arrays of either ab or a'b' now, otherwise the argument is just the same as for $\delta_{BB}$ or $\chi_{B, BB'}$. The expansion will be the same as for $\chi_{B, BB'}$

$$\delta_{BB, BB} = \Pi F_B .$$  
(4.3.3)

4.3.4 $\chi_{B, CC}$

The gametic arrays for ab, a'b' are now different, and are arrayed along the sides of a two-way table (Table 4.3). Linkage appears in the frequencies for that of ab, but not a'b' since a' and b' are on separate gametes. The difference to (4.2.6) arises because in the previous generation a' and b' may have been on the same gamete, which was not the case for $\chi_{B, CD}$ in the general pedigree.
Table 4.3 Expansion of $\chi_{B, \text{ CC}}$

<table>
<thead>
<tr>
<th>$a'b'$</th>
<th>$\frac{1}{4}$</th>
<th>$\frac{1}{4}$</th>
<th>$\frac{1}{4}$</th>
<th>$\frac{1}{4}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\chi_{B, \text{ CC}}$</td>
<td>$a_Gb_G$</td>
<td>$a_Hb_H$</td>
<td>$a_Gb_H$</td>
<td>$a_Hb_G$</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>$a'b'$</th>
<th>$\frac{1 + \lambda}{4} a_Db_D$</th>
<th>$\theta_{DG}$</th>
<th>$\theta_{DH}$</th>
<th>$\chi_D, \text{ GH}$</th>
<th>$\chi_D, \text{ HG}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$ab$</td>
<td>$\frac{1 + \lambda}{4} a_Eb_E$</td>
<td>$\theta_{EG}$</td>
<td>$\theta_{EH}$</td>
<td>$\chi_E, \text{ GH}$</td>
<td>$\chi_E, \text{ HG}$</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>$a'b'$</th>
<th>$\frac{1 - \lambda}{4} a_Db_D$</th>
<th>$\chi_G, \text{ ED}$</th>
<th>$\chi_H, \text{ ED}$</th>
<th>$\delta_{ED}, \text{ GH}$</th>
<th>$\delta_{ED}, \text{ HG}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$ab$</td>
<td>$\frac{1 - \lambda}{4} a_Eb_E$</td>
<td>$\chi_G, \text{ DE}$</td>
<td>$\chi_H, \text{ DE}$</td>
<td>$\delta_{DE}, \text{ GH}$</td>
<td>$\delta_{DE}, \text{ HG}$</td>
</tr>
</tbody>
</table>

The expansion is given in equation (4.3.4).

$$
\chi_{B, \text{ CC}} = \frac{1 + \lambda}{16} (\theta_{DG} + \theta_{DH} + \theta_{EG} + \theta_{EH}) + \frac{1 + \lambda}{8} (\chi_D, \text{ GH} + \chi_E, \text{ GH}) \\
+ \frac{1 - \lambda}{8} (\chi_G, \text{ ED} + \chi_H, \text{ ED}) + \frac{1 - \lambda}{4} \delta_{ED}, \text{ GH}.
$$

(4.3.4)

4.3.5 $\delta_{BB, \text{ CC}}$

The argument is the same as for $\chi_{B, \text{ CC}}$ except that linkage does not now affect the frequencies for $ab$ or $a'b'$. The appropriate
expansion, equation (4.3.5) is obtained by removing $\lambda$ from (4.3.4).

$$
\delta_{BB, CC} = \frac{1}{16} \left( \theta_{DG} + \theta_{DH} + \theta_{EG} + \theta_{EH} \right) + \frac{1}{8} \left( \gamma_{D, CH} + \gamma_{E, CH} + \gamma_{G, ED} + \gamma_{H, ED} \right) + \frac{1}{4} \theta_{ED, CH}. 
$$

(4.3.5)

4.3.6 $\gamma_{B, BC}$

For $\gamma_{B, BC}$, the gametic array for $ab$ is $(\frac{1 + \lambda}{4} a_D b_D, \frac{1 + \lambda}{4} a_E b_E, \frac{1 - \lambda}{4} a_D b_E, \frac{1 - \lambda}{4} a_E b_D)$. The gene $a'$ may be $a_D$ or $a_E$ with equal probability, and there is nothing to be gained by specifying $b'$, which is just written $b_C$. The two-way table for the first component is given (Table 4.4).

Table 4.4 Expansion of $\gamma_{11B, BC}$

<table>
<thead>
<tr>
<th>$\gamma_{11B, BC}$</th>
<th>$\frac{1 + \lambda}{4}$</th>
<th>$\frac{1 + \lambda}{4}$</th>
<th>$\frac{1 - \lambda}{4}$</th>
<th>$\frac{1 - \lambda}{4}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$a_D b_D$</td>
<td>$a_E b_E$</td>
<td>$a_D b_E$</td>
<td>$a_E b_D$</td>
<td></td>
</tr>
<tr>
<td>$\frac{1}{2} a_D b_C$</td>
<td>$\theta_{1DC}$</td>
<td>$\gamma_{11E, DE}$</td>
<td>$\theta_{1ED}$</td>
<td>$\gamma_{11D, EC}$</td>
</tr>
<tr>
<td>$a'b'$</td>
<td>$\frac{1}{2} a_E b_C$</td>
<td>$\gamma_{11D, EC}$</td>
<td>$\theta_{1EC}$</td>
<td>$\gamma_{11E, DC}$</td>
</tr>
</tbody>
</table>
Similar tables for the other three components lead to the expansion:

\[
\gamma_{B, BC} = \frac{1}{4} \Lambda (\theta_{CD} + \theta_{CE}) + \frac{1}{4} (\gamma_{D, CE} + \gamma_{E, CD}) \tag{4.3.6}
\]

where

\[
\Lambda = \begin{bmatrix}
1 & 0 & 1 & 0 \\
0 & 1 & 0 & 1 \\
0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0
\end{bmatrix}
\]

By symmetry the equation for \( \gamma_{B, CB} \) is:

\[
\gamma_{B, CB} = \frac{1}{4} \bar{\Psi} (\theta_{CD} + \theta_{CE}) + \frac{1}{4} (\gamma_{D, CE} + \gamma_{E, CE}) \tag{4.3.7}
\]

where

\[
\bar{\Psi} = \begin{bmatrix}
1 & 1 & 0 & 0 \\
0 & 0 & 0 & 0 \\
0 & 0 & 1 & 1 \\
0 & 0 & 0 & 0
\end{bmatrix}
\]

Combining (4.3.6) and (4.3.7) leads to the required expansion:

\[
\gamma_{B, CB} = \frac{1}{8} (\Lambda + \bar{\Psi}) (\theta_{CD} + \theta_{CE}) + \frac{1}{4} (\gamma_{D, CE} + \gamma_{E, CD}). \tag{4.3.8}
\]

4.3.7 \( \delta_{BB, BC} \)

In this case linkage does not affect the frequencies of ab, and the argument is as for \( \gamma_{B, BC} \). As linkage did not play any part in that expansion, equation (4.3.9) follows directly:

\[
\delta_{BB, CB} = \gamma_{B, CB} = \frac{1}{8} (\Lambda + \bar{\Psi}) (\theta_{CD} + \theta_{CE}) + \frac{1}{4} (\gamma_{D, CE} + \gamma_{E, CD}). \tag{4.3.9}
\]
4.3.8 \( \bar{\delta}_{BB, \bar{GH}} \)

The argument is just as for \( \bar{\lambda}_{B, \bar{GH}} \) except that linkage plays no part. Hence (4.3.10) follows from (4.2.6) by removing \( \lambda \).

\[
\bar{\delta}_{BB, \bar{GH}} = \frac{1}{\bar{\theta}} (\bar{\lambda}_{D, \bar{PH}} + \bar{\lambda}_{D, \bar{QH}} + \bar{\lambda}_{E, \bar{PH}} + \bar{\lambda}_{E, \bar{QH}}) \\
+ \frac{1}{\bar{\theta}} (\bar{\delta}_{DE, \bar{PH}} + \bar{\delta}_{DE, \bar{QH}}).
\]

(4.3.10)

As stated in section 4.2, the parents of \( H \) may also be brought in, but the expansion will still be in terms of trigametic and quadrigametic measures.

4.3.9 \( \bar{\delta}_{BC, \bar{BC}} \)

Table (4.5) shows the calculations for the first component of \( \bar{\delta}_{BC, \bar{BC}} \).

Table 4.5 Expansion of \( \bar{\delta}_{11BC, \bar{BC}} \)

<table>
<thead>
<tr>
<th>( \bar{\delta}_{11BC, \bar{BC}} )</th>
<th>( \bar{a} \bar{b}_G )</th>
<th>( \bar{a} \bar{E}_G )</th>
<th>( \bar{a} \bar{D}_H )</th>
<th>( \bar{a} \bar{E}_H )</th>
</tr>
</thead>
<tbody>
<tr>
<td>( \frac{1}{4} )</td>
<td>( \frac{1}{4} )</td>
<td>( \frac{1}{4} )</td>
<td>( \frac{1}{4} )</td>
<td>( \frac{1}{4} )</td>
</tr>
<tr>
<td>( \bar{a} \bar{b}_G )</td>
<td>( \bar{a} \bar{E}_G )</td>
<td>( \bar{a} \bar{D}_H )</td>
<td>( \bar{a} \bar{E}_H )</td>
<td></td>
</tr>
<tr>
<td>( \frac{1}{4} )</td>
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<tr>
<td>( \bar{a} \bar{E}_G )</td>
<td>( \bar{a} \bar{D}_H )</td>
<td>( \bar{a} \bar{E}_H )</td>
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<td>( \frac{1}{4} )</td>
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<td>( \frac{1}{4} )</td>
</tr>
<tr>
<td>( \bar{a} \bar{D}_G )</td>
<td>( \bar{a} \bar{E}_G )</td>
<td>( \bar{a} \bar{D}_H )</td>
<td>( \bar{a} \bar{E}_H )</td>
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<td>( \frac{1}{4} )</td>
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<td>( \frac{1}{4} )</td>
</tr>
<tr>
<td>( \bar{a} \bar{H}_G )</td>
<td>( \bar{a} \bar{D}_H )</td>
<td>( \bar{a} \bar{E}_H )</td>
<td></td>
<td></td>
</tr>
<tr>
<td>( \frac{1}{4} )</td>
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<td>( \frac{1}{4} )</td>
<td>( \frac{1}{4} )</td>
<td>( \frac{1}{4} )</td>
</tr>
<tr>
<td>( \bar{a} \bar{H}_H )</td>
<td>( \bar{a} \bar{E}_H )</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>( \frac{1}{4} )</td>
<td>( \frac{1}{4} )</td>
<td>( \frac{1}{4} )</td>
<td>( \frac{1}{4} )</td>
<td>( \frac{1}{4} )</td>
</tr>
</tbody>
</table>
Similar tables for the other three components lead to equation (4.3.11).

\[
\delta_{BC, \ CB} = \frac{1}{2} \sum \theta_{DE} + \frac{1}{2} \phi \theta_{GH} + \frac{1}{4} \delta_{DG, \ EH}
\]

\[
= \frac{1}{2} \sum F_B + \frac{1}{2} \phi F_C + \frac{1}{4} \delta_{DG, \ EH},
\]

(4.3.11)

where

\[
\begin{bmatrix}
1 & 1 & \frac{1}{2} & \frac{1}{2} \\
0 & 0 & 0 & 0 \\
0 & 0 & \frac{1}{2} & \frac{1}{2} \\
0 & 0 & 0 & 0
\end{bmatrix} = \begin{bmatrix}
1 & 1 & 1 & 1 \\
0 & \frac{1}{2} & 0 & \frac{1}{2} \\
0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0
\end{bmatrix}.
\]

4.3.10 $\delta_{BC, \ CB}$

Table 4.6 shows calculations for $\delta_{BC, \ CB}$, and the expansion is given in equation (4.3.12).

\[
\delta_{BC, \ CB} = \frac{1}{16} (\theta_{DG} + \theta_{EG} + \theta_{DH} + \theta_{EH}) + \frac{1}{8} (\zeta_D, \ \overline{GH} + \zeta_E, \ \overline{GH})
\]

\[
+ \zeta_G, \ \overline{DE} + \zeta_H, \ \overline{DE}) + \frac{1}{4} \delta_{GE, \ DH}.
\]

(4.3.12)
Table 4.6 Expansion of $\delta_{BC, CB}$

<table>
<thead>
<tr>
<th>$\delta_{BC, CB}$</th>
<th>$a^b_G$</th>
<th>$a^b_E$</th>
<th>$a^b_D$</th>
<th>$a^b_H$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\frac{1}{4}$</td>
<td>$\frac{1}{4}$</td>
<td>$\frac{1}{4}$</td>
<td>$\frac{1}{4}$</td>
<td>$\frac{1}{4}$</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>$\frac{1}{4} a^b_D$</th>
<th>$\theta_{DG}$</th>
<th>$\gamma_D$, $ED$</th>
<th>$\gamma_D$, $GH$</th>
<th>$\delta_{GD}$, $EH$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\frac{1}{4} a^b_E$</td>
<td>$\gamma_D$, $DE$</td>
<td>$\theta_{EG}$</td>
<td>$\delta_{GE}$, $DH$</td>
<td>$\gamma_E$, $GH$</td>
</tr>
<tr>
<td>$a^b$</td>
<td>$\frac{1}{4} a^b_D$</td>
<td>$\gamma_D$, $HG$</td>
<td>$\delta_{HD}$, $EG$</td>
<td>$\theta_{DH}$</td>
</tr>
<tr>
<td>$\frac{1}{4} a^b_E$</td>
<td>$\delta_{HE}$, $DG$</td>
<td>$\gamma_E$, $HG$</td>
<td>$\gamma_H$, $DE$</td>
<td>$\theta_{EH}$</td>
</tr>
</tbody>
</table>

4.3.11 $\delta_{BG, BH}$

Calculations for this final special case are indicated in Table 4.7. There is no point in expanding the two $b$ genes there. The expansion is given in equation (4.3.13).

$$\delta_{BG, BH} = \frac{1}{2} \Lambda \theta_{DG} + \frac{1}{2} \delta_{DH}, EG.$$ \hspace{1cm} (4.3.13)

By symmetry:

$$\delta_{GB, HB} = \frac{1}{2} \Psi \theta_{DG} + \frac{1}{2} \delta_{HD}, GE.$$ \hspace{1cm} (4.3.14)
Table 4.7  Expansion of $S_{11BG, BH}$

<table>
<thead>
<tr>
<th>$\frac{1}{2}$ $a'b'$</th>
<th>$a^b_G$</th>
<th>$a^b_G$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\frac{1}{2}$</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$S_{11BG, BH}$</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$\frac{1}{2}$ $a^b_H$</td>
<td>$\theta_{1GH}$</td>
<td>$S_{11DH, EG}$</td>
</tr>
<tr>
<td>$\frac{1}{2}$</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$S_{11EH, DG}$</td>
<td>$\theta_{1GH}$</td>
<td></td>
</tr>
</tbody>
</table>
5. GENERAL ANALYSIS OF INDIVIDUAL MATING SYSTEMS

5.1 Specific Pedigrees

With the measures defined generally, and all possibilities accounted for in the expansion equations, it is possible to determine the inbreeding function for any mating system.

The first type of pedigree to be considered is a specific one. Here an initial array of individuals, of known relationship and degree of inbreeding is specified. Usually they will be unrelated and non-inbred. It is required to determine the inbreeding function of some specified descendent of this initial array. There is no requirement of any pattern to the matings between the initial population and the individual of interest.

The method is straightforward. The inbreeding function of the individual is expanded back to digametic, trigametic, and quadrigametic measures of its parents. These measures, in turn, are further expanded back to measures involving their parents. This process continues until the inbreeding function under study has been expressed entirely in terms of measures involving the initial population, whereupon the numerical values for these measures are substituted.

Section 6.1 contains an example of the procedure.

5.2 Pedigree Systems of Mating

When there is a constant mating pattern between every generation, the above approach is neither practicable for long pedigrees, nor necessary. Instead, recurrence relations for the various measures are established.
Such relations are well established for the (one locus) inbreeding and panmictic coefficients. Moreover these coefficients form the marginal totals to the two by two tables of the components of the inbreeding function (Table 4.1). It is thus evident that, to determine the four components of the inbreeding function, the only information needed is one of the components in addition to the one-locus coefficients. It will be convenient to work with the two locus panmictic function, and corresponding (fourth) components of other measures.

Because the pedigree now has a recurring pattern, a new notational device is introduced. Instead of being subscripted according to individual, the measures will be superscripted according to generation. The subscripts refer to the individuals providing the gametes in the argument of the measures; the superscripts refer to the generation which is formed by the gametes.

The object is to find a minimal set of simultaneous transition equations for a set of (fourth components of) measures. The two locus panmictic function is necessarily a set of this smallest, or complete, set of measures. Any member of a complete set of measures in generation \((t+1)\) can be expressed in terms of the members of the set in generation \(t\).

The first step is to expand \(F_{00}^{t+1}\) back into measures of the previous generation. The types of additional measures necessary on the right hand side of this equation are noted, and transition equations established relating their values in generation \(t\) to values of measures in generation \(t-1\). The process continues until there are just enough (s) equations. The complete set of measures, then, of order \(s\), is such
that if any measure is removed from the set, the transition equations of the remaining \( s - 1 \) cannot be expressed in terms of only themselves, in the previous generation.

As \( F_{00}^{t+1} \) is of principal interest, the object is to use the \( s \) simultaneous transition equations to find \( F_{00}^{t+1} \). If \( s \) is sufficiently small this can be done directly. For selfing, \( s = 1 \) and for parent-offspring mating with one parent used repeatedly, \( s = 2 \) (see section 6.2). For larger \( s \), matrix techniques must be used.

The \( s \) transition equations are written in matrix form:

\[
\begin{bmatrix}
\vdots \\
\end{bmatrix}_{t+1} = \begin{bmatrix}
\vdots \\
\end{bmatrix}_{t} ,
\]

where \( \begin{bmatrix}
\vdots \\
\end{bmatrix}_{t} \) is the \( s \) vector \([F_{00}^{t}, X_{00}^{t}, \ldots, X_{00}^{t, s-1}]^{t}\) of complete measures, and \( \Omega \) is the \( s \times s \) transition matrix. Cockerham and Weir\(^2\) showed that the required recurrence formula for \( F_{00}^{t} \) is given directly by the minimal equation \( f(x) \) of \( \Omega \). Generally the minimal equation and characteristic equations of \( \Omega \) coincide. For \( \lambda = 0 \) or \( \lambda = 1 \), this minimal equation generally factors. The factor \( g(x) \) to be used for the recurrence formula for \( F_{00}^{t} \) is the factor of smallest order for which the vector \( g(\Omega)\begin{bmatrix}
\vdots \\
\end{bmatrix}_{t} \) has zero first component.

The transition matrix thus provides a recurrence formula for \( F_{00}^{t} \) which goes back \( s \) generations. For sib mating (Cockerham and Weir) \( s = 6 \); and for parent-offspring mating (section 6.3) with each parent used once, \( s = 4 \). Algebraic expressions for \( F_{00} \) (and hence the other components of \( F \)) in any generation will thus be extremely complicated. Numerical methods will generally be used to calculate values of \( F_{00} \) for various linkage values in successive generations.

\(^{2}\)Ibid.
In programming a computer to evaluate $F_{00}$, it is easiest to compute each of $s$ measures for each generation—a procedure equivalent to taking successive powers of the transition matrix.

### 5.3 Rate of Inbreeding

All the inbreeding systems studied in this work have known initial and final inbreeding functions—generally $F_0^0 = [0, 0, 0, 1]'$ and $F_0^\infty = [1, 0, 0, 0]'$. The systems differ however according to the rate at which double non-identity is replaced by double identity, and this rate provides a convenient characterization of a system.

