GROUP INBREEDING WITH TWO LINKED LOCI¹

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A convenient way of characterizing the effects of inbreeding is by means of the inbreeding coefficient, a probability measure that genes at one locus in an individual are identical by descent (MALÉCOT 1948). The probability arguments for determining the coefficient center on the identity relations between uniting gametes. A measure of the relationship between two individuals, the coancestry coefficient, is the probability measure for gametes provided by those individuals.

To accommodate inbreeding systems with matings between groups of individuals COCKERHAM (1967) defined group inbreeding and coancestry coefficients. These average quantities could be expressed in terms of individual inbreeding and coancestry coefficients. Their determination, however, rested upon additional probabilities of identity, defined for sets of gametes, which took account of the gametic sampling scheme. As were the individual coefficients, group inbreeding and coancestry coefficients were defined for pairs of gametes and are referred to as digametic measures.

Another extension of the inbreeding coefficient concept was to define and evaluate a measure of identity by descent for the genes at each of two linked, autosomal loci of a diploid individual. In two papers (COCKERHAM and WEIR 1968; WEIR and COCKERHAM 1968) the present authors first studied sib mating and then established methods for determining a two-locus inbreeding function for any pedigree or mating system of individuals. This function had four components which gave the probabilities of genes being identical by descent at both, the first, the second, or neither, of two loci, respectively. The first component was the inbreeding coefficient and the fourth the panmictic coefficient. It was necessary to introduce trigametic and quadrigametic measures in addition to the digametic ones.

This paper synthesizes the two extensions to establish two-locus inbreeding functions for groups of diploid individuals. As might be expected, the determination of the average inbreeding function for a group of individuals depends upon the definition of digametic, trigametic, and quadrigametic measures of the identity by descent, of genes at two linked loci, for sets of gametes. The measures are developed generally and applied to monoecious and dioecious populations.

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DEFINITIONS OF MEASURES

As before (COCKERHAM and WEIR 1968) a probability measure $\mathbf{X}(ab, a'b')$ is defined for any two distinct genes, a, a' at one locus and any two distinct genes b, b' at another locus.

$$\mathbf{X}(ab, a'b') = \begin{bmatrix} \bar{X}_{11}(ab, a'b') \\ \bar{X}_{10}(ab, a'b') \\ \bar{X}_{01}(ab, a'b') \\ \bar{X}_{00}(ab, a'b') \end{bmatrix} = \begin{bmatrix} \text{Prob}(a \equiv a', b \equiv b') \\ \text{Prob}(a \equiv a', b \not\equiv b') \\ \text{Prob}(a \not\equiv a', b \equiv b') \\ \text{Prob}(a \not\equiv a', b \not\equiv b') \end{bmatrix} \quad (1)$$

The identity sign $\equiv$ means identity by descent. No restriction is placed on the number of alleles per locus. Throughout this paper, each locus will be supposed to be equally inbred, so that $\bar{X}_{10} = \bar{X}_{01}$.

In analyzing individual mating schemes the general measure was subdivided into three classes according to whether the four genes a, a', b, b' were carried on two, three, or four gametes. The same distinction will be made here together with a further one. Gametes carrying the genes of interest are identified according to either the individuals from which they came (*average individual measures*) or to the set of gametes to which they belong (*gametic set measures*).

Three types of *average individual measures* are distinguished.

$$\bar{\theta}_{BC} = \mathbf{X}(ab \in B, a'b' \in C) \quad (2)$$

$$\bar{\gamma}_{B, DE} = \mathbf{X}(ab \in B, a' \in D, b' \in E) \quad (3)$$

$$\bar{\delta}_{BC, DE} = \mathbf{X}(a \in B, b \in C, a' \in D, b' \in E) \quad (4)$$

Each of these three is an average quantity. Equation (2) is a probability statement about genes at both loci carried on a gamete from an individual in group B and genes at both loci carried on a gamete from an individual in group C, and represents the average over all individuals in the two groups. If B and C were groups of size one, then, $\bar{\theta}_{BC} = \bar{\theta}_{BC}$, the usual individual measure (WEIR and COCKERHAM 1968). Similarly equation (3) is a probability statement about genes at both loci carried on a gamete from an individual in group B and genes at the a -locus and b -locus carried on gametes from individuals in groups D and E, respectively—averaged over all members of those three groups. Equation (4) refers to gametes from individuals in groups B, C, D, and E.

Various components of these measures are indicated by subscripts of 1 or 0, so that the fourth component of $\bar{\theta}_{BC}$ for example is written as $\bar{\theta}_{00BC}$.

In distinguishing the three types of *gametic set measures*, each set of gametes must be identified. It will usually be sufficient to specify the donor and recipient groups.

$$\bar{\psi}_{B_P C_Q} = \mathbf{X}(P \in ab \in B, Q \in a'b' \in C) \quad (5)$$

$$\bar{\gamma}_{B_P, D_R E_S} = \mathbf{X}(P \in ab \in B, R \in a' \in D, S \in b' \in E) \quad (6)$$

$$\bar{\delta}_{B_P C_Q, D_R E_S} = \mathbf{X}(P \in a \in B, Q \in b \in C, R \in a' \in D, S \in b' \in E) \quad (7)$$

Equation (5) is a probability statement about genes at both loci carried on one gamete in the gametic set that group P receives from group B and genes at both loci carried on one gamete in the gametic set that group Q receives from group C. This is an average over all the gametes in the two sets. Similarly equations (6) and (7) refer to three and four gametes in the indicated gametic sets.

The quantity to be determined for any group, A, is $\bar{F}_A$, the average of the

inbreeding functions for all members of group A. Each of its components is the average of the corresponding components of these inbreeding functions. It is called the *group inbreeding function of group A*. If A has groups B and C as parental groups, as in Figure 1, then

$$\bar{F}_A = \psi_{B_A C_A}. \quad (8)$$

The inbreeding function of a group in one generation is thus a measure defined on sets of output gametes from the previous generation.

For individual mating schemes, a set of measures defined on the output gametes of one generation is related to a set of such measures of the previous generation. One of these measures is the individual inbreeding function. As each gamete can be identified uniquely with one individual, these measures for which expansions back in time are defined are just individual measures.

For group mating schemes, relations will again be established between values in successive generations of measures defined on the output gametes of a generation. Expansions are thus performed on gametic set measures, and the expansion process will first be illustrated for a general pedigree of groups.

GENERAL EXPANSION

Expansions of measures make use of the linkage parameter λ which is defined so that an individual of genotype $a_1 b_1 / a_2 b_2$ produces an output gametic array of

$$\left(\frac{1+\lambda}{4} a_1 b_1, \frac{1+\lambda}