For any quantity $Y^t$ associated with generations, the usual rate of increase, $\rho^t$, of $Y^t$ at time $t$ is given by:

$$\rho^t = \frac{Y^t - Y^{t-1}}{(\lim_{t \to \infty} Y^t) - Y^{t-1}} \quad (5.3.1)$$

In the one locus case, the same rate is found whether the inbreeding or parmetric coefficients are used, since:

$$\rho^t = \frac{F_{1}^t - F_{1}^{t-1}}{1 - F_{1}^{t-1}} = \frac{F_{0}^t - F_{0}^{t-1}}{0 - F_{0}^{t-1}} \quad (5.3.2)$$

This "rate of inbreeding" will be constant for all generations only if $F_0^t = k F_0^{t-1}$ (k is a constant), which is the case for finite monoecious populations with random pairing of gametes. Self mating is such a case. For other systems however, an approximation can be made which does provide a constant rate of inbreeding. If the recurrence formula for $F_0^t$ is written as:
\[ F_{0}^{t+s} = \sum_{r=0}^{s-1} a_{r} F_{0}^{t+r} ; \]  

then the solution of this difference equation is:
\[ F_{0}^{t} = \sum_{r=0}^{s} b_{r} (x_{r})^{t} , \]

where \( x_{r} \) are the roots of the polynomial
\[ x^{t+s} - \sum_{r=0}^{s-1} a_{r} x^{t+r} = 0 . \]

Substituting \( F_{0}^{t} \) from (5.3.4) into (5.3.2) and dividing throughout by the \((t-1)\)th power of the largest root, \( x_{R} \), of (5.3.5) leads to:
\[ \rho^{t} = \sum_{r=0}^{s} b_{r} \frac{x_{r}^{t-1}}{x_{R}^{t-1}} (1-x_{r})/ \sum_{r=0}^{s} b_{r} \frac{x_{r}^{t-1}}{x_{R}^{t-1}} . \]

Hence, when \( t \) is large enough for \( \frac{x_{r}^{t-1}}{x_{R}^{t-1}} \) to be negligible for \( r \neq R \):
\[ \rho^{t} = 1 - x_{R} . \]

The same approximate (or limiting) rate of inbreeding would have resulted by working with \( F_{1}^{t} \) instead of \( F_{0}^{t} \). In the one locus case therefore, systems of mating may be compared by considering the quantity \( x_{R} \) for that system. Using the constant inbreeding rate also provides:
\[ F_{0}^{t} = x_{R} F_{0}^{t-1} \]

or
\[ F_{0}^{t} = (x_{R})^{t} \text{ if } F_{0}^{0} = 1 . \]
A similar theory is desired for the two locus case. Before a rate can be defined for the inbreeding function, the $4 \times 1$ vector $F$ must be reduced to a scalar by means of some suitable norm. The norm will also allow distances to be defined between vectors--so that, using the difference between $F^0$ and $F^t$, the degree of inbreeding can be specified.

The norm to be used is the two locus panmictic coefficient (the fourth component of $F$).

$$|| F^t || = F_{00}^t .$$

Hence $|| F^0 || = 1$ and $|| F^\infty || = 0$ and $|| F^t ||$ is a monotone decreasing function of $t$. The "degree of inbreeding", or distance from $F^0$ to $F^t$ is just $1 - F_{00}^t$, and the rate of inbreeding is:

$$\rho^t = \frac{F_{00}^{t-1} - F_{00}^t}{F_{00}^{t-1}} .$$

The limiting constant value of this rate is found just as in the one locus case. For pedigree systems of mating, when matrix techniques are used, the polynomial corresponding to (5.3.5) is the minimal polynomial of the transition matrix for the fourth components of the complete set of measures. Corresponding to $x_R$, the maximum eigenvalue $\mu(\lambda)$ of the transition matrix gives the rate of inbreeding:

$$\rho(t) = 1 - \mu(\lambda)$$

$$F_{00}^t = \mu(\lambda) F_{00}^{t-1} .$$

\[(5.3.7)\]
For complete linkage, \( F_{00}^t = F_{0.}^t = F_{.0}^t = F_0^t \), so that equation (5.3.7) gives:

\[
(F_{00}^t + F_{10}^t) = \mu(1)(F_{00}^{t-1} + F_{10}^{t-1}),
\]

\[
(F_{00}^t + F_{01}^t) = \mu(1)(F_{00}^{t-1} + F_{01}^{t-1}).
\]

These results, together with the requirement that \( F_{..}^t = 1 \), lead to, for sufficient large \( t \):

\[
P_{t+1}^t = \begin{bmatrix}
1 & 1-\mu(1) & 1-\mu(1) & 1+\mu(1) - 2\mu(1) \\
0 & \mu(1) & 0 & \mu(1) - \mu(1) \\
0 & 0 & \mu(1) & \mu(1) - \mu(1) \\
0 & 0 & 0 & \mu(1) \\
\end{bmatrix} P_t.
\]

If \( P_0^t = [0, 0, 0, 1]' \), the inbreeding function can thus be approximated by:

\[
P_t = \begin{bmatrix}
1 + (\mu(1))^t - 2(\mu(1))^t \\
(\mu(1))^t - (\mu(1))^t \\
(\mu(1))^t - (\mu(1))^t \\
(\mu(1))^t \\
\end{bmatrix}.
\]

(5.3.8)

When two linked loci are considered, then, the inbreeding of any system of mating is characterized by the two quantities \( \mu(1) \) and \( \mu(\lambda) \).
The maximum eigenvalue $\mu(\lambda)$ is a monotone increasing function of $\lambda$, so that $\mu(\lambda) \leq \mu(1)$.

While this monotonicity will be demonstrated numerically, it will not be proven analytically. A verbal proof can be given though.

In any inbreeding system, when there is independent assortment of genes at the two loci ($\lambda = 0$), the fact that uniting gametes carry copies of a single ancestral gene at one locus does not imply that they do for the other locus also. (This is quite apart from the fact that the probability that each locus, considered separately, carried identical genes is the same for both loci). On the other hand, as linkage increases, there is greater tendency for genes originally on one chromosome to stay together. Hence identity at one locus is more likely to imply simultaneous identity at the other locus. The proportion of double identity (and hence $F_{11}$) is thus a monotone increasing function of the linkage parameter $\lambda$.

Equation (5.3.8) thus implies that $\mu(\lambda)$ (and $F_{00}$) is a monotone increasing function of $\lambda$.

By its very nature, inbreeding implies a decrease in double non-identity regardless of the degree of linkage, so that $\mu(1) < 1$. On the other hand, the fastest form of inbreeding is selfing, for which $\mu(\lambda) = (1 + \lambda^2)/4$. Finally, for pedigree systems of mating, the gametes $ab$ and $a'b'$ uniting to form an individual are specified and $F_{00}$ may be written:

$$F_{00} = \Pr(a \neq a', b \neq b')$$

$$= \Pr(a \neq a' \mid b \neq b') \Pr(b \neq b') .$$
For complete linkage:

\[ \Pr(a \neq a' \mid b \neq b') = 1, \]

which implies

\[ F_{00}(1) = F_0, \]

and for zero linkage:

\[ \Pr(a \neq a' \mid b \neq b') = P(a \neq a'), \]

so that:

\[ F_{00}(0) = F_0^2, \]

and

\[ \mu(0) = \mu(1)^2. \]

The previous paragraph leads to two inequalities, the first for all inbreeding systems and the second for pedigree systems. They are:

\[ (1 + \lambda^2)/4 \leq \mu(\lambda) < 1, \]

\[ \mu(1)^2 \leq \mu(\lambda) \leq \mu(1). \]
6. EXAMPLES OF INDIVIDUAL MATING SYSTEMS

6.1 Specific Pedigree

An example of a specific pedigree will be given to illustrate the procedures outlined in section 5.1. The pedigree is shown in Figure 6.1.

For the one locus inbreeding coefficient, direct application of Wright's general formula gives:

\[ F_A = \left( \frac{1}{2} \right)^4 (1 + F_G) + \left( \frac{1}{2} \right)^5 (1 + F_K) + \left( \frac{1}{2} \right)^4 (1 + F_E), \]

i.e., \( F_{A_{1.1}} = 5/32 \), if G, K, E are each non-inbred and unrelated.

![Figure 6.1 Specific pedigree](image-url)
For the two locus case, \( F_A \) will be expanded back until all measures involve gametes from \( G, K, E \) only.

\[
F_A = \theta_{BC}
\]

\[
= \frac{1 + \lambda}{4} (\theta_{DC} + \theta_{EC}) + \frac{1 - \lambda}{2} \gamma_{C, DE}
\]

\[
= \left( \frac{1 + \lambda}{4} \right)^2 (\theta_{DG} + \theta_{DH} + \theta_{EG} + \theta_{EH})
\]

\[
+ \frac{1 - \lambda^2}{8} (\gamma_D, HG + \gamma_E, HG + \gamma_G, DE + \gamma_H, DE)
\]

\[
+ \left( \frac{1 - \lambda}{4} \right)^2 \delta_{GH}, DE
\].

This first stage follows directly from equation (4.2.3). Each of the measures on the right hand side still needs expanding though.

\[
\theta_{DG} = \frac{1 + \lambda}{4} (\theta_{GG} + \theta_{KG}) + \frac{1 - \lambda}{2} \gamma_{G, GK},
\]

\[
\theta_{DH} = \left( \frac{1 + \lambda}{4} \right)^2 (\theta_{GK} + \theta_{GE} + \theta_{KE} + \theta_{KK})
\]

\[
+ \frac{1 - \lambda^2}{8} (\gamma_G, KE + \gamma_K, KE + \gamma_E, GK + \gamma_K, GK)
\]

\[
+ \left( \frac{1 - \lambda}{4} \right)^2 \delta_{GK}, KE
\],

\[
\theta_{EH} = \frac{1 + \lambda}{4} (\theta_{EK} + \theta_{EE}) + \frac{1 - \lambda}{2} \gamma_{E, KE},
\]

\[
\gamma_D, HG = \frac{1 + \lambda}{8} (\gamma_G, GH + \gamma_G, GE + \gamma_K, GK + \gamma_K, GE)
\]

\[
+ \frac{1 - \lambda}{4} (\delta_{GK}, GK + \delta_{GK}, GE),
\]
\[ \gamma_E, \overline{HG} = \frac{1}{2} (\gamma_E, \overline{KG} + \gamma_E, \overline{GE}) , \]

\[ \gamma_G, \overline{DE} = \frac{1}{2} (\gamma_G, \overline{KE} + \gamma_E, \overline{GE}) , \]

\[ \gamma_H, \overline{DE} = \frac{1}{8} \left( \gamma_E, \overline{GE} + \gamma_E, \overline{KE} + \gamma_K, \overline{GE} + \gamma_K, \overline{KE} \right) + \frac{1 - \lambda}{4} (\delta_{\overline{KE}}, \overline{GE} + \delta_{\overline{KE}}, \overline{KE}) , \]

\[ \delta_{\overline{GH}}, \overline{DE} = \frac{1}{4} \left( \delta_{\overline{GE}}, \overline{GE} + \delta_{\overline{GE}}, \overline{KE} + \delta_{\overline{GE}}, \overline{GE} + \delta_{\overline{GE}}, \overline{KE} \right) . \]

Substitution of the expansions of these last eight equations into equation (6.1.1) leads to:

\[ F_A = \left( \frac{1 + \lambda}{4} \right)^3 (\Theta_{\overline{GG}} + \Theta_{\overline{EE}} + \frac{1 + \lambda}{4} \Theta_{\overline{KK}} + \frac{5 + \lambda}{4} \Theta_{\overline{GK}} + \frac{5 + \lambda}{4} \Theta_{\overline{EK}}) \]

\[ + \left( \frac{1 + \lambda}{4} \right)^2 \left( \frac{17 + 2\lambda + \lambda^2}{16} \right) \Theta_{\overline{GE}} \]

\[ + \frac{1 - \lambda^2}{8} \left( \frac{5 + \lambda}{8} (\gamma_G, \overline{GE} + \gamma_E, \overline{GE}) + \frac{3(1 + \lambda)}{8} (\gamma_G, \overline{KE} + \gamma_E, \overline{KE}) \right) + \frac{9 + \lambda + \lambda^2}{16} (\gamma_G, \overline{KE} + \gamma_E, \overline{KG}) \]

\[ + \frac{(1 + \lambda)(3 + \lambda)}{16} (\gamma_K, \overline{KE} + \gamma_E, \overline{KE}) + \frac{1 + \lambda}{4} \gamma_K, \overline{GE} \]

\[ + \frac{(1 - \lambda)^2}{4} \left( \frac{5 + 2\lambda + \lambda^2}{16} \delta_{\overline{GE}}, \overline{GE} + \frac{1 + \lambda}{8} (\delta_{\overline{GE}}, \overline{KE} + \delta_{\overline{KE}}, \overline{KE}) \right) + \frac{\lambda}{4} (\delta_{\overline{GE}}, \overline{GE} + \frac{3 + \lambda}{8} (\delta_{\overline{GE}}, \overline{GE} + \delta_{\overline{GE}}, \overline{KE})) . \]
With $F_A$ now expanded back as far as possible, it remains to replace each of the initial measures in the expansion by its numerical value.

Since $E$, $K$, $G$ are each non-inbred:

$$
\Theta_{EE} = \Theta_{GG} = \Theta_{KK} = \left[ \frac{1 + \lambda^2}{4}, \frac{1 - \lambda^2}{4}, \frac{1 - \lambda^2}{4}, \frac{1 + \lambda^2}{4} \right],
$$

(6.1.3)

from equation (4.3.1). If the three initial individuals are also assumed to be unrelated:

$$
\Theta_{EK} = \Theta_{KE} = \Theta_{GE} = [0, 0, 0, 1]^T
$$

(6.1.4)

since there is no chance of gametes from different individuals being identical by descent. Any other measure with distinct subscripts has the same value:

$$
\gamma_G, \overline{KE} = \gamma_E, \overline{KG} = \gamma_K, \overline{GE} = [0, 0, 0, 1]^T.
$$

(6.1.5)

The remaining measures have repeated subscripts, and their expansions follow from section 4.3. From equation (4.3.8):

$$
\gamma_G, \overline{GE} = \gamma_E, \overline{EC} = \gamma_G, \overline{KG} = \gamma_E, \overline{EK} = \gamma_K, \overline{KE} = \gamma_K, \overline{KG} = [0, \frac{1}{4}, \frac{1}{4}, \frac{1}{2}]^T.
$$

(6.1.6)

These values could have been written down immediately. In $\gamma_G, GE$ for example there is a probability of one half that the two a genes were copies of one gene in $G$ and hence identical. There is no chance of the two $b$ genes being identical.

Hence

$$
\gamma_G, GE = [0, \frac{1}{2}, 0, \frac{1}{2}]^T.
$$
By symmetry:

\[ \gamma_G, \ \gamma_C = [0, 0, \frac{1}{6}, \frac{1}{6}]', \]

and hence the equation (6.1.6).

For the quadrigametic measures, equations (4.3.10), (4.3.13) and (4.3.14) give:

\[ \beta_{GRK}, \ \beta_{KE} = \beta_{ERK}, \ \beta_{GC} = \beta_{GRK}, \ \beta_{GE} = [0, \frac{1}{8}, \frac{1}{8}, \frac{3}{4}]', \quad (6.1.7) \]

and equations (4.3.11) and (4.3.12) lead to:

\[ \beta_{GRK}, \ \beta_{CK} = \beta_{ERK}, \ \beta_{KE} = \beta_{GRK}, \ \beta_{GE} = [\frac{1}{8}, \frac{1}{8}, \frac{1}{8}, \frac{5}{8}]'. \quad (6.1.8) \]

Combining equations (6.1.2), \ldots, (6.1.8) then gives the value of the inbreeding function of individual A to be:

\[
F_A = \begin{bmatrix}
(25 + 4\lambda + 39\lambda^2 + 48\lambda^3 + 31\lambda^4 + 12\lambda^5 + \lambda^6)/1024 \\
(135 - 4\lambda - 39\lambda^2 - 48\lambda^3 - 31\lambda^4 - 12\lambda^5 - \lambda^6)/1024 \\
(135 - 4\lambda - 39\lambda^2 - 48\lambda^3 - 31\lambda^4 - 12\lambda^5 - \lambda^6)/1024 \\
(729 + 4\lambda + 39\lambda^2 + 48\lambda^3 + 31\lambda^4 + 12\lambda^5 + \lambda^6)/1024
\end{bmatrix}
\]

When linkage is complete (\( \lambda = 1 \)), it can be seen from this result, and that obtained above for the one locus coefficient that:

\[ F_{11A} = F_{1.A} = F_{A} \frac{5}{32}, \]

and that for independently segregating loci (\( \lambda = 0 \)),

\[ F_{11A} = (F_{1.A}) (F_{.A}) = \frac{25}{1024}. \]
The effect of linkage is thus seen to be to increase the relative frequency of double identity and double non-identity ($F_{11}$ and $F_{00}$) at the expense of the frequencies of single identities.

6.2 Repeated Parent-Offspring Mating

Consider the parent-offspring pedigree of Figure 6.2 where one parent ($U$) is used repeatedly. Individuals A, B, C are in generations $t + 2$, $t + 1$, $t$ respectively. The initial pair $U$ and $V$ are not related. The case where they are also non-inbred will be considered first. The method of section 5.2 will be used.

![Figure 6.2 Repeated parent-offspring mating](image)
From equation (4.2.1):

\[ F_{00A} = \theta_{00BU} = \frac{1 + \lambda}{4} (\theta_{0UU} + \theta_{0CU}) + \frac{1 - \lambda}{2} \gamma_{0UU}, \overline{CU}, \quad (6.2.1) \]

and from equation (4.3.1):

\[ \theta_{00UU} = \frac{1 + \lambda^2}{4}, \]

so that (6.2.1) may be written:

\[ F_{00}^{t+2} = \frac{(1 + \lambda)(1 + \lambda^2)}{16} + \frac{1 + \lambda}{4} F_{00}^{t+1} + \frac{1 - \lambda}{2} \alpha^{t+1}. \quad (6.2.2) \]

From equation (4.3.8):

\[ \gamma_{0UU}, \overline{BU} = \frac{1}{2} \gamma_{0UU}, \overline{UU} + \frac{1}{2} \gamma_{0UU}, \overline{CU}, \quad (6.2.3) \]

and from equation (4.3.2):

\[ \gamma_{0UU}, \overline{UU} = \frac{1}{4}, \]

so that (6.2.3) may be written:

\[ \alpha^{t+2} = \frac{1}{8} + \frac{1}{2} \alpha^{t+1}. \quad (6.2.4) \]

The use of \( \alpha^t \) for \( \gamma_{0UU}, \overline{BU} \) is an abbreviation consistent with remarks on notation in section 5.2. Eliminating \( \alpha \) from (6.2.3), (6.2.4) provides the recurrence relation for the two locus panmictic coefficient:

\[ F_{00}^{t+2} = \frac{3 + \lambda}{4} F_{00}^{t+1} - \frac{1 + \lambda}{8} F_{00}^t + \frac{3 - \lambda + \lambda^2 + \lambda^3}{32}. \quad (6.2.5) \]

Provided the first individual (generation 1) to mate with U
(generation 0) was not inbred:

\[ F_{00}^0 = F_{00}^1 = 1. \]

From previous authors (e.g., Kempthorne, 1957), or from direct substitution of \( \lambda = 1 \) into (6.2.2), the recurrence formula for the (one locus) coefficient of parentage is known to be:

\[ F_0^{t+1} = \frac{1}{4} + \frac{1}{2} F_0^t, \quad F_0^0 = 1. \]  \hspace{1cm} (6.2.6)

Using (6.2.5), (6.2.6) and the fact that \( F_0 = F_0, = F_0 \), the following inbreeding functions for this system are found to be:

\[ F_0^0 = [0, 0, 0, 1]' \]

\[ F_0^1 = [0, 0, 0, 1]' \]

\[ F_0^2 = \begin{bmatrix}
(1 + \lambda + \lambda^2 + \lambda^3)/16 \\
(3 - \lambda - \lambda^2 - \lambda^3)/16 \\
(3 + \lambda - \lambda^2 - \lambda^3)/16 \\
(9 + \lambda + \lambda^2 + \lambda^3)/16
\end{bmatrix} \]

\[ F_0^3 = \begin{bmatrix}
(9 + 2\lambda + 6\lambda^2 + 6\lambda^3 + \lambda^4)/64 \\
(15 - 2\lambda - 6\lambda^2 - 6\lambda^3 - \lambda^4)/64 \\
(15 - 2\lambda - 6\lambda^2 - 6\lambda^3 - \lambda^4)/64 \\
(25 + 2\lambda + 6\lambda^2 + 6\lambda^3 + \lambda^4)/64
\end{bmatrix} \]
\[ F^\infty = \begin{bmatrix}
(3 - \lambda + \lambda^2 + \lambda^3)/4(3-\lambda) \\
(3 - \lambda - \lambda^2 - \lambda^3)/4(3-\lambda) \\
(3 - \lambda - \lambda^2 - \lambda^3)/4(3-\lambda) \\
(3 - \lambda + \lambda^2 + \lambda^3)/4(3-\lambda)
\end{bmatrix} .
\]

In each generation therefore, when \( \lambda = 1 \), \( F_{00}^\infty = F_0 = F_{0}^\cdot \) which is to be expected as completely linked genes are transmitted as one unit. When \( \lambda = 0 \), \( F_{00}^\infty = F_0 = F_{0}^\cdot \), which shows that in the absence of linkage the two genes are transmitted independently.

A more practical case may now be considered. This mating scheme is often used when the initial pair \( U \) and \( V \) are unrelated but each has double identity. Each is completely inbred. Equation (6.2.1) still holds, but because any two genes from \( U \) at one locus must now be identical, \( \theta_{00UU} = \gamma_{00U}, \overline{\theta U} = 0 \). The desired recurrence formula is then, from (6.2.2):

\[
F_{00}^{t+2} = \frac{1+\lambda}{4} F_{00}^{t} . \tag{6.2.7}
\]

The corresponding one locus equation is thus:

\[
F_{0}^{t+2} = \frac{1}{2} F_{0}^{t+1} . \tag{6.2.8}
\]

These last two equations may now be combined to provide the recurrence relation for the vector \( F \). For convenience, the superscripts \( t, t+1 \) are used.
$$F^{t+1} = \begin{bmatrix}
1 & \frac{1}{2} & \frac{1}{2} & \frac{1+\lambda}{4} \\
0 & \frac{1}{2} & 0 & \frac{1-\lambda}{4} \\
0 & 0 & \frac{1}{2} & \frac{1-\lambda}{4} \\
0 & 0 & 0 & \frac{1+\lambda}{4}
\end{bmatrix} F^t,$$

(6.2.9)

$$F^1 = [0, 0, 0, 1]^T.$$

This system is very similar to self mating. The appropriate transition equation for selfing follows immediately from (4.3.1):

$$F^{t+1} = \Theta F^t.$$

The matrix $\Theta$ differs from that in (6.2.9) only by having each $\lambda$ replaced by $\lambda^2$. This form of repeated parent-offspring mating differs from selfing then only when linkage is neither absent nor complete ($0 < \lambda < 1$).

6.3 Successive Parent-Offspring Mating

The pedigree is shown in Figure 6.3 and the procedure of section 5.2 is used. Individual A belongs to generation $(t+1)$.

$$F_{00}^{t+1} = \delta_{00CB}$$

$$= \frac{1+\lambda}{4} \left( \delta_{00CC} + \delta_{00CD} \right) + \frac{1-\lambda}{2} \left( \gamma_{00C, CD} \right)$$

i.e.

$$F_{00}^{t+1} = \frac{1+\lambda}{4} \left( \delta^t + F_{00}^t \right) + \frac{1-\lambda}{2} \alpha^t.$$  

(6.3.1)
From equation (4.3.1):

$$\Theta_{OBB} = \frac{1 + \lambda^2}{4} F_{00B}$$

i.e. $$\phi^{t+1} = \frac{1 + \lambda^2}{4} F_{00}^t$$

From equation (4.3.8):

$$\gamma_{OBB, BC} = \frac{1}{n} \left( \gamma_{OOO, CC} + \gamma_{OOD, CC} \right)$$

i.e. $$\alpha^{t+1} = \frac{1}{n} \left( \alpha^t + \beta^t \right)$$

Figure 6.3 Successive parent-offspring mating
From equation (4.3.3):

\[ \gamma_{OOC, BB} = \frac{1}{4} (\theta_{OOC} + \theta_{OCD}) + \frac{1}{2} \gamma_{OOC, CD} \]

i.e. \( \beta^{t+1} = \frac{1}{4} (\phi^t + F_{00}^t) + \frac{1}{2} \alpha^t \). (6.3.4)

The complete set, \( (F_{00}, \phi, \alpha, \beta) \) is thus of order 4, and the transition matrix equation is:

\[
\begin{bmatrix}
F_{00} \\
\phi \\
\alpha \\
\beta
\end{bmatrix}^{t+1} =
\begin{bmatrix}
\frac{1 + \lambda}{4} & \frac{1 + \lambda}{4} & \frac{1 - \lambda}{2} & 0 \\
\frac{1 + \lambda^2}{4} & 0 & 0 & 0 \\
0 & 0 & \frac{1}{4} & \frac{1}{4} \\
\frac{1}{4} & \frac{1}{4} & \frac{1}{2} & 0
\end{bmatrix}
\begin{bmatrix}
F_{00} \\
\phi \\
\alpha \\
\beta
\end{bmatrix}^t.
\] (6.3.5)

For non-inbred unrelated initial individuals, the initial vector is \( u_0^t = [1, 1, 1, 1] \).

The characteristic function for the transition matrix is:

\[ x^4 - \frac{2 + \lambda}{4} x^3 - \frac{2 + \lambda^2 + \lambda^3}{16} x^2 + \frac{1 + 5\lambda + \lambda^2 + \lambda^3}{64} x + \frac{\lambda(1 + \lambda^2)}{128} \]

This leads directly to the following recurrence relation for the two locus pammctic coefficient.

\[
F_{00}^{t+4} = \frac{2 + \lambda}{4} F_{00}^{t+3} + \frac{2 + \lambda^2 + \lambda^3}{16} F_{00}^{t+2} - \frac{1 + 5\lambda + \lambda^2 + \lambda^3}{64} F_{00}^{t+1} - \frac{\lambda(1 + \lambda^2)}{128} F_{00}^t.
\] (6.3.6)
When \( \lambda = 1 \) this reduces to:

\[
F_{00}^{t+2} = \frac{1}{2} F_{00}^{t+1} + \frac{1}{4} F_{00}^t ,
\]

which is the usual one locus equation (Jennings, 1916) so that

\[
F_{00}^{t+1} = F_0^t .
\]

When \( \lambda = 0 \), it reduces to:

\[
F_{00}^{t+3} = \frac{1}{2} F_{00}^{t+2} + \frac{1}{8} F_{00}^{t+1} + \frac{1}{64} F_{00}^t ,
\]

which is satisfied by \( F_{00} F_0 = F_0^2 \) and is the same as the corresponding one for sib mating as given by Cockerhan and Weir (1968). The difference between full sib mating and this scheme of parent-offspring mating with each parent used once, is only reflected in the inbreeding function when linkage is neither complete nor zero.

Table 6.1 gives the value of \( F_{11}^t \) for various generations and linkage values.

Table 6.2 lists \( \mu(\lambda) \), the dominant root of the transition matrix. Values there marked with an asterisk were given by Bennett (1954a). All agree, except that for \( \lambda = 0.90 \) for which Bennett gave the value 0.77154 instead of the correct 0.771158. While his approach was different, the dominant root of his \( 8 \times 8 \) matrix also gave the value of the limiting rate of decrease of double non-identity.
Table 6.1 Values of $F_{11}$ for successive parent-offspring mating

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<th>0.6</th>
<th>0.7</th>
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Table 6.2 Dominant root of transition matrix for successive parent-offspring mating

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<th>λ</th>
<th>μ</th>
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</tr>
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</tr>
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<td>.80902*</td>
</tr>
</tbody>
</table>

*Values also found by Bennett (1954a).
7. GROUP MEASURES

7.1 Definitions

The previous work on inbreeding functions will now be extended to include groups of individuals using the concepts and notations of Cockerham (1967) who extended one locus inbreeding measures for groups. The general pedigree of Figure 1.1 is still appropriate here, except that the letters now refer to groups of individuals rather than single individuals. Groups A, B, ... have $N_A$, $N_B$, ... individuals in them.

Corresponding to the definitions of section 4.1, group measures are defined as:

\[ F_{lA} = \frac{X(ab \in A, a'b' \in A)}{A} \]  
\[ \Theta_{lBC} = \frac{X(ab \in B, a'b' \in C)}{B} \]  
\[ Z_{lB, DE} = \frac{X(ab \in B, a' \in D, b' \in E)}{D} \]  
\[ \delta_{lBC, DE} = \frac{X(a \in B, b \in C, a' \in D, b' \in E)}{E} \]  

Equation (7.1.3), for example, states that ab is a random gamete from a random individual of group B and $a'$, $b'$ are on random gametes from random individuals in groups D and E respectively. $F_{lA}$ is called the group inbreeding function of group A, and $\Theta_{lBC}$ the group coancestry function of groups B and C. The relationship between the two is no longer as simple as that for individual measures, and is considered in the next section.
Each of the group measures is related directly to the individual measures. The group inbreeding function \( F_{-IA} \) demonstrates this. It is the average of \( 2N_A (2N_A - 1) \) probabilities, one for each pairing of the \( 2N_A \) gametes that united to form group A; of these pairs, \( N_A \) are within individuals and the remainder are among individuals. Hence equation (7.1.5):

\[
F_{-IA} = \frac{1}{2N_A - 1} F_{-A} + \frac{2(N_A - 1)}{2N_A - 1} \theta_{-AA}.
\]  

(7.1.5)

The quantity \( F_{-A} \) is the average of the \( N_A \) inbreeding functions of individuals in group A. As it is usual to assign the expected value of the inbreeding function to all members of the group, the bar will be dropped. The quantity \( \theta_{-AA} \) is the average of the \( N_A (N_A - 1)/2 \) coancestry functions of distinct individuals in group A. Once again, the expected value of the coancestry for each pair is the same so that the bar may be dropped. In this case though, the measure will be written \( \theta_{-AA'} \), to emphasize that distinct individuals are involved in the measure.

This notation is extended to the other group measures in the equations below. The subscripts on each of the group measures refer to groups. The subscripts on each individual measure refer to individuals within groups, and primes denote distinct individuals. Each individual measure is an average value—the averages being for all individuals within groups.

\[
\theta_{-BC} = \theta_{BC}.
\]  

(7.1.6)

\[
\theta_{-AA} = \frac{1}{N_A} \theta_{AA} + \frac{N_A - 1}{N_A} \theta_{AA'}.
\]  

(7.1.7)
\[ \chi_{IB, \text{ GH}} = \chi_{B, \text{ GH}} \] (7.1.8)

\[ \chi_{IB, \text{ CC}} = \frac{1}{N_C} \chi_{B, \text{ CC}} + \frac{N_C - 1}{N_C} \chi_{B, \text{ CC'}}. \] (7.1.9)

\[ \chi_{IB, \text{ BC}} = \frac{1}{N_B} \chi_{B, \text{ BC}} + \frac{N_B - 1}{N_B} \chi_{B, \text{ B'C}}. \] (7.1.10)

\[ \chi_{IA, \text{ AA}} = \frac{1}{N_A^2} \chi_{A, \text{ AA}} + \frac{N_A - 1}{N_A^2} (\chi_{A', \text{ AA}} + 2 \chi_{A, \overline{\text{AA'}}}) \]
\[ + \frac{(N_A - 1)(N_A - 2)}{N_A^2} \chi_{A, \overline{\text{AA''}}}. \] (7.1.11)

\[ \delta_{DE, \text{ GH}} = \delta_{DE, \text{ GH}}. \] (7.1.12)

\[ \delta_{DE, \text{ BC}} = \frac{1}{N_D} \delta_{DB, \text{ BC}} + \frac{N_D - 1}{N_D} \delta_{DE, \text{ D'C}}. \] (7.1.13)

\[ \delta_{IB, \text{ CC}} = \frac{1}{N_C} \delta_{B, \text{ CC}} + \frac{N_C - 1}{N_C} \delta_{B, \text{ CC'}} + \frac{N_B - 1}{N_B} \delta_{B', \text{ CC'}}. \] (7.1.14)

\[ \delta_{IB, \text{ BC}} = \frac{1}{N_B} \delta_{B, \text{ BC}} + \frac{N_C - 1}{N_B} \delta_{B, \text{ BC'}} + \frac{N_{B'C} - 1}{N_B} \delta_{B'C, \text{ B'C'}}. \] (7.1.15)
\[ \delta_{BB, BC} = \frac{1}{N_B^2} \delta_{BB, BC} + \frac{N_B - 1}{N_B^2} \left( \delta_{BB', BC} + 2\delta_{BB, BC'} \right) \]

\[ = \frac{(N_B - 1)(N_B - 2)}{N_B^2} \delta_{BB', BC'} \tag{7.1.16} \]

\[ \delta_{AA, AA} = \frac{1}{N_A^3} \delta_{AA, AA} + \frac{N_A - 1}{N_A^3} \left( \delta_{AA, AA'} + 2\delta_{AA', AA'} \right) \]

\[ + \frac{2(N_A - 1)(N_A - 2)}{N_A^3} \left( \delta_{AA', AA''} + \delta_{AA', AA'''} \right) \]

\[ + \frac{(N_A - 1)(N_A - 2)(N_A - 3)}{N_A^3} \delta_{AA', AA'''} \tag{7.1.17} \]

### 7.2 General Expansions

Two rules given by Cockerham (1967) will be restated here. They are:

1. The numbers of gametes in uniting input sets are equal,
2. Gametes from one input set unite at random with gametes from the other input set.

With these rules it is clear that the probability of a random gamete in one uniting set being identical by descent with a random gamete in the other uniting set is the same as the inbreeding function of an individual in the offspring group, and as the coancestry function of the parental groups. For Figure 1.1 for example:

\[ F_A = \delta_{IBC} \tag{7.2.1} \]
For the same pedigree, the expansion of the remaining three group measures proceeds just as in section 4.2. For example:

\[
\Theta_{\ell BC} = \frac{1 + \lambda}{4} (\Theta_{\ell BG} + \Theta_{\ell BH}) + \frac{1 - \lambda}{4} (\gamma_{\ell B, GH} + \gamma_{\ell B, HG}),
\]

\[
\gamma_{\ell B, GH} = \frac{1 + \lambda}{4} (\gamma_{\ell D, GH} + \gamma_{\ell E, GH}) + \frac{1 - \lambda}{4} (\delta_{\ell DE, GH} + \delta_{\ell ED, GH}),
\]

\[
\delta_{\ell DE, GH} = \frac{1}{2} (\delta_{\ell KE, GH} + \delta_{\ell LE, GH}).
\]

These general expansions only apply for group measures for different groups. This is evident from equations (7.1.6), (7.1.8) and (7.1.12), where it is seen that these group measures are the averages of individual measures that could be expanded by the general methods of section 4.2.

When the group measures involve gametes from the same group however, the remaining equations at the end of the last section show that they are functions of the special individual measures which were expanded in section 4.3. Whenever one group provides more than one gamete for a measure, there is the possibility that these gametes come from the same individual and thus may be automatically identical. The next section will consider these cases.

### 7.3 Special Expansions

Unlike the individual measures, group measures with repeated subscripts depend upon the gametic sampling plan appropriate to the system. Two basic sampling plans will be considered: independent and combined sampling of gametic sets from the same group.
For the independent sampling plan, the probability that any individual of a parental group contributes a random gamete in an output set of gametes is the same for all members and not dependent on gametes in the other output sets from the same group. In the combined sampling plan, all output gametes from one group are considered together, rather than in separate output sets.

In independent sampling situations it may happen that every parent contributes two gametes to the next generation. For a dioecious system with equal numbers of males and females this would be the case if every parent gave exactly one gamete to one offspring of each sex. Thus, if A is a group of males, and B is its group of fathers, the two gametes for $\theta_{AA}'$ cannot both have originated from one member of B --each father has only one son. The expansion of $\theta_{AA}'$ then cannot include the group measure $\theta_{BB}'$. Instead a new class of measures--gametic set measures--which take account of the gametic sampling plan, must be defined. These are:

$$y_{X, Y}^{BC} = X(ab, a'b' \text{ are two gametes received by groups } x, y \text{ from parental groups } B, C \text{ respectively}),$$

$$y_{X, Y}^{BC} = X(ab, a', b' \text{ are three gametes received by groups } x, y, z \text{ from parental groups } B, D, E \text{ respectively}),$$

$$y_{X, Y}^{BC} = X(a, b, a', b' \text{ are four gametes received by groups } x, y, z, w \text{ from parental groups } B, C, D, E \text{ respectively}).$$

These gametic set measures can differ from the three group measures only when at least one parental group gives more than one gamete
to an offspring group. While the expansion of $\Theta_{BC}$ may be made in terms of group measures, such as $\Theta_{iDH}$ (Figure 1.1), the expansion of $\Theta_{BB}$ must involve gametic set measures, such as $\Psi_{BB}$. For combined sampling of gametes however, all output gametes are considered together, so that, if the subdivision of the combined set into input sets for various offspring groups is random with respect to parents, the gametic set measures must be equal to the corresponding group measures.

For combined sampling schemes in this work then, for example,

$$\Psi_{BC} = \Theta_{iBC} \text{ for all } x, y.$$ 

Notwithstanding this sometime equivalence of gametic set measures and group measures, expansion of the individual measures appearing in equations (7.1.6), . . . , (7.1.17) will be given in terms of gametic set measures. Once again tables showing identity relations between gametic arrays may be used to obtain the expansions. The subscripts on gametic arrays for ab, a'b' now refer to groups instead of individuals though. The pedigree of Figure 1.1 is still appropriate.

From Table 7.1, the expansion of $\Theta_{AA'}$ for a group pedigree is:

$$\Theta_{AA'} = \left(\frac{1 + \lambda}{4}\right)^2 \left(\Psi_{BB} + \frac{\Psi_{BA} + 2\Psi_{CA} + \Psi_{CC}}{4}\right)$$

$$+ \frac{1 - \lambda^2}{8} \left(\Psi_{BA} + \frac{\Psi_{BA} + \Psi_{CA} + \Psi_{CA}}{4}\right) + \frac{(1 - \lambda)^2}{4} \frac{\Psi_{BA}}{4} \frac{\Psi_{BA}}{4} \frac{\Psi_{CA}}{4}.$$ 

(7.3.1)
7.3.1 $\chi_{B', C'C'}$

The expansion of the trigametic measure $\chi_{B', C'C'}$ is shown in equation (7.3.2). In that equation the dot subscript for individual B means that the particular offspring group that the gamete from group B goes to can have no influence on the measure concerned.

$$\chi_{B', C'C'} = \frac{1}{4} (\nu_B, C_G C_c + \nu_B, H_C H_c + 2 \nu_B, C_c H_c) .$$  \hfill (7.3.2)

The measure $\delta_{BB', C'C'}$ has the same expansion, and $\delta_{BB', C'C}$ has a similar one.

7.3.2 $\Theta_{AA'}$

Table 7.1 Expansion of $\Theta_{AA'}$

<table>
<thead>
<tr>
<th>$a'b'$</th>
<th>$\frac{1 + \lambda}{4}$</th>
<th>$\frac{1 + \lambda}{4}$</th>
<th>$\frac{1 - \lambda}{4}$</th>
<th>$\frac{1 - \lambda}{4}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\Theta_{AA'}$</td>
<td>$a_B b_B$</td>
<td>$a_C b_C$</td>
<td>$a_B b_C$</td>
<td>$a_C b_B$</td>
</tr>
<tr>
<td>$\frac{1 + \lambda}{4} a_{B'C'}$</td>
<td>$\Psi_{B'A} A_A$</td>
<td>$\Psi_{B'A} C_A$</td>
<td>$\nu_{B'A}, B_A C_A$</td>
<td>$\nu_{B'A}, C_A A_A$</td>
</tr>
<tr>
<td>$\frac{1 + \lambda}{4} a_{C'B'}$</td>
<td>$\Psi_{C'A} A_A$</td>
<td>$\Psi_{C'A} C_A$</td>
<td>$\nu_{C'A}, B_A C_A$</td>
<td>$\nu_{C'A}, C_A A_A$</td>
</tr>
<tr>
<td>$\frac{1 - \lambda}{4} a_{B'C'}$</td>
<td>$\nu_{B'A}, B_A C_A$</td>
<td>$\nu_{C'A}, B_A C_A$</td>
<td>$\kappa_{B'A}, B_A C_A$</td>
<td>$\kappa_{C'A}, B_A C_A$</td>
</tr>
<tr>
<td>$\frac{1 - \lambda}{4} a_{C'B'}$</td>
<td>$\nu_{B'A}, C_A A_A$</td>
<td>$\nu_{C'A}, C_A A_A$</td>
<td>$\kappa_{C'A}, B_A C_A$</td>
<td>$\kappa_{C'A}, C_A A_A$</td>
</tr>
</tbody>
</table>
7.3.3 $s_{BB', CC'}$

The expansion of a quadrigametic measure for a group pedigree is shown in equation (7.3.3).

\[
\begin{align*}
    s_{BB', CC'} &= \frac{1}{16} \left( \xi_{D_B D_B'} C_C C_C + \xi_{D_B D_B'} H_C H_C + \xi_{E_B E_B'} C_C C_C \\
    &\quad + \xi_{E_B E_B'} H_C H_C \right) \\
    &\quad + \frac{1}{8} \left( \xi_{D_B D_B'} C_C H_C + \xi_{E_B E_B'} C_C H_C + \xi_{H_C H_C} D_B E_B - 3 \xi_{E_B E_B'} C_C H_C \right) \\
    &\quad + \frac{1}{4} \xi_{D_B D_B'} H_C C_C .
\end{align*}
\]

(7.3.3)

There is little point in listing all possible transition equations. In the next chapter, where examples are considered, those expansions that are needed will be shown. The next step is to derive expressions for the various probabilities of gametes originating from the same or different parents.

7.4 Gametic Sampling Probabilities

For a group B with $N_B$ members, there are seven probabilities to be defined. These are for the possible origins of the gametes:

\[
\begin{align*}
P_{B_1} &= \text{Prob(two gametes from one individual in group B)}, \\
P_{B_2} &= \text{Prob(three gametes from one individual in group B)}, \\
P_{B_3} &= \text{Prob(three gametes from two individuals in group B)},
\end{align*}
\]
\[ P_{B_4} = \text{Prob(four gametes from one individual in group B)}, \]
\[ P_{B_5} = \text{Prob(three gametes from one individual and one gamete from another individual in group B)}, \]
\[ P_{B_6} = \text{Prob(two gametes from each of two individuals in group B)}, \]
\[ P_{B_7} = \text{Prob(two gametes from one individual, and one gamete from each of two other individuals in group B)}. \]

The remaining three possible origins for the gametes are: two gametes from two individuals in group B (with probability \(1 - P_{B_1}\)), three gametes from three individuals in group B (with probability \(1 - P_{B_2} - P_{B_3}\)), and four gametes from four individuals in group B (with probability \(1 - P_{B_4} - P_{B_5} - P_{B_6} - P_{B_7}\)).

For independent sampling of gametic sets, in one set let \(k_i\) be the number of gametes contributed by the \(i^{th}\) parent. If this set is an input set for group A, the total number of gametes is the same as the number of offspring:

\[ \sum k_i = N_A, \]

with a mean of

\[ k_{AB} = \frac{\sum k_i}{N_B} = \frac{N_A}{N_B}. \]

For combined sampling, \(k_i\) will refer to the total number of gametes contributed by the \(i^{th}\) individual, and A will refer to the total collection of offspring individuals.

Each summation in the expressions for the seven probabilities listed below is over the integers 1 to \(N_B\).
\[ P_{B_1} = \frac{\sum k_i(k_i-1)}{N_B \bar{\kappa}_{AB} (N_B \bar{\kappa}_{AB} - 1)} , \]

\[ P_{B_2} = \frac{\sum k_i(k_i-1)(k_i-2)}{N_B \bar{\kappa}_{AB} (N_B \bar{\kappa}_{AB} - 1)(N_B \bar{\kappa}_{AB} - 2)} , \]

\[ P_{B_3} = \frac{3 \sum k_i(k_i-1)(N_B \bar{\kappa}_{AB} - k_i)}{N_B \bar{\kappa}_{AB} (N_B \bar{\kappa}_{AB} - 1)(N_B \bar{\kappa}_{AB} - 2)} , \]

\[ P_{B_4} = \frac{\sum k_i(k_i-1)(k_i-2)(k_i-3)}{N_B \bar{\kappa}_{AB} (N_B \bar{\kappa}_{AB} - 1)(N_B \bar{\kappa}_{AB} - 2)(N_B \bar{\kappa}_{AB} - 3)} , \]

\[ P_{B_5} = \frac{4 \sum k_i(k_i-1)(N_B \bar{\kappa}_{AB} - k_i)}{N_B \bar{\kappa}_{AB} (N_B \bar{\kappa}_{AB} - 1)(N_B \bar{\kappa}_{AB} - 2)(N_B \bar{\kappa}_{AB} - 3)} , \]

\[ P_{B_6} = \frac{3 \sum k_i(k_i-1)k_j(k_j-1)}{N_B \bar{\kappa}_{AB} (N_B \bar{\kappa}_{AB} - 1)(N_B \bar{\kappa}_{AB} - 2)(N_B \bar{\kappa}_{AB} - 3)} , \]

\[ P_{B_7} = \frac{6 \sum k_i(k_i-1)k_j(N_B \bar{\kappa}_{AB} - k_i - k_j)}{N_B \bar{\kappa}_{AB} (N_B \bar{\kappa}_{AB} - 1)(N_B \bar{\kappa}_{AB} - 2)(N_B \bar{\kappa}_{AB} - 3)} . \]

If each of the \( k_i \) are identically distributed, each of the probabilities can be replaced by its expected value, making use of these central moments:

\[ \sigma_{AB}^2 = E(\sum_{i} k_i - \bar{\kappa}_{AB})^2/N_B , \]

\[ m_{22}^{AB} = E(\sum_{i \neq j} (k_i - \bar{\kappa}_{AB})^2 (k_j - \bar{\kappa}_{AB})^2/N_B) , \]
\begin{align*}
\Delta m_{2}^{2} & = E\left( \sum_{i} (k_{\downarrow} - k_{AB})^{3}/N_{B} \right), \\
\Delta m_{4}^{2} & = E\left( \sum_{i} (k_{\downarrow} - k_{AB})^{4}/N_{B} \right). \\
\text{The probabilities now take the form:} \\
\frac{P_{B_1}}{P_{B_2}} & = \frac{\frac{\sigma^{2}_{AB} + k_{AB}(k_{AB} - 1)}{k_{AB}(N_{B} / k_{AB} - 1)} - 3(k_{AB} - 1)\sigma^{2}_{AB} + k_{AB}(k_{AB} - 1)(k_{AB} - 2)}{\frac{\sigma^{2}_{AB} + k_{AB}(k_{AB} - 1)}{k_{AB}(N_{B} / k_{AB} - 1)(N_{B} / k_{AB} - 2)}}, \\
\frac{P_{B_3}}{P_{B_2}} & = \frac{3(P_{B_1} - P_{B_2})}{P_{B_4}} \\
\frac{P_{B_5}}{P_{B_4}} & = \frac{\sigma^{2}_{AB} + 2(2k_{AB} - 3)m_{3}^{2}_{AB} + \frac{6(k_{AB} - 1)\sigma^{2}_{AB} + k_{AB}(k_{AB} - 1)(k_{AB} - 2)(k_{AB} - 3)}{k_{AB}(N_{B} / k_{AB} - 1)(N_{B} / k_{AB} - 2)(N_{B} / k_{AB} - 3)},} \\
\frac{P_{B_6}}{P_{B_5}} & = \frac{3(N_{B} - 1)m_{22}^{2}_{AB} + 6(1 - 2k_{AB})m_{3}^{2}_{AB} + \frac{3[2N_{B} \sigma_{AB}(k_{AB} - 1) - (6k_{AB} - 6k_{AB}^{2}) + 1] \sigma^{2}_{AB} + 3(N_{B} - 1)k_{AB}^{2}(k_{AB} - 1)^{2}}{k_{AB}(N_{B} / k_{AB} - 1)(N_{B} / k_{AB} - 2) / k_{AB}(N_{B} / k_{AB} - 1)(N_{B} / k_{AB} - 2)} - 2)}/(N_{B} / k_{AB} - 3),}
\end{align*}
\[ P_{B_7} = \left( 6m_{AB}^4 - 6(N_B - 1)m_{AB}^2 + 12(\frac{4}{5}k_{AB}^2 - N_B k_{AB} - 1)m_{AB}^3 + 6(12k_{AB}^2 - 8N_B k_{AB} - 6k_{AB}^2 + 2N_B k_{AB} + 2N_B k_{AB}^2 + 3N_B k_{AB}) + 6k_{AB}^3 (k_{AB}^{-1})(N_B - 1)(N_B - 2) \right) / k_{AB}^2 (N_B k_{AB} - 1)(N_B k_{AB} - 2)(N_B k_{AB} - 3). \]

Note that the reciprocal of \( P_{B_1} \) is usually called the (two gamete) effective population number (Wright, 1931). Similarly, the reciprocals of \( P_{B_2} \) and \( P_{B_4} \) could be called three and four gamete effective population numbers respectively for group B.

When two groups are considered, additional probabilities are needed. For groups B and C with \( N_B \) and \( N_C \) members respectively:

\[ P_{BC_1} = \text{Prob(} \text{two gametes from one individual in group B, and two gametes from one individual in group C)}, \]

\[ P_{BC_2} = \text{Prob(} \text{two gametes from one individual in group B, and two gametes from two individuals in group C)}, \]

\[ P_{BC_3} = \text{Prob(} \text{two gametes from two individuals in group B, and two gametes from one individual in group C}). \]

Hence, for two gametes from two individuals in group B, and two gametes from two individuals in group C, the probability is

\[ 1 - P_{BC_1} - P_{BC_2} - P_{BC_3}. \]

Sampling within one group is supposed to be independent of that in another group, so:
\[ p_{B_1} = \frac{P_B}{P_C}, \quad (7.4.1) \]
\[ p_{B_2} = P_B \left(1 - \frac{P_C}{P_C}\right), \quad (7.4.2) \]
\[ p_{B_3} = \left(1 - \frac{P_B}{P_C}\right) \frac{P_C}{P_C}. \quad (7.4.3) \]

Two gametic distributions commonly considered are "equal chance" and a distribution as close as possible to a constant number of gametes per parent.

For equal chance, each member of a group has equal probability of providing any of the gametes in an output set of that group.

For the gametic set transmitted from B to A then, the \( k_1 \) are distributed binomially \( Bi(N_B, \frac{k_{AB}}{N_B}, \frac{1}{N_B}) \) and the central moments are:

\[ \sigma_{AB}^2 = \frac{k_{AB}(N_B - 1)}{N_B}, \]
\[ m_{22}_{AB} = \frac{k_{AB}^2(N_B^2 - 2N_B + 3)}{N_B^2} - \frac{k_{AB}^2(N_B^2 - 4N_B + 6)}{N_B^2}, \]
\[ m_{33}_{AB} = \frac{k_{AB}(N_B - 1)(N_B - 2)}{N_B}, \]
\[ m_{44}_{AB} = 3\frac{k_{AB}^2(N_B - 1)^2}{N_B^2} + \frac{k_{AB}(N_B - 1)(N_B^2 - 6N_B + 6)}{N_B^2}. \]

Substitution of these values into the above definitions leads to:

\[ p_{B_1} = \frac{1}{N_B}, \quad (7.4.4) \]
\[ p_{B_2} = \frac{1}{N_B^2}, \quad (7.4.5) \]
\[ p_{B_3} = 3(N_B - 1)/N_B^2, \quad (7.4.6) \]
\[ P_{B_4} = \frac{1}{N_B^3}, \quad (7.4.7) \]

\[ P_{B_5} = \frac{4(N_B-1)}{N_B^3}, \quad (7.4.8) \]

\[ P_{B_6} = \frac{3(N_B-1)}{N_B^3}, \quad (7.4.9) \]

\[ P_{B_7} = \frac{6(N_B-1)(N_B-2)}{N_B^3}. \quad (7.4.10) \]

The other special case considered may be where every member of B contributes exactly the same number of gametes. All moments about the mean of the \( k_1 \) distribution are then zero, and the probabilities become:

\[ P_{B_1} = \frac{k_{AB}^{-1}}{N_B k_{AB}^{-1}}, \]

\[ P_{B_2} = \frac{(k_{AB}^{-1})(k_{AB}^{-2})}{(N_B k_{AB}^{-1})(N_B k_{AB}^{-2})}, \]

\[ P_{B_3} = 3(P_{B_1} - P_{B_2}) \]

\[ P_{B_4} = \frac{(k_{AB}^{-1})(k_{AB}^{-2})(k_{AB}^{-3})}{(N_B k_{AB}^{-1})(N_B k_{AB}^{-2})(N_B k_{AB}^{-3})}, \]

\[ P_{B_5} = 4(P_{B_2} - P_{B_4}). \]
\[ p_{B_6} = \frac{3 k_{AB}(N_B - 1)(k_{AB} - 1)^2}{(N_B k_{AB} - 1)(N_B k_{AB} - 2)(N_B k_{AB} - 3)} \]

\[ p_{B_7} = \frac{6k_{AB}^2(N_B - 1)(N_B - 2)}{(N_B k_{AB} - 1)(N_B k_{AB} - 2)(N_B k_{AB} - 3)} \]

In combined sampling plans, and equal sized groups, \( k_{AB} = 2 \), so that the probabilities are:

\[ p_{B_1} = 1/(2N_B - 1) \] \hspace{2cm} (7.4.11)

\[ p_{B_2} = 0 \] \hspace{2cm} (7.4.12)

\[ p_{B_3} = 3/(2N_B - 1) \] \hspace{2cm} (7.4.13)

\[ p_{B_4} = 0 \] \hspace{2cm} (7.4.14)

\[ p_{B_5} = 0 \] \hspace{2cm} (7.4.15)

\[ p_{B_6} = 3/(2N_B - 1)(2N_B - 3) \] \hspace{2cm} (7.4.16)

\[ p_{B_7} = 12(N - 2)/(2N_B - 1)(2N_B - 3) \] \hspace{2cm} (7.4.17)

For independent sampling plans, each parent generally gives just one gamete to an output set, so \( k_{AB} = 1 \), and:

\[ p_{B_1} = 0 \quad i = 1, \ldots, 7 \] \hspace{2cm} (7.4.18)

A result that follows almost trivially from definitions can now be shown for the three measures \( \Psi, \nu, \kappa \). Consider \( \Psi_{B_1}^{B_A A_A} \) for example.

From its definition, and that of the above probabilities:

\[ \Psi_{B_1}^{B_A A_A} = p_{B_1}^{BB} \theta_{BB} + (1 - p_{B_1}) \theta_{BB}' \] \hspace{2cm} (7.4.18)
For equal chance gamete distribution, $P_{BA} = \frac{1}{N_B}$ from (7.4.4) so that (7.4.18) just reduces to (7.3.1). In other words:

$$\Psi_{BA,BA} = \frac{\theta}{BB} .$$

The same procedure for the other two measures leads to:

$$\Psi_{B'BA, B'BA} = P_{B2} \frac{\delta}{BB} + P_{B3} (\frac{\gamma}{BB}, BB + \frac{\gamma}{BB}, BB) / 3$$

$$+ (1 - P_{B2} - P_{B3}) \frac{\gamma}{BB}, B'B''$$

$$= \frac{\gamma}{BB}, BB'$$

$$\Xi_{B'BA, B'BA} = P_{B4} \frac{\delta}{BB}, BB + P_{B5} \frac{\delta}{BB}, BB + P_{B6} \frac{\delta}{BB}, B'B'$$

$$+ 2 \frac{\delta}{BB}, \frac{BB'}{BB'} / 3 + P_{B7} \frac{\delta}{BB}, B'B''$$

$$+ 2 \frac{\delta}{BB}, \frac{BB''}{BB''} / 3 + (1 - P_{B4} - P_{B5} - P_{B6})$$

$$- P_{B7} \frac{\delta}{BB'}, B''B''$$

$$= \frac{\delta}{BB}, BB' .$$

Similar equations lead to the result that, for equal chance gamete formation, there is no difference between group measures and gametic set measures, and hence no difference between various sampling plans.

For one gamete per parent to a particular offspring group,

$$\Psi_{BA,BA} = \frac{\theta}{BB'} ,$$

and both of $\Psi_{B'BA, B'BA}$ and $\Xi_{B'BA, B'BA}$ must be zero.
There is now sufficient theory developed to consider some examples, as in the next chapter.
8. EXAMPLES OF GROUP MATING SYSTEMS

8.1 Monoecious Populations: General Sampling Scheme

The group measures are now applied to finite monoecious populations. Inbreeding arises because of the finite size of each generation (group). The mating scheme is shown in Figure 8.1, where B, C are the groups of individuals comprising generations t, t+1 respectively. With sexuality of gametes, gametic sets are involved, and the numbers of each, male and female, must be the same.

There is only one group in each generation, and hence only three types of group measures: \( \Theta_{lBB}, \gamma_{lB, BB} \) and \( \delta_{lBB, BB} \). The number of gametic set measures however is nine. These, together with an abbreviated notation, are now listed.

\[
\begin{align*}
\text{B} & \quad t \quad \text{C} \quad t+1 \\
\end{align*}
\]

Figure 8.1 Monoecious mating
\[ \Delta_{\alpha}^{t+1} = \frac{\Gamma_{m}^{t+1}}{\Gamma_{m}^{t+1}} = \frac{\psi_{B_{m}B_{f}}^{t+1}}{\psi_{B_{m}B_{f}}^{t+1}} , \]

\[ \Lambda_{\alpha}^{t+1} = \frac{\psi_{B_{m}B_{m}}^{t+1}}{\psi_{B_{m}B_{m}}^{t+1}} = \frac{\psi_{B_{f}B_{m}}^{t+1}}{\psi_{B_{f}B_{m}}^{t+1}} , \]

\[ \Delta_{\beta}^{t+1} = \frac{\psi_{B_{m}B_{f}}^{t+1}}{\psi_{B_{m}B_{f}}^{t+1}} = \frac{\psi_{B_{f}B_{f}}^{t+1}}{\psi_{B_{f}B_{f}}^{t+1}} , \]

\[ \Lambda_{\beta}^{t+1} = \frac{\psi_{B_{m}B_{f}}^{t+1}}{\psi_{B_{m}B_{f}}^{t+1}} = \frac{\psi_{B_{m}B_{m}}^{t+1}}{\psi_{B_{m}B_{m}}^{t+1}} , \]

In these equations, an \( m \) subscript indicates a male gamete and an \( f \) denotes a female gamete. Because there are the same number of male and female gametes formed each generation, there is nothing to be gained by distinguishing between, say, \( \psi_{B_{m}B_{m}}^{t+1} \) and \( \psi_{B_{m}B_{f}}^{t+1} \). Instead they are given the common value \( \Delta_{\alpha}^{t+1} \). As any male and any female gamete from group B may unite to form an individual in generation \((t+1)\):
\[ P_C = \frac{T_{t+1}}{F} = \frac{\psi_{B_m} B_f}{T_{t+1}}. \]

Hence the measure \( T_{t+1} \) is just the inbreeding function, and this is the function the value of which is to be determined.

Each of the nine gametic set measures will now be expressed in terms of individual measures, making use of the probabilities defined in section 7.4.

The two digametic measures each have the form of equation (8.1.1), where \( B \) and \( B' \) are any distinct individuals in group \( B \). Until the gametic sampling plan is specified, the values of \( P_B \) appropriate for \( T_1 \) and \( T_2 \) cannot be given. They may of course be different.

\[ T_{t+1} = P_B \frac{\theta_{BB}}{t} + (1-P_B) \frac{\theta_{BB'}}{t} \quad i = 1, 2. \quad (8.1.1) \]

If \( B, B', B'' \) are any three distinct individuals of group \( B \), then equation (8.1.2) holds for each of the trigametic measures.

\[ \Gamma_{t+1} = P_B \gamma_B, BB + P_B \left( \gamma_{B', BB'} + 2 \gamma_{B', BB''} \right) + (1-P_B - P_{B''}) \left( \gamma_{B', BB''} \right) \quad i = 1, 2, 3. \quad (8.1.2) \]

The four quadrigametic measures have the form of equation (8.1.3), where \( B, B', B'', B''' \) are any four distinct individuals of group \( B \).

\[ \Delta_{t+1} = P_B \delta_{BB}, BB + P_B \left( \delta_{BB}, BB'' \right) + P_B \left( 2 \delta_{BB}, BB'' \right) \]

\[ + (1-P_B - P_{B''}) \frac{\delta_{BB'}}{3} + P_B \left( 2 \delta_{BB'}, BB'B'' \right) + \frac{\delta_{BB''}}{3} \]

\[ + (1-P_B - P_{B''}) \frac{\delta_{BB'}}{3} + P_B \left( 2 \delta_{BB'}, BB'B'' \right) + \frac{\delta_{BB''}}{3} \]

\[ \quad i = 1, 2, 3, 4. \quad (8.1.3) \]
There are thus thirteen individual measures to expand back in terms of gametic set measures of the previous generation. The methods for obtaining such expansions were outlined in the previous chapter. They are all listed in Table 8.1 where, for convenience, just the fourth component of individual and gametic set measures are shown. The double zero subscript has been dropped.

When the sampling plan is specified, values of the probabilities $P_{B_1}$ can be given, and equations (8.1.1), (8.1.2) and (8.1.3) together with Table 8.1 lead to simultaneous transition equations for the gametic set measures. At this stage the methods of Chapter 4 are employed to give values of the inbreeding function for the system. The next two sections consider combined and independent sampling of gametic sets.

Regardless of the sampling plan however, when the groups are single individuals, the system reduces to a selfing pedigree. For any value of $t$ then:

$$F^t + 1 = \Theta B^t + 1 = \Theta F^t$$

from equation (4.3.1). Hence

$$F^t = (\Theta)^t F^0,$$

and if the initial individual was not inbred, so that $F^0 = [0, 0, 0, 1]'$:
Table 8.1 Expansion of individual measures in terms of gametic set measures for a monoocious population

<table>
<thead>
<tr>
<th></th>
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<th>$T_2$</th>
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<th>$\Gamma_2^t$</th>
<th>$\Gamma_3^t$</th>
<th>$\Delta_1^t$</th>
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<td>0</td>
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<tr>
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<td>$\frac{(1+\lambda)^2}{8}$</td>
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<td>$\frac{(1-\lambda)^2}{2}$</td>
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<td>0</td>
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<td>$\frac{(1+\lambda)}{6}$</td>
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<td>$\frac{(1-\lambda)}{6}$</td>
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<td>$\frac{(1+\lambda)}{6}$</td>
<td>0</td>
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<td>$\frac{1}{4}$</td>
<td>$\frac{1}{4}$</td>
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</tbody>
</table>
8.2 Monoecious Populations: Combined Sampling Scheme

Great simplification arises when the combined sampling of gametes is considered—the sex of each gamete being random with respect to its parents. From section 7.3 it is known that the gametic set measures are not different from the group measures in this case. The following relations thus hold:

\[
\begin{align*}
T_{1}^{t+1} &= T_{2}^{t+1} = \theta_{tBB}, \\
\Gamma_{1}^{t+1} &= \Gamma_{2}^{t+1} = \Gamma_{3}^{t+1} = \gamma_{tB}, \quad BB, \\
\Delta_{1}^{t+1} &= \Delta_{2}^{t+1} = \Delta_{3}^{t+1} = \Delta_{4}^{t+1} = \delta_{tBB}, \quad BB.
\end{align*}
\]

The common values of equations (8.2.1), (8.2.2) and (8.2.3) will be labelled \(T^{t+1}\), \(\Gamma^{t+1}\) and \(\Delta^{t+1}\) respectively. Table 8.1 may be modified simply by adding the first two columns and labelling the resulting column \(T^{t}\), and labelling the sum of the third, fourth and fifth columns by \(\Gamma^{t}\) and that of the last four columns by \(\Delta^{t}\). The table now,
together with equations (8.1.1), (8.1.2) and (8.1.3) leads to the transition equations:

$$u_{t+1} = \Omega u_t,$$

where $$u_t' = [T, \Gamma, \Delta]^t$$ and the transition matrix $$\Omega$$ has the form below (equation 8.2.5).

$$\Omega = \begin{bmatrix}
\dfrac{(1+\lambda)^2}{4} - \lambda \dfrac{P_{B_1}}{2} & \dfrac{(1-\lambda^2)(1-P_{B_1})}{2} & \dfrac{(1-\lambda^2)(1-P_{B_1})}{4} \\
\dfrac{P_{B_2}}{4} + \dfrac{(1+\lambda)P_{B_2}}{12} & \dfrac{(1+\lambda)(1-P_{B_1})}{2} - \lambda \dfrac{P_{B_2}}{2} & \dfrac{(1-\lambda)(1-P_{B_2})}{2} - \dfrac{5(1-\lambda)P_{B_3}}{12} \\
\dfrac{P_{B_4}}{4} + \dfrac{P_{B_6}}{6} & \dfrac{P_{B_5}P_{B_6}P_{B_7}}{3} & \dfrac{1-P_{B_4}-P_{B_5}-3P_{B_6}}{4} - \dfrac{P_{B_7}}{2}
\end{bmatrix}$$

(8.2.5)

Now if each generation is constrained to be of the same size, so that the mean number of gametes per parent is $$k = 2$$, the probabilities $$P_{B_1}, \ldots, P_{B_7}$$ are constant for all generations, so that $$\Omega$$ is the same for all generations and (8.2.4) holds for all consecutive generations $$t, t+1$$. The initial vector is $$u_0' = [1, 1, 1]$$.

For an equal chance gametic distribution, ($$k = 2$$), the values of $$P_{B_1}, \ldots, P_{B_7}$$ were given in equations (7.1.4), \ldots, (7.1.10) and substitution of these into equation (8.2.5) gives the following transition matrix (equation 8.2.6).
\[
\Omega = \begin{bmatrix}
\frac{(1+\lambda)^2}{4} - \frac{\lambda}{2N} & \frac{(N-1)(1-\lambda^2)}{2N} & \frac{(N-1)(1-\lambda)^2}{4N} \\
\frac{(1+\lambda)}{4N} - \frac{\lambda}{4N^2} & \frac{(N-1)(N+1+\lambda(N-2))}{2N^2} & \frac{(N-1)(1-\lambda)(2N-3)}{4N^2} \\
\frac{(2N-1)}{4N^3} & \frac{(N-1)(2N-1)}{N^3} & \frac{(N-1)(2N-1)(2N-3)}{4N^3}
\end{bmatrix}.
\]

The common size of each generation has been written as \( N \). The recurrence formula for the two locus panmictic coefficient goes back three generations. For complete linkage however it reduces to:

\[
T^{t+1} = \left( \frac{2N-1}{2N} \right) T^t,
\]

or:

\[
F_{00}^{t+1} = \left( \frac{2N-1}{2N} \right) F_{00}^t,
\]

which is the usual (one locus) panmictic coefficient equation (Wright, 1931). Setting \( \lambda = 0 \) however does not lead to an equation satisfied by \( F_0 \). \( F_0 \) as was the case for pedigree systems of mating (section 5.3).

For any group mating scheme, for an offspring \( A \) of parental groups \( B \) and \( C \):

\[
F_{00A}(\lambda) = \theta_{\text{XO}BC}(\lambda) = \sum_i p_i x_{100}(\lambda),
\]

where the sum is over a number of individual measures \( x_i \) which may be di-, tri-, or quadrigametic. The coefficients \( p_i \) are just the probabilities introduced in section 7.4. Since
\[ \sum_{i} p_i x_{100}(0) \neq (\sum_{i} p_i x_{100}(1))^2, \]

then

\[ F_{00A}^{(0)} \neq (F_{00}^{(1)})^2. \]

This matter will be discussed later.

The equal chance system was studied numerically, and values of the dominant root of the transition matrix are listed in Table 8.2. There the root is clearly a monotone function of \( \lambda \) as discussed previously. It is also a monotone increasing function of \( N \), agreeing with the general result that larger populations are less inbred. Values of the two locus inbreeding function \( F_{11} \) are displayed in Figure 8.2.

If the gametic distribution is such that every parent gives exactly two gametes, the probabilities \( p_{B_1}^+, \ldots, p_{B_7}^+ \) are given by equations (7.4.11), \ldots, (7.4.17), and the transition matrix takes the following form (equation 8.2.7).

\[
\Omega = \begin{bmatrix}
\frac{(1+\lambda)^2}{4} - \frac{\lambda}{2(N-1)} & \frac{(1-\lambda^2)(N-1)}{2N-1} & \frac{(1-\lambda)^2(N-1)}{2(2N-1)} \\
\frac{1+\lambda}{4(2N-1)} & \frac{1}{2} + \frac{\lambda(N-2)}{2N-1} & \frac{(1-\lambda)(4N-7)}{4N-1} \\
\frac{1}{2(2N-1)(2N-3)} & \frac{4N-7}{(2N-1)(2N-3)} & \frac{16N^2 - 56N + 51}{4(2N-1)(2N-3)}
\end{bmatrix}. \quad (8.2.7)
\]

For complete linkage, the recurrence formula for the two locus

panmictic coefficient reduces to:
Table 8.2  Dominant root of transition matrix for monoecious populations with equal chance gamete formation

<table>
<thead>
<tr>
<th>Linkage Parameter, $\lambda$</th>
<th>Population Size, N</th>
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<th>8</th>
<th>16</th>
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</tr>
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<td></td>
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</table>
Figure 8.2 $F_{11}$ for monoecious populations with equal chance gamete formation.
\[ F_{00}^{t+1} = \left( \frac{\lambda N - 3}{\lambda N - 2} \right) F_{00}^t, \]

but for the other values of \( \lambda \), it goes back three generations.

Numerical values of the dominant root of \( \Omega \) are listed in Table 8.3 where, once again, \( \mu(\lambda) \) increases with both \( \lambda \) and \( N \). Values of \( F_{11}^t \) are shown in Figure 8.3.

8.3 Monoecious Populations: Independent Sampling Scheme

From section 7.4 it is known that there can be no difference between gametic set measures and group measures for an equal chance gametic distribution. However, the expansion of group measures is independent of the gametic sampling plan, so that independent sampling of gametic sets is the same as combined sampling for an equal chance distribution.

The results of the previous section for equal chance thus also hold for this section. In particular, equation (8.2.6) gives the appropriate transition matrix, and Table 8.2 and Figure 8.2 give numerical characteristics of the system.

The two gametic sampling plans do differ however when the gametic distribution is such that every parent gives exactly two gametes. In this independent sampling plan, every parent is supposed to contribute one male and one female gamete to the next generation. It is this system that shows up the differences in the general equations, (8.1.1), (8.1.2) and (8.1.3) according to which particular measure is being discussed. The differences arise between measures when the gametes for which the measure is defined are located in the same or different output sets.
Table 8.3 Dominant root of transition matrix for monoecious populations with combined sampling and two gametes per parent

<table>
<thead>
<tr>
<th>Linkage Parameter, ( \lambda )</th>
<th>Population Size, ( N )</th>
<th>2</th>
<th>4</th>
<th>8</th>
<th>16</th>
<th>32</th>
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</table>
Figure 8.3 $F_{11}$ for monoecious populations with combined sampling and two gametes per parent
For gametes going to the same set (the set of male or female gametes), the probabilities for one gamete per parent (equation (7.4.18)) are appropriate. For gametes going to different sets, the probabilities for two gametes per parent (equation (7.4.11), . . . , (7.4.17)) are appropriate. Combinations of the two sets of probabilities must be used when the gametes for the measure are such that some go to one output set, and some to the other. As an example, consider the three cases of equation (8.1.2):

\[ \Gamma_1 = \lambda B', B'B'' \]

\[ \Gamma_2 = \frac{1}{N} \lambda B, BB' + \frac{1}{N} \lambda B, B'B' + \frac{N-2}{N} \lambda B, B'B'' \]

\[ \Gamma_3 = \frac{2}{N} \lambda B, BB' + \frac{N-2}{N} \lambda B, B'B'' \]

With the proper probabilities in equations (8.1.1), (8.1.2), (8.1.3), using the expansions of Table 8.1 leads to the 9 x 9 transition matrix in equation (8.3.1).

With complete linkage, there are only two equations to consider since the complete set of measures is then just \((T_1, T_2)\). This can be seen from the matrix by substituting \(\lambda = 1\). The two transition equations are:

\[ T_{1t+1}^t = T_{1t}^t/2 + (N-1) T_{2t}^t/2N \]

\[ T_{2t+1}^t = T_{1t}^t/2 + T_{2t}^t/2 \]

so that

\[ T_{1t+1}^t = T_{1t}^t - T_{1t}^t/4N \]
\[
\begin{array}{cccccccc}
\frac{(1+\lambda)^2}{6N} + \frac{(1+\lambda)^2(N-1)}{6N} & \frac{(1-\lambda)^2(N-1)}{6N} & 0 & \frac{(1-\lambda)^2(N-1)}{4N} & 0 & 0 & 0 & \frac{(1-\lambda)^2(N-1)}{8N} \\
\frac{(1+\lambda)^2}{6} & 0 & \frac{1-\lambda^2}{2} & 0 & 0 & 0 & \frac{(1-\lambda)^2}{8} & \frac{(1-\lambda)^2}{8} \\
0 & 0 & \frac{1+\lambda}{8} & \frac{1+\lambda}{4N} & \frac{1+\lambda}{8} & 0 & \frac{1-\lambda}{4} & \frac{1-\lambda}{8} \\
\frac{1+\lambda}{6N} & \frac{1+\lambda}{8N} & \frac{(1+\lambda)(N-2)}{6N} & \frac{3}{4N} + \frac{(1+\lambda)(N-2)}{4N} & \frac{1}{4N} & \frac{(1-\lambda)(N-2)}{8N} & 0 & \frac{(1-\lambda)(N-2)}{8N} \\
0 & 0 & \frac{(1+\lambda)(N-2)}{6N} & \frac{1}{2N} + \frac{(1+\lambda)(N-2)}{4N} & \frac{1}{2N} + \frac{(1+\lambda)(N-2)}{8N} & 0 & \frac{(1-\lambda)(N-2)}{4N} & \frac{(1-\lambda)(N-2)}{8N} \\
0 & 0 & 0 & 0 & 0 & \frac{1}{8} & \frac{1}{2} & \frac{1}{4} & \frac{1}{8} \\
0 & 0 & \frac{1}{4N} & \frac{1}{2N} & \frac{1}{4N} & \frac{N-3}{8N} & \frac{2N-3}{8N} & \frac{N-1}{4N} & \frac{N-1}{8N} \\
\frac{(N-3)}{8N^2} & \frac{(N-1)}{8N^2} & \frac{(N-2)}{4N(N-1)} & \frac{1}{2N} & \frac{N-2}{4N(N-1)} & \frac{(N-2)(N-3)}{8N(N-1)} & \frac{N-2}{2N} & \frac{2N^2-4N+3}{8N(N-1)} & \frac{N^2-3N+3}{8N(N-1)} \\
\frac{3}{4N(N-1)} & \frac{1}{4N(N-1)} & \frac{N-2}{2N(N-1)} & \frac{1}{N} & \frac{N-2}{2N(N-1)} & \frac{(N-2)(N-3)}{6N(N-1)} & \frac{N-2}{2N} & \frac{N^2-3N+3}{6N(N-1)} & \frac{1}{8}
\end{array}
\]
\[ F_{00}^{t+1} = F_{00}^t - F_{00}^{t-1/2N}, \]

which is the result given by Cockerham (1967). For non inbred initial populations, \( F_{00}^0 = 1 \) and \( F_{00}^1 = 1/2N \). Values of the dominant root for the 9 x 9 transition matrix are displayed in Table 8.4, while values of \( F_{11}^t \) are given in Figure 8.4.

Tables 8.2, 8.3 and 8.4, together with Figures 8.2, 8.3 and 8.4 allow conclusions to be drawn for monoecious mating systems and comparisons to be made between the three systems studied here. In each system inbreeding starts in the first generation.

Firstly, the graphs show immediately that an equal chance gamete formation scheme leads to a more inbred population than do either of the two gametes per parent (controlled mating) schemes. For any generation, in populations of the same size and between loci for which there is the same amount of linkage, the value of \( F_{11} \) for equal chance gamete formation is greater than that for either scheme of two gametes per parent. For these two controlled systems, \( F_{11} \) for the combined sampling plan is initially less but later greater than \( F_{11} \) for the independent sampling plan. The generation in which inbreeding is equal increases with population size. Since these comments apply for all linkage values, including complete linkage, they are also true for the one locus coefficient \( F_1 \), and as such may be termed "first order" effects.

The "second order", or linkage, effects are indicated by the three lines for each population size in the graphs. The greatest
Table 8.4 Dominant root of transition matrix for monoecious populations with independent sampling and two gametes per parent

<table>
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<tr>
<th>Linkage Parameter, $\lambda$</th>
<th>Population Size, $N$</th>
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</tbody>
</table>
Figure 8.4 $F_{11}$ for monoecious populations with independent sampling and two gametes per parent.
effect due to linkage, $F_{11}(1) - F_{11}(0)$, is seen to have a maximum in an early generation and decrease to zero at complete double identity. For any population size, this maximum (effect of linkage) is least for equal chance gamete formation and greatest for two gametes per parent with independent sampling. The curve for $\lambda = 0.9$ is seen to lie about midway between the two extreme lines ($\lambda = 0.0$, $\lambda = 1.0$) in the first few generations and then tend towards the $\lambda = 0.0$ line. This demonstrates the non-linear way in which linkage effects inbreeding: 90 per cent linkage gives only about half the effect of 100 per cent linkage. Whereas the rate of increase of $F_{11}(1)$ is monotone, the curve for $F_{11}(0)$ first has a decreasing rate and then an increasing (or at least non-decreasing) rate. The same is true for other small linkage values. This results in populations of different sizes being able to be equally inbred at the points where, say the $F_{11}(0)$ line of one intersects the other lines of another.

The generation at which combined and independent sampling plans with two gametes per parent have equal values of $F_{11}$ is altered by linkage. As linkage decreases from complete to zero, this generation is later. In other words, as linkage decreases the combined sampling controlled plan avoids inbreeding for a longer time than does the independent sampling controlled plan. The final behavior is unchanged.

Limiting behavior for the three systems is summarized by the values of the dominant roots of the transition matrices. In keeping with the higher rate of inbreeding for equal chance gamete formation shown in the graphs, the dominant roots are less than the corresponding ones for either system with two gametes per parent. Of these two
systems, combined sampling gives smaller roots than does independent sampling. The difference between the latter two sets of values however is less than that between either one and that of equal chance gamete formation—which is reflected in the greater similarity of the graphs for the two controlled systems.

8.4 Dioecious Populations: General Sampling Scheme

The next group pedigree involves two groups (males and females) per generation. Population size is assumed constant at \( N_m \) males and \( N_f \) females per generation. The mating scheme is shown in Figure 8.5, where groups are labelled with \( m \) or \( f \) for males or females. Measures will be superscripted according to generation.

When \( N_m = N_f = 1 \), the system is a full sib pedigree, which has been studied by Cockerham and Weir (1968)

\[4\]  

---

\[4\] Ibid.
With two groups per generation, there are nine group measures (assuming equal inbreeding of males and females), and twenty-three gametic set measures. These latter, together with abbreviated notation, are now listed.

\[ T_{11} = \psi_{m.f.} \]

\[ T_{21} = \psi_{m.f} \]

\[ T_{22} = \left( \frac{m}{\psi_{m.f}} + \frac{m}{\psi_{m.f}} \right)/2 \]

\[ \Gamma_{11} = \nu_{m.f} \]

\[ \Gamma_{12} = \left( \nu_{m.f} + \nu_{m.f} \right)/2 \]

\[ \Gamma_{21} = \nu_{m.f} \]

\[ \Gamma_{22} = \left( \nu_{m.f} + \nu_{m.f} \right)/2 \]

\[ \Gamma_{31} = \left( \nu_{m.f} + \nu_{m.f} \right)/2 \]

\[ \Gamma_{32} = \left( \nu_{m.f} + \nu_{m.f} \right)/2 \]

\[ \Gamma_{33} = \left( \nu_{m.f} + \nu_{m.f} \right)/2 \]

\[ \Delta_{11} = \xi_{f.f} \]

\[ \Delta_{12} = \left( \xi_{m.f} + \xi_{f.f} \right)/2 \]

\[ \Delta_{13} = \left( \xi_{m.f} + \xi_{f.f} \right)/2 \]
\[ \Delta_{21} = \frac{\zeta_{m_m f_m}}{m_m f_f}, \]
\[ \Delta_{22} = \frac{\zeta_{m_m f_m} f_m + \zeta_{m_f f_f}}{m_f f_f}/2, \]
\[ \Delta_{23} = \frac{\zeta_{m_m f_m} + \zeta_{m_f f_f}}{m_f f_m}/2, \]
\[ \Delta_{31} = \frac{\zeta_{m_m} m_f + \zeta_{m_f}}{m_m m_f}/2, \]
\[ \Delta_{32} = \frac{\zeta_{m_m} m_f + \zeta_{m_f}}{m_f m_f}/2, \]
\[ \Delta_{33} = \frac{\zeta_{m_m} m_f + \zeta_{m_f}}{m_f m_f}/2, \]
\[ \Delta_{41} = \frac{\zeta_{m_m} m_m + \zeta_{m_f m_f}}{m_m m_f}/2, \]
\[ \Delta_{42} = \frac{\zeta_{m_m} m_f + \zeta_{m_f}}{m_f m_m}/2, \]
\[ \Delta_{43} = \frac{\zeta_{m_m} m_f + \zeta_{m_f}}{m_f m_f}/2, \]
\[ \Delta_{44} = \frac{\zeta_{m_f}}{m_m}, \frac{m_m}{f_f}. \]

Every quantity in these equations is understood to have the same
(t+1) superscript indicating generation.

Because there may be unequal numbers of males and females in each
generation, it is not possible to equate such measures as \( \Psi_{m_m} \)
and \( \Psi_{m_f m_f} \). However, each has a very similar expansion, so it is convenient
to work with their average. There is another average implicit, but
not expressed, in the above equations. Each gametic set measure listed
there represents the average of itself and that measure obtained by re-
placing m by f and f by m in all positions of the subscripts.
A dot subscript indicated that the gamete from that group goes to
either male or female offspring groups. As any male gamete and any
female gamete—i.e., a gamete from the male group, and a gamete from
the female group—from a generation may unite to form an individual
in the next generation.

\[ \frac{F^{t+1}}{F} = \frac{Y^{t+1}}{Y} = F^{t+1} \]

Hence the measure \( T_{11} \) is just the inbreeding function, and this is the
quantity to be determined for all generations.

Each of the twenty-three gametic set measures will now be ex-
pressed in terms of individual measures, making use of the probabili-
ties defined in section 7.4. As for the monoecious case, some of the
digametic, trigametic or quadrigametic set measures have the same
general expansions. Differences do not appear until the gametic
sampling plan is specified.

For the digametic measures, \( T_{11} \) has the form of (8.4.1) and both
\( T_{21} \) and \( T_{22} \) have that of (8.4.2). In these equations, \( m, m' \) are any
distinct males and \( f, f' \) are any distinct females in generation \( t \).

\[ T_{11} = \frac{\theta}{m f} \quad (8.4.1) \]

\[ T_{2i} = \left( P_m \frac{\theta_{mm}}{l} + P_f \frac{\theta_{ff}}{l} \right) / 2 + \left( (1-P_m) \frac{\theta_{mm}}{l} + (1-P_f) \frac{\theta_{ff}}{l} \right) / 2. \quad (8.4.2) \]

\[ i = 1, 2. \]

For the trigametic measures, where \( m, m', m'' \) are any three
distinct males and \( f, f', f'' \) are any three distinct females in genera-
tion \( t \):
\( \Gamma_{1i} = (P_{m_1} \chi_m, ff + P_{m_1} \chi_f, mm)/2 + ((1-P_{m_1}) \chi_m', ff') + (1-P_{m_1}) \chi_f, mm')/2, \)
\[ i = 1, 2. \quad (8.4.3) \]
\( \Gamma_{2i} = (P_{m_2} \chi_m, mm + P_{m_2} \chi_f, mf)/2 + ((1-P_{m_2}) \chi_m', mf') + (1-P_{m_2}) \chi_f', mf')/2, \)
\[ i = 1, 2. \quad (8.4.4) \]
\( \Gamma_{3i} = (P_{m_3} \chi_m, mm + P_{m_3} \chi_f, ff)/2 + (P_{m_3} \chi_m, mm' + P_{m_3} \chi_f, ff')/6 + (P_{m_3} \chi_m, mm'' + P_{m_3} \chi_f, ff'')/3 + ((1-P_{m_2} - P_{m_3}) \chi_m, mm') \]
\[ + (1-P_{m_2} - P_{m_3}) \chi_f, ff'')/2, \quad i = 1, 2, 3. \quad (8.4.5) \]

For the quadrigametic measures, where primes indicate distinct individuals in generation \((t)\): 

\( \Delta_{1i} = P_{mf_1} \delta_{mm}, ff + P_{mf_2} \delta_{mm'}, ff + P_{mf_3} \delta_{mm}, ff' \)
\[ + (1-P_{mf_1} - P_{mf_2} - P_{mf_3}) \delta_{mm'}, ff', \quad i = 1, 2, 3. \quad (8.4.6) \]
\( \Delta_{2i} = P_{mf_1} (\delta_{mf}, mf + \delta_{fm}, fm)/2 + P_{mf_2} \delta_{mf}, m'f + P_{mf_3} \delta_{mf}, mf' \)
\[ + (1-P_{mf_1} - P_{mf_2} - P_{mf_3}) (\delta_{mf}, m'f' + \delta_{fm}, f'm')/2, \quad (8.4.7) \]
\[ i = 1, 2, 3. \]
\[ \Delta_{31} = \left( P_{m_2} \delta_{mm}, \overline{mm} + P_{f_2} \delta_{ff}, \overline{ff} \right)/2 + \left( P_{m_3} \delta_{mm}, \overline{m'f} + P_{f_3} \delta_{ff}, \overline{f'm} \right)/3 \]

\[ + \left( P_{m_2} \delta_{mm}, \overline{mfm} + \delta_{m'm}, \overline{fm} \right) + P_{f_3} \left( \delta_{ff}, \overline{fm} + \delta_{f'm}, \overline{mf} \right)/12 \]

\[ + \left( 1 - P_{m_2} - P_{m_3} \right) \delta_{mm}, \overline{m''f} + \left( 1 - P_{f_2} - P_{f_3} \right) \delta_{ff}, \overline{f''m} \right)/2, \quad (8.4.8) \]

\[ i = 1, 2, 3. \]

\[ \Delta_{41} = \left( P_{m_4} \delta_{mm}, \overline{mm} + P_{f_4} \delta_{ff}, \overline{ff} \right)/4 + \left( P_{m_5} \delta_{mm}, \overline{m'm} + P_{f_5} \delta_{ff}, \overline{f'f} \right)/2 \]

\[ + \left( P_{m_6} \delta_{mm}, \overline{m'm} \right) + P_{f_6} \delta_{ff}, \overline{f'f} \right)/3 + P_{m_6} \delta_{mm}, \overline{m'm} \]

\[ + P_{f_6} \delta_{ff}, \overline{f'f} \right)/6 + \left( P_{m_7} \delta_{mm}, \overline{m'm} + P_{f_7} \delta_{ff}, \overline{f'f} \right)/3 \]

\[ + \left( P_{m_7} \delta_{mm}, \overline{m'm} + \delta_{m'm}, \overline{m'm} \right) + P_{f_7} \delta_{ff}, \overline{f'f} \right)/2 + \left( 1 - P_{m_4} - P_{m_5} - P_{m_6} - P_{m_7} \right) \delta_{mm}, \overline{m'm} \]

\[ + \left( 1 - P_{f_4} - P_{f_5} - P_{f_6} - P_{f_7} \right) \delta_{ff}, \overline{f'f} \right)/2. \quad i = 1, 2, 3, 4. \quad (8.4.9) \]

In these nine equations, every group and individual measure is understood to have the superscript \((t+1)\).

There are thus 57 individual measures to expand back in terms of gametic set measures of the previous generation. However, there are only 28 distinct expansions--a result of the averaging that took place in defining the gametic set measures. These 28 expansions are listed in Table 8.5 for the fourth component of each measure. Of the 28 individual measures listed there; 3 have subscripts symmetric in \(m\) and \(f\), 23 represent the average of that measure and that obtained by
Table 8.5 Expansion of individual measures in terms of gametic set measures for a dioecious population

|                | $\Delta t_{11}$ | $\Delta t_{12}$ | $\Delta t_{13}$ | $\Delta t_{14}$ | $\Delta t_{21}$ | $\Delta t_{22}$ | $\Delta t_{23}$ | $\Delta t_{24}$ | $\Delta t_{31}$ | $\Delta t_{32}$ | $\Delta t_{33}$ | $\Delta t_{34}$ | $\Delta t_{41}$ | $\Delta t_{42}$ | $\Delta t_{43}$ | $\Delta t_{44}$ |
|----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|
| $t_{t+1}$ m_f  | $(1+\lambda)^2/2$ | $(1+\lambda)^2/2$ | 0               | 0               | 0               | 0               | 0               | 0               | $(1-\lambda)^2/2$ | 0               | 0               | 0               | 0               | 0               | 0               | 0               |
| $t_{t+1}$ m_m  | $1+\lambda^2/4$ | 0               | 0               | 0               | 0               | 0               | 0               | 0               | 0               | 0               | 0               | 0               | 0               | 0               | 0               | 0               |
| $t_{t+1}$ m_m' | $(1+\lambda)^2/2$ | 0               | 0               | 0               | 0               | 0               | 0               | 0               | 0               | 0               | 0               | 0               | 0               | 0               | 0               | 0               |
| $t_{t+1}$ m_f' | 0               | 0               | 0               | 0               | 0               | 0               | 0               | 0               | $(1-\lambda)^2/2$ | 0               | 0               | 0               | 0               | 0               | 0               | 0               |
| $t_{t+1}$ m_m' | $1+\lambda^2/4$ | 0               | 0               | 0               | 0               | 0               | 0               | 0               | 0               | 0               | 0               | 0               | 0               | 0               | 0               | 0               |
| $t_{t+1}$ m_m  | 0               | 0               | 0               | 0               | 0               | 0               | 0               | 0               | 0               | 0               | 0               | 0               | 0               | 0               | 0               | 0               |
| $t_{t+1}$ m_m' | 0               | 0               | 0               | 0               | 0               | 0               | 0               | 0               | 0               | 0               | 0               | 0               | 0               | 0               | 0               | 0               |
Table 8.5 (continued)

|  | \( \Delta^t_{11} \) | \( \Delta^t_{21} \) | \( \Delta^t_{22} \) | \( \Delta^t_{12} \) | \( \Delta^t_{13} \) | \( \Delta^t_{23} \) | \( \Delta^t_{33} \) | \( \Delta^t_{11} \) | \( \Delta^t_{21} \) | \( \Delta^t_{22} \) | \( \Delta^t_{12} \) | \( \Delta^t_{13} \) | \( \Delta^t_{23} \) | \( \Delta^t_{33} \) | \( \Delta^t_{11} \) | \( \Delta^t_{21} \) | \( \Delta^t_{22} \) | \( \Delta^t_{12} \) |
| \( \tau^t \) | \( \tau^t \) | \( \tau^t \) | \( \tau^t \) | \( \tau^t \) | \( \tau^t \) | \( \tau^t \) | \( \tau^t \) | \( \tau^t \) | \( \tau^t \) | \( \tau^t \) | \( \tau^t \) | \( \tau^t \) | \( \tau^t \) | \( \tau^t \) | \( \tau^t \) | \( \tau^t \) | \( \tau^t \) | \( \tau^t \) |
| \( m, m \) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| \( m, f' \) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1/2 | 0 | 0 | 0 | 1/2 | 0 | 0 | 1/2 | 0 | 0 | 1/2 |
| \( m, f \) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1/2 | 0 | 0 | 0 | 1/2 | 0 | 0 | 1/2 | 0 | 0 | 1/2 |
| \( m, m, m \) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1/4 | 0 | 0 | 0 | 1/4 | 0 | 0 | 1/4 | 0 | 0 | 1/4 |
| \( m, m, m' \) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1/4 | 0 | 0 | 0 | 1/4 | 0 | 0 | 1/4 | 0 | 0 | 1/4 |
| \( m, m, m'' \) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1/4 | 0 | 0 | 0 | 1/4 | 0 | 0 | 1/4 | 0 | 0 | 1/4 |
| \( m, m, m'' \) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1/4 | 0 | 0 | 0 | 1/4 | 0 | 0 | 1/4 | 0 | 0 | 1/4 |
| \( m, m, m'' \) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1/4 | 0 | 0 | 0 | 1/4 | 0 | 0 | 1/4 | 0 | 0 | 1/4 |
| \( m, m, m'' \) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1/4 | 0 | 0 | 0 | 1/4 | 0 | 0 | 1/4 | 0 | 0 | 1/4 |
| \( m, m, m'' \) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1/4 | 0 | 0 | 0 | 1/4 | 0 | 0 | 1/4 | 0 | 0 | 1/4 |
| \( m, m, m'' \) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1/4 | 0 | 0 | 0 | 1/4 | 0 | 0 | 1/4 | 0 | 0 | 1/4 |
| \( m, m, m'' \) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1/4 | 0 | 0 | 0 | 1/4 | 0 | 0 | 1/4 | 0 | 0 | 1/4 |
| \( m, m, m'' \) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1/4 | 0 | 0 | 0 | 1/4 | 0 | 0 | 1/4 | 0 | 0 | 1/4 |
| \( m, m, m'' \) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1/4 | 0 | 0 | 0 | 1/4 | 0 | 0 | 1/4 | 0 | 0 | 1/4 |
replacing \( m \) with \( f \) and \( f \) with \( m \) in the subscript, and the remaining 2 are the averages of four measures. These last two, and the averages they represent are:

\[
\bar{\delta}_{m'm', mf} = (\bar{\delta}_{m'm}, mf + \bar{\delta}_{ff', fm} + \bar{\delta}_{m'm', fm} + \bar{\delta}_{f'f, mf})/4,
\]

\[
\bar{\delta}_{m'm', mm'} = (\bar{\delta}_{m'm}, mm + \bar{\delta}_{ff', fm} + \bar{\delta}_{m'm', mm} + \bar{\delta}_{f'f, ff})/4.
\]

As in the monoecious case, values for the \( P_m, P_f, P_{mf} \) probabilities can be given when the gametic sampling plan is specified. Special cases are considered in the next two sections.

8.5 **Dioecious Populations: Combined Sampling Scheme**

As in the monoecious case, great simplification arises when combined sampling of gametes from each group is considered. Since the gametic set measures are equivalent to the group measures in this case, the following relations hold. The first term in each of these nine equations will be the notation used for the remainder of this section.

\[
T_{11}^{t+1} = T_{11}^{t+1} = \theta_{m' m} ,
\]

\[
T_{12}^{t+1} = T_{21}^{t+1} = (\theta_{m'm} + \theta_{lff})/2 , \quad i = 1, 2.
\]

\[
T_{11}^{t+1} = T_{11}^{t+1} = (\gamma_{lmm}, ff + \gamma_{lff}, mm)/2 , \quad i = 1, 2.
\]

\[
T_{22}^{t+1} = T_{22}^{t+1} = (\gamma_{lmm}, mm + \gamma_{lff}, ff)/2 , \quad i = 1, 2.
\]

\[
T_{33}^{t+1} = T_{33}^{t+1} = (\gamma_{lmm}, mm + \gamma_{lff}, ff)/2 , \quad i = 1, 2, 3.
\]
\[ \Delta_{1}^{t+1} = \Delta_{1}^{t+1} = \delta_{lmm}^{t+1}, \quad i = 1, 2, 3. \]

\[ \Delta_{2}^{t+1} = \Delta_{2}^{t+1} = \delta_{lmf}^{t+1}, \quad i = 1, 2, 3. \]

\[ \Delta_{3}^{t+1} = \Delta_{3}^{t+1} = \delta_{lff}^{t+1} / 2, \quad i = 1, 2, 3. \]

\[ \Delta_{4}^{t+1} = \Delta_{4}^{t+1} = \delta_{mmf}^{t+1} / 2, \quad i = 1, 2, 3, 4. \]

By adding together appropriate columns as for the monoecious case, Table 8.5 will now have only nine columns. The expansions represented by that table, together with equations (8.4.1), . . ., (8.4.9) lead to nine simultaneous transition equations:

\[ u_{t+1} = \Omega u_{t}, \]

where \( u_{t}' = [T_{1}, T_{2}, \Gamma_{1}, \Gamma_{2}, \Gamma_{3}, \Delta_{1}, \Delta_{2}, \Delta_{3}, \Delta_{4}]^{t} \) and \( u_{0}' = [1, 1, 1, 1, 1, 1, 1, 1, 1]. \) The two locus panmictic function is \( T_{1}. \) The form of this transition matrix is displayed. First however, some new notation must be introduced to reduce the size of each element. Let:

\[ P_{1} = \frac{P_{m_{1}} + P_{f_{1}}}{2}, \quad P_{2} = \frac{P_{m_{2}} + P_{f_{2}}}{2}; \]

\[ P_{4} = \frac{P_{m_{4}} + P_{f_{4}}}{2}, \quad P_{6} = \frac{P_{m_{6}} + P_{f_{6}}}{2}; \]

\[ P_{7} = \frac{P_{m_{7}} + P_{f_{7}}}{2}, \quad Q_{1} = P_{mf_{1}}, \]

\[ Q_{2} = P_{mf_{2}}, \quad Q_{3} = P_{mf_{3}}, \quad Q_{4} = 1 - P_{mf_{1}} - P_{mf_{2}} - P_{mf_{3}}. \]

The matrix follows in equation (8.5.1). In the matrix, use has been made of the relations between \( P_{m_{3}}, P_{f_{3}}, P_{f_{5}} \) and the other measures, as given in section 7.4.
\[
\begin{pmatrix}
\frac{(1+\lambda)^2}{8} & \frac{(1+\lambda)^2}{8} & 0 & \frac{1+\lambda}{2} & 0 & \frac{(1-\lambda)^2}{8} & \frac{(1-\lambda)^2}{8} & 0 & 0 \\
\frac{1+\lambda}{2} \cdot P_1 + \frac{(1+\lambda)^2}{8} (1-P_1) & 0 & \frac{1+\lambda}{2} & 0 & \frac{(1-\lambda)^2}{8} & \frac{(1-\lambda)^2}{8} (1-P_1) & 0 & 0 \\
\frac{1+\lambda}{8} \cdot P_1 & 0 & \frac{1+\lambda}{8} (1-P_1) & \frac{P_1}{2} + \frac{1+\lambda}{4} (1-P_1) & \frac{1+\lambda}{8} (1-P_1) & \frac{1-\lambda}{8} & \frac{1-\lambda}{8} & 0 & 0 \\
0 & \frac{\frac{1}{8} \cdot P_1 + \frac{1+\lambda}{8} (1-P_1)}{2} & \frac{\frac{1}{8} \cdot P_1 + \frac{1+\lambda}{8} (1-P_1)}{2} & \frac{1+\lambda}{8} (1-P_1) & \frac{1-\lambda}{8} (1-P_1) & \frac{1-\lambda}{8} (1-P_1) & \frac{1-\lambda}{8} (1-P_1) & \frac{1-\lambda}{8} (1-P_1) & 0 \\
\frac{1+\lambda}{8} (P_1 - P_2) + \frac{P_2}{4} & 0 & \frac{\frac{1}{8} \cdot P_1 + \frac{1+\lambda}{8} (1-P_1)}{2} & \frac{1+\lambda}{8} (1+2P_2 - 3P_1) & \frac{1-\lambda}{8} (1+2P_2 - 3P_1) & \frac{1-\lambda}{8} (1+2P_2 - 3P_1) & \frac{1-\lambda}{8} (1+2P_2 - 3P_1) & \frac{1-\lambda}{8} (1+2P_2 - 3P_1) & 0 \\
\end{pmatrix}
\]

(8.5.1)

\[
\begin{pmatrix}
\begin{array}{ccccccccc}
\frac{Q_3}{8} & 0 & \frac{Q_4 + Q_5}{6} & \frac{1+Q_1 - Q_4}{4} & \frac{Q_4 - Q_3}{6} & \frac{1+Q_4}{6} & \frac{1-\lambda}{4} & \frac{1-\lambda}{4} & \frac{1-\lambda}{4} \\
0 & 0 & 0 & 0 & \frac{1}{6} & \frac{Q_1}{6} & \frac{1+Q_1 - Q_4}{4} & \frac{1-\lambda}{4} & \frac{Q_4}{6} \\
0 & 0 & \frac{\frac{1}{6} \cdot P_1}{2} & \frac{\frac{1+\lambda}{8} (1-P_1)}{2} & \frac{\frac{1}{8} \cdot P_1 - P_2}{2} & \frac{P_1 - P_2}{4} & \frac{\frac{1}{8} \cdot P_1}{2} & \frac{2+2P_2 - 3P_1}{4} & \frac{1-3P_1 + P_2}{8} \\
\frac{P_6}{12} & \frac{\frac{1}{12} \cdot P_2 - P_4}{6} & \frac{\frac{1}{8} \cdot P_2}{6} & \frac{\frac{1}{8} \cdot P_2}{6} + \frac{P_2 - P_4}{6} & \frac{P_1}{12} & \frac{1+3P_1 - 2P_2}{6} & \frac{1-4P_2 + 3P_1}{6} & \frac{1-4P_2 + 3P_1}{6} & \frac{1-4P_2 + 3P_1}{6} \\
\end{array}
\end{pmatrix}
\]

\[\sum_{i=1}^{n}\]
Two checks on this matrix are possible. When \( \lambda = 1 \), the system should reduce to a one locus dioecious scheme for the combined sampling plan. This value substituted into the matrix shows that \( (T_1, T_2) \) form a complete set, and that the two transition equations are:

\[
T_{1}^{t+1} = T_{1}^{t} / 1 + T_{2}^{t} / 2,
\]
\[
T_{2}^{t+1} = P_{1} T_{1}^{t} / 2 + (1-P_{1}) T_{2}^{t} / 2,
\]
so that:

\[
T_{1}^{t+1} = T_{1}^{t} + (T_{1}^{t-1} - 2T_{1}^{t} P_{1} / 4,
\]

or, using the symbol \( F_{0} \) for (one locus) panmictic function:

\[
F_{0}^{t+1} = F_{0}^{t} + (F_{0}^{t-1} - 2F_{0}^{t} P_{1} / 4.
\]

This is the form of the result given by Wright (1931), where \( 2/P_{1} \) is the "overall (digametic) effective number."

The other check comes from setting \( N_{m} = N_{f} = 1 \). This implies that \( P_{1} = Q_{1} = 1 \) and that the other \( P_{1} \) and \( Q_{1} \) are zero. These values in the matrix show that the complete set is now \( (T_{1}, T_{2}, P_{1}, P_{2}, \Delta_{1}, \Delta_{2}) \), and the \( 6 \times 6 \) matrix for these measures is just that given by Cockerham and Weir (1968)\(^5\) for a sib mating pedigree—as it should be.

For an equal chance gametic distribution \( (k=2) \), the values of \( P_{m}^{1}, \ldots, P_{m}^{7} \) and \( P_{f}^{1}, \ldots, P_{f}^{7} \) are given by equations (7.4.4), \( \ldots \), (7.4.10). From equations (7.4.1), (7.4.2) and (7.4.3) then the

\[^{5}\text{Ibid.}\]
values of $P_{m_1 f}$, $P_{m_2 f}$, $P_{m_3 f}$ can be found. The following quantities, needed for the matrix, are given values then:

\[ P_1 = \frac{(N_m + N_f)}{2N_m N_f} \]
\[ P_2 = \frac{(N_m^2 + N_f^2)}{2N_m^2 N_f^2} \]
\[ P_4 = \frac{(N_m^3 + N_f^3)}{2N_m^3 N_f^3} \]
\[ P_6 = 3(P_2 - P_4) \]
\[ P_7 = 6P_1 - 18P_2 + 12P_4 \]
\[ Q_1 = \frac{1}{N_m N_f} \]
\[ Q_2 = \frac{(N_f - 1)}{N_m N_f} \]
\[ Q_3 = \frac{(N_m - 1)}{N_m N_f} \]
\[ Q_4 = \frac{(N_m - 1)(N_f - 1)}{N_m N_f} \]

From the value of $P_1$, it can be seen that the "overall (digametic) effective number" is $\frac{4N_m N_f}{N_m + N_f}$, as given by Wright (1931). Now equation (8.5.2) shows that the limiting rate of inbreeding for complete linkage (1-\(\mu(1)\)) is a monotone increasing function of $P_1$. Hence $\mu(1)$ will be an increasing function of the overall effective number $N_e = \frac{4N_m N_f}{N_m + N_f}$. The system was studied numerically and dominant roots displayed in Table 8.6, where the relation between the root and effective population number is seen to be the same for all linkage values. The values of $F_{11}^t$ for four populations with equal numbers, $N/2$, of males and females are displayed in Figure 8.6.
Table 8.6 Dominant root of transition matrix for dioecious populations with equal chance gamete formation

<table>
<thead>
<tr>
<th>Population Size</th>
<th>( N_m )</th>
<th>( N_f )</th>
<th>( N_e )</th>
<th>Linkage Parameter, ( \lambda )</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.00</td>
</tr>
<tr>
<td>1</td>
<td>1</td>
<td>2.000</td>
<td>.65451</td>
<td>.65699</td>
</tr>
<tr>
<td>1</td>
<td>2</td>
<td>2.667</td>
<td>.71747</td>
<td>.71950</td>
</tr>
<tr>
<td>1</td>
<td>3</td>
<td>3.000</td>
<td>.74094</td>
<td>.74293</td>
</tr>
<tr>
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<td>10</td>
<td>3.636</td>
<td>.77646</td>
<td>.77847</td>
</tr>
<tr>
<td>2</td>
<td>2</td>
<td>4.000</td>
<td>.79404</td>
<td>.79514</td>
</tr>
<tr>
<td>2</td>
<td>3</td>
<td>4.800</td>
<td>.82281</td>
<td>.82366</td>
</tr>
<tr>
<td>2</td>
<td>4</td>
<td>5.333</td>
<td>.83791</td>
<td>.83866</td>
</tr>
<tr>
<td>3</td>
<td>3</td>
<td>6.000</td>
<td>.85365</td>
<td>.85420</td>
</tr>
<tr>
<td>3</td>
<td>4</td>
<td>6.857</td>
<td>.86984</td>
<td>.87027</td>
</tr>
<tr>
<td>3</td>
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<td>7.500</td>
<td>.87914</td>
<td>.88019</td>
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<tr>
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<td>4</td>
<td>8.000</td>
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<td>.88691</td>
</tr>
<tr>
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<td>8.000</td>
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<td>.88692</td>
</tr>
<tr>
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<td>.89718</td>
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<tr>
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<td>6</td>
<td>9.600</td>
<td>.90394</td>
<td>.90415</td>
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<td>5</td>
<td>10.000</td>
<td>.90748</td>
<td>.90767</td>
</tr>
<tr>
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<td>.91463</td>
<td>.91479</td>
</tr>
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<td>10.909</td>
<td>.91458</td>
<td>.91481</td>
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<tr>
<td>5</td>
<td>7</td>
<td>11.667</td>
<td>.91980</td>
<td>.91994</td>
</tr>
<tr>
<td>6</td>
<td>6</td>
<td>12.000</td>
<td>.92188</td>
<td>.92201</td>
</tr>
<tr>
<td>7</td>
<td>7</td>
<td>14.000</td>
<td>.93241</td>
<td>.93250</td>
</tr>
<tr>
<td>8</td>
<td>8</td>
<td>16.000</td>
<td>.94044</td>
<td>.94051</td>
</tr>
<tr>
<td>9</td>
<td>9</td>
<td>18.000</td>
<td>.94677</td>
<td>.94682</td>
</tr>
<tr>
<td>10</td>
<td>10</td>
<td>20.000</td>
<td>.95189</td>
<td>.95192</td>
</tr>
<tr>
<td>100</td>
<td>100</td>
<td>200.000</td>
<td>.99502</td>
<td>.99502</td>
</tr>
</tbody>
</table>
Figure 8.6 $F_{11}$ for dioecious populations with equal chance gamete formation
Table 8.6 shows two cases where different numbers of males and females give the same effective population number. These combinations are: $N_m = N_f = 4$ and $N_m = 3$, $N_f = 6$ both giving $N_e = 8$ and $N_m = 5$, $N_f = 6$ and $N_m = 3$, $N_f = 30$ both giving $N_e = 10.909$. For complete linkage the dominant roots must be equal for each pair because of this equality of effective number. The roots also stay close for other linkage values but the relation is not a simple one, and must depend on the three and four gamete effective numbers also. These latter numbers are different for the different pairs of $N_m$, $N_f$.

With unequal numbers in each sex, $N_m < N_f$ say, it is not possible for every parent to contribute the same number of gametes—males contribute an average of $(N_m + N_f)/N_m$ and females an average of $(N_m + N_f)/N_f$. For integral values of $(N_m + N_f)/N_m$ however, the moments of the gametic distribution for males may be made zero. From equations (7.4.11), 

\[ P_m = \frac{N_f}{N_m (N_m + N_f - 1)} , \]

\[ P_{m_2} = \frac{N_f(N_f - N_m)}{N_m^2(N_m + N_f - 1)(N_m + N_f - 2)} , \]

\[ P_{m_4} = \frac{N_f(N_f - N_m)(N_f - 2N_m)}{N_m^3(N_m + N_f - 1)(N_m + N_f - 2)(N_m + N_f - 3)} , \]
\[
\begin{align*}
\mathcal{P}_{m_6} &= \frac{3(N_m-1)(N_m+N_f)N_f^2}{N_m^3(N_m+N_f-1)(N_m+N_f-2)(N_m+N_f-3)}, \\
\mathcal{P}_{m_7} &= \frac{6(N_m+N_f)^2 N_f(N_m-1)(N_m-2)}{(N_m+N_f-1)(N_m+N_f-2)(N_m+N_f-3)}.
\end{align*}
\]

One distribution of female gametes in this case is for \(N_m\) of the females to contribute two gametes each, and the remaining \((N_f-N_m)\) to contribute just one each. The probabilities \(P_{m_2}, P_{m_3}, P_{m_4}\) and \(P_{m_5}\) are all zero, and the remaining probabilities found using the moments:

\[
\sigma_f^2 = N_m(N_f-N_m)/N_f^2,
\]

\[
m_{m_3} = N_m(N_f-N_m)(N_f-2N_m)/N_f^3,
\]

\[
m_{m_4} = N_m(N_f^2-2N_fN_m+3N_m^2)(N_f-N_m)/N_f^4,
\]

\[
m_{m_22} = 2N_m^2(N_f-N_m)^2(N_f+N_m-N_m^2)/N_f^6.
\]

It is then possible to calculate the \(P_i\) and \(Q_i\) needed for the transition matrix.

Matters are simplified for an equal number, \(N\), of males and females in each generation. Each parent may be supposed to contribute exactly two gametes, so that:

\[
P_i = \mathcal{P}_{m_i} = \mathcal{P}_{m_i}
\]

and the common value comes from setting \(N = N_B\) in equations (7.4.11),
\( \ldots, (7.4.17) \). From equations (7.4.1), (7.4.2), (7.4.3) then:

\[
Q_1 = \frac{1}{(2N-1)^2},
\]

\[
Q_2 = Q_3 = \frac{(2N-2)}{(2N-1)^2},
\]

so that

\[
Q_4 = \frac{(2N-2)^2}{(2N-1)^2}.
\]

This case of equal numbers of males and females was studied numerically, and the dominant root of the transition matrix shown in Table 8.7. In that table, the population size is the number of males plus the number of females. Figure 8.7 shows values of the two locus inbreeding coefficient \( F_{11} \) for \( N/2 \) males and females.

8.6 Dioecious Populations: Independent Sampling Scheme

For equal chance gamete formation, both the combined and the independent sampling schemes lead to the same equations. This case was discussed in the last section and the results displayed in equation (8.5.1), Table 8.6 and Figure 8.6.

For a system with as little variation as possible in the number of gametes per parent the algebra for independent sampling is very complex. The complexity was suggested for combined sampling, even when it was possible to work with 9 group measures instead of 23 gametic set measures.

To reduce the complexity the simplifying assumption of equal numbers, \( N/2 \), of each sex will be made. Each male and each female is supposed to contribute one male and one female gamete. The
Table 8.7 Dominant root of transition matrix for dioecious populations with combined sampling and two gametes per parent

<table>
<thead>
<tr>
<th>Linkage Parameter, $\lambda$</th>
<th>Population Size, N</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>2</td>
</tr>
<tr>
<td>0.0</td>
<td>0.65451</td>
</tr>
<tr>
<td>0.1</td>
<td>0.65484</td>
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<td>0.65600</td>
</tr>
<tr>
<td>0.3</td>
<td>0.65832</td>
</tr>
<tr>
<td>0.4</td>
<td>0.66231</td>
</tr>
<tr>
<td>0.5</td>
<td>0.66879</td>
</tr>
<tr>
<td>0.6</td>
<td>0.67906</td>
</tr>
<tr>
<td>0.7</td>
<td>0.69524</td>
</tr>
<tr>
<td>0.8</td>
<td>0.72031</td>
</tr>
<tr>
<td>0.9</td>
<td>0.75758</td>
</tr>
<tr>
<td>1.0</td>
<td>0.80902</td>
</tr>
</tbody>
</table>
Figure 8.7 $F_{11}$ for dioecious populations with combined sampling and two gametes per parent.
probabilities needed in equations (8.4.1), . . . , (8.4.9) may be
determined from equation (7.4.11), . . . , (7.4.18). As in the
monoecious case, distinction must be made, on the basis of whether
the gametes in question are in the same or different output sets,
between using a mean number of one ((7.4.18)) or two ((7.4.11) . . .
(7.4.17)) gametes per parent.

By way of illustration consider the two cases of equation
(8.4.3):

\[ \Gamma_{11} = \frac{2}{N} \gamma_m, \text{ ff} + \frac{N-2}{N} \gamma_m, \text{ ff'}, \]

\[ \Gamma_{12} = \gamma_m, \text{ ff'}. \]

Substitution of the values of these probabilities, and the
combining of the equations with the expansions of Table 8.5 leads to
23 simultaneous transition equations. The corresponding transition
matrix, \( \Omega \), will be displayed, but because of its size will be sub-
divided:

\[
\Omega = \begin{bmatrix}
\Omega_1 & \Omega_2 \\
10 \times 10 & 10 \times 13 \\
\Omega_3 & \Omega_4 \\
13 \times 10 & 13 \times 13
\end{bmatrix}.
\]

Each of the four sub-matrices is now displayed with the appropriate
measures listed along the edges of each.
\[
\begin{array}{cccccccccccc}
& r_{11}^t & r_{21}^t & r_{12}^t & r_{22}^t & r_{11}^t & r_{12}^t & r_{21}^t & r_{22}^t & r_{51}^t & r_{52}^t & r_{53}^t \\
\hline
r_{11}^{t+1} & \frac{(1+\lambda)^2}{8} & \frac{(1+\lambda)^2}{8} & 0 & 0 & 0 & 0 & \frac{1-\lambda^2}{2} & 0 & 0 & 0 & 0 \\
r_{21}^{t+1} & \frac{1+\lambda}{2N} + \frac{(1+\lambda)^2}{8} \frac{N-2}{N} & 0 & \frac{(1+\lambda)^2}{8} \frac{N-2}{N} & 0 & 0 & 0 & \frac{1-\lambda^2}{2} \frac{N-2}{N} & 0 & 0 & 0 & 0 \\
r_{22}^{t+1} & \frac{(1+\lambda)^2}{8} & 0 & \frac{(1+\lambda)^2}{8} & 0 & 0 & 0 & \frac{1-\lambda^2}{2} & 0 & 0 & 0 & 0 \\
r_{11}^{t+1} & \frac{1+\lambda}{4N} & \frac{1+\lambda}{4N} & 0 & 0 & \frac{1+\lambda}{8} \frac{N-2}{N} & \frac{1}{N} + \frac{1+\lambda}{4} \frac{N-2}{N} & 0 & 0 & 0 & \frac{1+\lambda}{8} \frac{N-2}{N} & \frac{1+\lambda}{N} \\
r_{12}^{t+1} & 0 & 0 & 0 & 0 & \frac{1+\lambda}{8} & \frac{1+\lambda}{4} & 0 & 0 & 0 & \frac{1+\lambda}{8} & 0 \\
r_{21}^{t+1} & 0 & 0 & 0 & \frac{1+\lambda}{8} \frac{N-2}{N} & 0 & \frac{1}{N} + \frac{1+\lambda}{4} \frac{N-2}{N} & \frac{1+\lambda}{8} \frac{N-2}{N} & 0 & 0 & \frac{1+\lambda}{8} \frac{N-2}{N} & 0 \\
r_{22}^{t+1} & 0 & 0 & 0 & \frac{1+\lambda}{8} & 0 & \frac{1+\lambda}{4} & 0 & 0 & 0 & \frac{1+\lambda}{8} & 0 \\
r_{11}^{t+1} & 0 & 0 & 0 & 0 & \frac{1+\lambda}{8} & 0 & \frac{1+\lambda}{4} & \frac{1+\lambda}{8} & 0 & 0 & 0 \\
r_{12}^{t+1} & \frac{1+\lambda}{4N} & \frac{1+\lambda}{4N} & 0 & 0 & \frac{1}{2N} + \frac{1+\lambda}{8} \frac{N-2}{N} & \frac{5}{2N} + \frac{1+\lambda}{4} \frac{N-2}{N} & \frac{3+\lambda}{8} \frac{N-2}{N} & 0 & 0 & \frac{1+\lambda}{8} \frac{N-2}{N} & 0 \\
r_{22}^{t+1} & 0 & 0 & 0 & 0 & \frac{1}{N} + \frac{1+\lambda}{8} \frac{N-2}{N} & 0 & \frac{1}{2N} + \frac{1+\lambda}{4} \frac{N-2}{N} & \frac{3+\lambda}{8} \frac{N-2}{N} & 0 & 0 & 0 \\
\end{array}
\]
\[
\begin{array}{cccccccccccc}
\Delta_{11} & \Delta_{12} & \Delta_{13} & \Delta_{21} & \Delta_{22} & \Delta_{23} & \Delta_{31} & \Delta_{32} & \Delta_{33} & \Delta_{41} & \Delta_{42} & \Delta_{43} & \Delta_{44} \\
\hline
1^{t+1} & 0 & (1-\lambda)^2 & N-2 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
2^{t+1} & 0 & (1-\lambda)^2 & N-2 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
2^{t+1} & 0 & (1-\lambda)^2 & N-2 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
3^{t+1} & 0 & (1-\lambda)^2 & N-2 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
3^{t+1} & 0 & (1-\lambda)^2 & N-2 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
3^{t+1} & 0 & (1-\lambda)^2 & N-2 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
3^{t+1} & 0 & (1-\lambda)^2 & N-2 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
3^{t+1} & 0 & (1-\lambda)^2 & N-2 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
3^{t+1} & 0 & (1-\lambda)^2 & N-2 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
\end{array}
\]

\[\omega_2 = \frac{1}{8} \begin{bmatrix}
\frac{1-\lambda}{N} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & \frac{1-\lambda}{N} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & \frac{1-\lambda}{N} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & \frac{1-\lambda}{N} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & \frac{1-\lambda}{N} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & \frac{1-\lambda}{N} & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & \frac{1-\lambda}{N} & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & \frac{1-\lambda}{N} & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \frac{1-\lambda}{N} & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \frac{1-\lambda}{N} & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \frac{1-\lambda}{N} & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \frac{1-\lambda}{N} & 0 \\
\end{bmatrix}\]
\[
\begin{bmatrix}
\Delta_{11}^{t+1} & 1/2N^2 & 1/2N^2 & 0 & 0 & N-2/2N^2 & 1/N & 0 & 0 & 0 & 0 & N-2/2N^2 \\
\Delta_{12}^{t+1} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
\Delta_{13}^{t+1} & 0 & 0 & 0 & 0 & 1/4N & 1/2N & 0 & 0 & 0 & 0 & 1/4N \\
\Delta_{21}^{t+1} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
\Delta_{22}^{t+1} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
\Delta_{23}^{t+1} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
\Delta_{31}^{t+1} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
\Delta_{32}^{t+1} & 0 & 0 & 0 & 0 & 1/4N & 0 & 1/4N & 1/4N & 0 & 1/4N & 0 \\
\Delta_{33}^{t+1} & 0 & 0 & 0 & 0 & 1/2N & 0 & 1/2N & 1/2N & 0 & 1/2N & 0 \\
\Omega_{3}^{t+1} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
\Delta_{41}^{t+1} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
\Delta_{42}^{t+1} & 0 & 0 & 0 & 0 & 0 & 1/2N & 0 & 1/2N & 0 & 0 & 0 \\
\Delta_{43}^{t+1} & 1/2N(N-2) & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
\Delta_{44}^{t+1} & 1/N(N-2) & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 
\end{bmatrix}
\]
\[
\begin{array}{cccccccccccc}
\Delta_{t+1}^{11} & \Delta_{t+1}^{12} & \Delta_{t+1}^{13} & \Delta_{t+1}^{21} & \Delta_{t+1}^{22} & \Delta_{t+1}^{23} & \Delta_{t+1}^{31} & \Delta_{t+1}^{32} & \Delta_{t+1}^{33} & \Delta_{t+1}^{41} & \Delta_{t+1}^{42} & \Delta_{t+1}^{43} & \Delta_{t+1}^{44} \\
1/8 & (N-2)^2/8N & 0 & 1/8 & 0 & 0 & 0 & 1/N & 0 & 0 & 0 & (N-2)^2/8N & 0 \\
1/8 & 1/8 & 0 & 1/8 & 0 & 0 & 0 & 1/8 & 0 & 0 & 0 & 1/8 & 0 \\
1/8 & N-2/8N & 0 & 1/8 & 0 & 0 & 0 & N-1/2N & 0 & 0 & 0 & N-2/8N & 0 \\
1/4 & 0 & 0 & 0 & (N-2)^2/8N & 0 & 0 & 0 & N-2/2N & 0 & 0 & 0 & (N-2)^2/8N \\
1/4 & 0 & 0 & 0 & 1/8 & 0 & 0 & 0 & 1/2 & 0 & 0 & 0 & 1/8 \\
1/4 & 0 & 0 & 0 & N-2/8N & 0 & 0 & 0 & N-1/2N & 0 & 0 & 0 & N-2/8N \\
1/4 & 0 & 0 & 0 & 1/8 & 0 & 0 & 0 & 1/8 & 0 & 0 & 0 & 1/8 \\
\end{array}
\]

\[\alpha_t = \frac{\Delta_{t+1}^{31}}{\frac{N-1}{4N}}\]

\[
\begin{array}{cccccccccccc}
\Delta_{t+1}^{32} & \Delta_{t+1}^{33} & \Delta_{t+1}^{42} & \Delta_{t+1}^{43} & \Delta_{t+1}^{44} \\
0 & 0 & N-2/8N & 0 & 0 & N-2/8N & N-1/4N & N-1/2N & N-2/8N & 0 & N-1/8N & 0 & 0 \\
0 & 0 & N-2/4N & 0 & 0 & 1/8 & N-1/4N & N-2/8N & 1/8 & 0 & N-1/8N & 0 & 0 \\
0 & 0 & 1/4 & 0 & 0 & 1/8 & 0 & 1/2 & 0 & 0 & 1/8 & 0 & 0 \\
0 & N-2/8N & 0 & 0 & N-2/2N & 0 & 0 & N-3/2N & 0 & 0 & N-6/8N & 0 & 0 \\
0 & N-2/4N & 0 & 0 & N-2/2N & 0 & 0 & N-3/2N & 0 & 0 & N-6/8N & 0 & 0 \\
0 & N-2/4N & 0 & 0 & N-2/2N & 0 & 0 & N-3/2N & 0 & 0 & N-6/8N & 0 & 0 \\
0 & N-2/4N & 0 & 0 & N-2/2N & 0 & 0 & N-3/2N & 0 & 0 & N-6/8N & 0 & 0 \\
0 & N-2/4N & 0 & 0 & N-2/2N & 0 & 0 & N-3/2N & 0 & 0 & N-6/8N & 0 & 0 \\
\end{array}
\]
Here again, two checks are possible for these equations. For complete linkage ($\lambda=1$), the complete set is $(T_{11}, T_{21}, T_{22})$ and the corresponding transition matrix is:

$$
\Omega = \begin{bmatrix}
\frac{1}{2} & \frac{1}{2} & 0 \\
\frac{1}{2} & 0 & \frac{(N-2)}{2N} \\
\frac{1}{2} & 0 & \frac{1}{2}
\end{bmatrix}.
$$

This leads to the following recurrence formula for the (one locus) panmictic coefficient:

$$F_0^{t+1} = F_0^t - F_0^{t-2}/4N,$$

which is just that given by Cockerham (1967).

By setting $N=2$, the complete set is $(T_{11}, T_{21}, T_{11}', T_{21}', \Delta_{11}, \Delta_{21})$ and the $6 \times 6$ transition matrix is the same as that given by Cockerham and Weir (1968) for a sib mating pedigree.

Table 8.8 shows the dominant root of the $23 \times 23$ transition matrix while values of $F_{11}$ are graphed in Figure 8.8.

The three tables of dominant roots (Tables 8.6, 8.7 and 8.8) and the three graphs of $F_{11}$ (Figures 8.6, 8.7 and 8.8) may now be employed to evaluate the three dioecious systems here. Substantially the same conclusions apply as were made in section 8.3 for monoecious mating systems, although inbreeding now starts in the second generation, and

\[6\text{Ibid.}\]
Table 8.8 Dominant root of transition matrix for dioecious populations with independent sampling and two gametes per parent

<table>
<thead>
<tr>
<th>Linkage Parameter, $\lambda$</th>
<th>Population Size, $N$</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>2</td>
</tr>
<tr>
<td>0.0</td>
<td>.65451</td>
</tr>
<tr>
<td>0.1</td>
<td>.65484</td>
</tr>
<tr>
<td>0.2</td>
<td>.65600</td>
</tr>
<tr>
<td>0.3</td>
<td>.65832</td>
</tr>
<tr>
<td>0.4</td>
<td>.66231</td>
</tr>
<tr>
<td>0.5</td>
<td>.66879</td>
</tr>
<tr>
<td>0.6</td>
<td>.67906</td>
</tr>
<tr>
<td>0.7</td>
<td>.69524</td>
</tr>
<tr>
<td>0.8</td>
<td>.72031</td>
</tr>
<tr>
<td>0.9</td>
<td>.75758</td>
</tr>
<tr>
<td>1.0</td>
<td>.80902</td>
</tr>
</tbody>
</table>
Figure 8.8 $F_{11}$ for dioecious populations with independent sampling and two gametes per parent.
all systems are identical for $N = 2$ (just one male and one female each generation).

As far as first order effects are concerned, once again the equal chance gamete formation scheme has smaller dominant roots and greater $F_{11}$ values than do the controlled mating schemes. Although the combined sampling plan with two gametes per parent has greater late values of $F_{11}$ (and hence smaller dominant roots) than does the corresponding independent sampling plan, initially it does not. To a greater extent than even in the monoecious systems though these two plans are very similar.

Linkage effects also present a similar story. The logistic-type curve for $F_{11}(0)$ provides an early maximum for $F_{11}(1) - F_{11}(0)$ and enables populations of unequal sizes and unequal linkage values to be equally inbred in early generations.

Finally, comparisons can be made between monoecious and dioecious populations of the same total size.

For equal chance gamete formation schemes, the smaller dominant roots for the monoecious populations indicate larger values of $F_{11}$ than for dioecious populations. The graphs of $F_{11}$ values confirm this, and show that the relation holds for all generations. This relation is in no way affected by linkage, and holds equally well for $F_{1}$.

When each parent is constrained to produce exactly two gametes (with either sampling plan) the dioecious populations have smaller dominant roots and greater final rates of inbreeding. The graphs are not sufficiently large to illustrate this relation, for in the larger populations the roots are very close in value. However the graphs do
illustrate the higher initial rate of inbreeding for monoecious populations—which is largely a result of inbreeding starting a generation earlier. These observations are also independent of linkage. The generation in which a dioecious population becomes as inbred as a corresponding monoecious one is a function of the linkage parameter though. As linkage decreases, this generation becomes later.
9. DISCUSSION

The machinery to allow the analysis of any inbreeding system when two linked autosomal loci are considered has now been developed and demonstrated. In contrast to the one locus case where only two gametes need be taken account of, genes for two loci are necessarily carried on two, three, or four gametes between generations. The analyses thus make use of digametic, trigametic or quadrigametic measures--each being a probability statement concerning the identity of descent of genes at the two loci on the appropriate gametes.

For pedigrees of individuals, just these three types of individual measures are needed. When pedigrees of groups are involved though, additional analogous quantities--group measures, and gametic set measures--must be used and related to the individual measures.

The methods of determining one of the digametic measures, the in-breeding function, in given situations were specified in Chapter 5. At any stage, it is the inbreeding function for one individual that is to be determined, and the analysis of all systems depends upon the expansion of this measure into a combination of measures involving individuals of the previous generations. In specific pedigrees the expansions are taken back to the initial population while for pedigree systems of mating a set of simultaneous transition equations connecting values in successive generations of a minimal, complete, set of measures is derived.

Detailed instructions for expanding the measures were given in Chapter 4. Each of the pairs of genes ab, a'b', in the argument of
$X(ab, a'b')$ may be replaced by the gametic array which identifies the individuals from which the pairs came. These arrays are used as headings in a two-way table, the cells of which are filled with the measures appropriate to the marginal genes for that cell. This method is formally correct, and is the basis for all of the work of Chapter 4. In particular cases, the results given there may be consulted and applied. Measures which do not involve repeated subscripts (or one individual supplying more than one gamete) may be expanded directly however.

Such direct expansions are performed for one gamete at a time. The individual, B say, from which it came is replaced by its two parents, (DE) in parentheses in the subscript. For example, $\Theta_{BC}$ becomes $\Theta_{(DE)C}$ and $\gamma_{G, HB}$ becomes $\gamma_{G, H(DE)}$. If both genes on the gamete are being considered, as in $\Theta_{BC}$, the bracketed pair (DE) is replaced by D, E, DE or ED with probabilities $(1+\lambda)/4$, $(1+\lambda)/4$, $(1-\lambda)/4$, or $(1-\lambda)/4$,

\[ i.e., \quad \Theta_{(DE)C} = \frac{1+\lambda}{4} (\Theta_{DC} + \Theta_{EC}) + \frac{1-\lambda}{4} (\gamma_{C, DE} + \gamma_{C, ED}) \]

This is merely a statement that a gene from B has two ways of being parental and two of being recombinant. If only one gene on the gamete is being considered, the pair (DE) is replaced by D or E with probability 1/2 each,

\[ i.e., \quad \gamma_{G, H(DE)} = \frac{1}{2} (\gamma_{G, HD} + \gamma_{G, HE}) \]

Each of the subscripts is treated in the same way. Such general rules cannot be given though when a subscript is repeated.
For the specific pedigrees, expansion through all generations back to the original population completes the problem—the required inbreeding function has been found. For the pedigree systems of mating, the transition matrix for the fourth components of the complete set of measures also essentially completes the problem. The matrix acts upon a vector whose first component is \( F_{00} \), and the one locus coefficients are assumed known. Hence the matrix leads to the whole function \( F \), but the particular way in which it is used can vary.

If only the first few generations are of interest, the first few powers of the matrix can be calculated to provide algebraic expressions for \( F_{00} \), and hence \( F \). This is only practicable for small matrices. When the whole course of the inbreeding process is to be studied the characteristic equation of the matrix provides a recurrence formula for \( F_{00} \) and thus all values of \( F_{00} \) can be found. The number of generations this formula goes back is given immediately by the number of measures in the complete set, or the size of the transition matrix. There is some question as to the purpose to be served by displaying the recurrence formula, especially when the order of the equation is large. For example, calculating all the coefficients in the equation of degree 23 for the dioecious system of section 8.6, would be of little use. On the other hand an adequate picture of the system can be drawn by calculating \( F_{00} \) numerically for specific linkage values by taking successive powers of the matrix with a computer. A final use for the matrix is in using it to characterize the limiting behavior of the system. Any inbreeding system has its limiting behavior completely specified by \( \mu(\lambda) \) and \( \mu(1) \) when \( \lambda \neq 1 \); no two systems will have the same values
for both of these quantities. The stage at which equation (5.3.8)
becomes appropriate varies with the linkage parameter. In the
monoecious population with equal chance gamete formation for example,
the ratio between successive values of $F_{00}$ is constant to 5 decimal
places (and hence equal to $\mu(\lambda)$) after no more than 10 generations for
$\lambda = 0$. For $0 < \lambda < 0.5$, the number of generations is not greater than
20, but for higher $\lambda$ the number rapidly increases. It can take 60
generations to reach the steady decrease when $\lambda = 0.9$.

It has been shown that the complexity of the analysis, as indi-
cated by the size of the transition matrix, depends on the number of
measures needed to form a complete set. There seems to be no way in
which this total number of measures can be written down for any mating
system, although the maximum number needed depends only on the size of
each generation. These maxima are shown in Table 9.1.

The table shows, for example, that if each generation has only two
members, no mating system can lead to a matrix greater than $9 \times 9$. The
number of measures for a dioecious system is shown in Table 9.2.

The results of applying these techniques and determining the
effects of linkage on inbreeding can now be discussed, although some
comments have already been made earlier.

The obvious quantity to characterize the effects of linkage on the
identity of two pairs of linked genes in an individual of genotype
$ab/a'b'$ is:

$$\eta_{ij}(\lambda) = F_{ij}(\lambda) - F_i F_j,$$

i.e. $\eta_{11}(\lambda) = \text{Prob}(a=a',b=b') - \text{Prob}(a=a')\text{Prob}(b=b')$. 

Table 9.1  Maximum number of measures needed for regular pedigrees and monoecious populations

<table>
<thead>
<tr>
<th>Population Size, N</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4^+</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of Digametic Measures</td>
<td>1</td>
<td>2</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>Number of Trigametic Measures</td>
<td>0</td>
<td>3</td>
<td>4</td>
<td>4</td>
</tr>
<tr>
<td>Number of Quadrigametic Measures</td>
<td>0</td>
<td>4</td>
<td>6</td>
<td>7</td>
</tr>
<tr>
<td>Total Number of Measures</td>
<td>1</td>
<td>9</td>
<td>12</td>
<td>13</td>
</tr>
</tbody>
</table>

Table 9.2  Maximum number of measures needed for dioecious populations

<table>
<thead>
<tr>
<th>Number in Each Sex, N/2</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4^+</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of Digametic Measures</td>
<td>2</td>
<td>3</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>Number of Trigametic Measures</td>
<td>3</td>
<td>7</td>
<td>8</td>
<td>8</td>
</tr>
<tr>
<td>Number of Quadrigametic Measures</td>
<td>4</td>
<td>13</td>
<td>16</td>
<td>17</td>
</tr>
<tr>
<td>Total Number of Measures</td>
<td>9</td>
<td>23</td>
<td>27</td>
<td>28</td>
</tr>
</tbody>
</table>
This quantity, the "identity disequilibrium function" was used in discussing sib mating by Cockerham and Weir (1968). The four components of the function have the same numerical value:

\[ \eta_{ll}(\lambda) = - \eta_{l0}(\lambda) = - \eta_{0l}(\lambda) = \eta_{00}(\lambda). \]

For pedigree systems of mating, as discussed in section 5.3, \( F_{ij}(0) \) has the same value as \( F_{i}F_{j} \), so that the identity disequilibrium function may also be written as \( F_{ij}(\lambda) - F_{ij}(0) \). Both initially and finally this quantity is zero. It reaches a maximum quickly and then decreases, but not at a constant rate. The maximum value and generation of its attainment for successive parent-offspring mating is shown in Table 9.3. For complete linkage, \( \eta_{ll}(1) = F_{l}(1-F_{l}) \) which has a maximum of 0.25.

For group mating systems it was shown in section 8.2 that \( F_{ij}(0) \) is not equal to \( F_{i}F_{j} \). It becomes convenient then to divide the identity disequilibrium function into two components:

\[ F_{ij}(\lambda) - F_{i}F_{j} = (F_{ij}(0) - F_{i}F_{j}) + (F_{ij}(\lambda) - F_{ij}(0)). \]

The first component gives the disequilibrium in the absence of linkage and will be designated \( \eta_{Nij} \). It is a function of the population size \( N \). The second term, written as \( \eta_{Lij}(\lambda) \), shows the effects of linkage on the identity disequilibrium. Hence:

\[ \eta_{ll}(\lambda) = \eta_{Nll} + \eta_{Lll}(\lambda) \]

or:

\[ F_{ll}(\lambda) = F_{l}^{2} + \eta_{Nll} + \eta_{Lll}(\lambda). \]

\(^{7}\)Ibid.
Table 9.3 Maximum value of identity disequilibrium and generation of attainment for successive parent-offspring mating

<table>
<thead>
<tr>
<th>Linkage Parameter, $\lambda$</th>
<th>Maximum Value</th>
<th>Generation</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>0.1</td>
<td>0.0069</td>
<td>2</td>
</tr>
<tr>
<td>0.2</td>
<td>0.0155</td>
<td>2</td>
</tr>
<tr>
<td>0.3</td>
<td>0.0261</td>
<td>2</td>
</tr>
<tr>
<td>0.4</td>
<td>0.0390</td>
<td>2</td>
</tr>
<tr>
<td>0.5</td>
<td>0.0550</td>
<td>2</td>
</tr>
<tr>
<td>0.6</td>
<td>0.0748</td>
<td>3</td>
</tr>
<tr>
<td>0.7</td>
<td>0.1037</td>
<td>3</td>
</tr>
<tr>
<td>0.8</td>
<td>0.1394</td>
<td>3</td>
</tr>
<tr>
<td>0.9</td>
<td>0.1883</td>
<td>4</td>
</tr>
<tr>
<td>1.0</td>
<td>0.2500</td>
<td>4</td>
</tr>
</tbody>
</table>
For any group mating system the family of $F_{\lambda}(\lambda)$ curves for a particular population size has the same characteristics. The family is bounded above by the curve for $F_{\lambda}(1) = F_{\lambda}$, and bounded below by $F_{\lambda}(0)$. Now $F_{\lambda}(0)$ is at a distance $\eta_{N\lambda\lambda}$ above $F_{\lambda}^2$, and this difference has an early maximum after which $F_{\lambda}(0)$ converges to $F_{\lambda}^2$. The maximum value of $\eta_{N\lambda\lambda}(1)$ (the difference between $F_{\lambda}$ and $F_{\lambda}^2$) occurs when $F_{\lambda} = 0.5$, but at this stage $\eta_{N\lambda\lambda}$ is small. This accounts for the divergence of $F_{\lambda}$ and $F_{\lambda}(0)$ in the graphs of Chapter 8 until about the time when $F_{\lambda} = 0.5$, whereupon they converge. As linkage increases, $\eta_{N\lambda\lambda}(\lambda)$ becomes increasingly greater than $\eta_{N\lambda\lambda}$ and the generation of its maximum value moves later in time towards that of $\eta_{N\lambda\lambda}(1)$. Finally it should be noted that the overall identity disequilibrium $\eta_{\lambda\lambda}(\lambda)$ has a maximum value greater than either of those of its two components and at a time between those of the components. These concepts are illustrated in Table 9.4 where $\eta_{\lambda\lambda}(\lambda)$, $\eta_{N\lambda\lambda}$ and $\eta_{L\lambda\lambda}(\lambda)$ are shown for a monoecious population of size eight with equal chance gamete formation. In that table asterisks denote maximum values.

Table 9.4, the graphs, and tables of dominant roots in Chapter 8 all show that the effects of linkage do not increase linearly with the linkage parameter $\lambda$—which was not to be expected since both $F(\lambda)$ and $\mu(\lambda)$ involve polynomials in $\lambda$ of degree greater than one. It is only for high values of $\lambda$ (say 0.9) that linkage produces significant effects, and even then the effects are not as great as those of population size. At best then, linkage plays a transient role, and is most important at high values, small populations, and early generations.
Table 9.4  Identity disequilibrium functions for a monoecious population of size eight with equal chance gamete formation

<table>
<thead>
<tr>
<th>Generation</th>
<th>$\eta_{N11}$</th>
<th>$\eta_{L11}$</th>
<th>$\eta_{11}$</th>
<th>$\eta_{L11}$</th>
<th>$\eta_{11}$</th>
<th>$\eta_{L11}$</th>
<th>$\eta_{11}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>0.0274</td>
<td>0.0078</td>
<td>0.0352</td>
<td>0.0253</td>
<td>0.0527</td>
<td>0.0312</td>
<td>0.0586</td>
</tr>
<tr>
<td>2</td>
<td>0.0308*</td>
<td>0.0187</td>
<td>0.0495</td>
<td>0.0600</td>
<td>0.0908</td>
<td>0.0756</td>
<td>0.1064</td>
</tr>
<tr>
<td>3</td>
<td>0.0292</td>
<td>0.0248</td>
<td>0.0540*</td>
<td>0.0886</td>
<td>0.1178</td>
<td>0.1158</td>
<td>0.1450</td>
</tr>
<tr>
<td>4</td>
<td>0.0266</td>
<td>0.0271</td>
<td>0.0537</td>
<td>0.1094</td>
<td>0.1360</td>
<td>0.1491</td>
<td>0.1757</td>
</tr>
<tr>
<td>5</td>
<td>0.0240</td>
<td>0.0272*</td>
<td>0.0512</td>
<td>0.1237</td>
<td>0.1477</td>
<td>0.1758</td>
<td>0.1998</td>
</tr>
<tr>
<td>6</td>
<td>0.0215</td>
<td>0.0261</td>
<td>0.0476</td>
<td>0.1335</td>
<td>0.1550</td>
<td>0.1965</td>
<td>0.2180</td>
</tr>
<tr>
<td>7</td>
<td>0.1092</td>
<td>0.1247</td>
<td>0.0439</td>
<td>0.1373</td>
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</tr>
<tr>
<td>8</td>
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<td>0.0229</td>
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</tr>
<tr>
<td>9</td>
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<td>0.0210</td>
<td>0.0364</td>
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<tr>
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<td>0.1490</td>
<td>0.2356</td>
<td>0.2494</td>
</tr>
<tr>
<td>11</td>
<td>0.0122</td>
<td>0.0176</td>
<td>0.0298</td>
<td>0.1313</td>
<td>0.1435</td>
<td>0.2377*</td>
<td>0.2499*</td>
</tr>
<tr>
<td>12</td>
<td>0.0110</td>
<td>0.0160</td>
<td>0.0270</td>
<td>0.1263</td>
<td>0.1373</td>
<td>0.2375</td>
<td>0.2485</td>
</tr>
<tr>
<td>13</td>
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<td>0.0146</td>
<td>0.0243</td>
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</tr>
<tr>
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<td>0.0132</td>
<td>0.0219</td>
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<td>0.1234</td>
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<td>0.2410</td>
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<td>0.0120</td>
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</tr>
<tr>
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<td>0.0073</td>
<td>0.0117</td>
<td>0.0783</td>
<td>0.0827</td>
<td>0.1950</td>
<td>0.1994</td>
</tr>
<tr>
<td>30</td>
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<td>0.0025</td>
<td>0.0040</td>
<td>0.0354</td>
<td>0.0369</td>
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<td>0.1235</td>
</tr>
<tr>
<td>40</td>
<td>0.0005</td>
<td>0.0009</td>
<td>0.0014</td>
<td>0.0148</td>
<td>0.0153</td>
<td>0.0695</td>
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<tr>
<td>50</td>
<td>0.0001</td>
<td>0.0003</td>
<td>0.0004</td>
<td>0.0059</td>
<td>0.0060</td>
<td>0.0380</td>
<td>0.0381</td>
</tr>
</tbody>
</table>

a* - Maximum values.
The discussion of genotype frequencies (or at least the frequencies of double identity and double non-identity) in the presence of linkage is one use for the inbreeding function found in this work. Another was discussed by Schnell (1961).

For a random member of a group of individuals with the same history of inbreeding, each with \( n \) loci under consideration, the number, \( m \), of loci carrying genes identical by descent has expected value \( E m = n F \). If each pair of loci, \( p \) and \( q \), has linkage parameter \( \lambda_{pq} \), the covariance between the numbers of the two loci identical by descent among individuals is:

\[
\sigma_{pq} = F_{11}(\lambda_{pq}) - F_{1}^2,
\]

so that, as given by Schnell, the variance of \( m \) among individuals is:

\[
\sigma_m^2 = n F_{1}(1-F_{1}) + \sum_{p \neq q} \sigma_{pq}.
\]

The summation is over all distinct pairs \( p, q \) and thus has \( n(n-1) \) terms. As Schnell says, this variance is a desirable supplement to \( F_1 \) in describing the effect of a mating scheme on the homozygosity by descent in resulting individuals. The variance can be seen to increase with the amount of linkage.

Complete descriptions though can only be given by an \( n \)-locus inbreeding function. Certainly a vector valued measure \( X \) with \( 2n \) components could be defined. As discussed in Cockerham and Weir (1968)\textsuperscript{8},

\textsuperscript{8}Ibid.
such measures must now be x-gametic, where x may range from 2 to n subject to $x < 2N$ for a population of size N. The preliminary algebra would follow in the same manner as in this work but would be very extensive, and a computer could be employed to solve the resulting transition equations numerically. Haldane and Waddington (1931) do show how some three loci results can follow from these for two loci.
10. SUMMARY

Various systems of inbreeding, including specific pedigrees, pedigree mating systems and group mating systems are studied when two linked autosomal loci of a diploid organism are considered.

A general function with four components, each of which is a probability statement concerning the identity by descent of any two pairs of genes is defined. Three broad classes, digametic, trigametic and quadrigametic, of the function are discussed. When the two pairs of genes are on uniting gametes, the digametic function is called the two locus inbreeding function, and this is the quantity to be determined for the inbreeding systems.

For pedigree and group mating systems transition equations connecting values in successive generations for one component of each member of a complete set of functions are derived. The complete set includes the inbreeding function. The equations are displayed in matrix form for each system of inbreeding. The characteristic equation of the transition matrix furnishes a recurrence formula for the two locus panmictic function, and the largest eigenvalue, which is tabulated, affords a characterization of the limiting values of the inbreeding function. Values of the two locus inbreeding coefficient for the systems studied are presented in either tables or graphs.

Some general conclusions regarding the effects of linkage on inbreeding are drawn and some applications of the inbreeding function are discussed.
11. LIST OF REFERENCES


Jennings, H. S. 1917. The numerical results of diverse systems of breeding, with respect to two pairs of characters, linked or independent, with special relation to the effects of linkage. Genetics 2:97-154.


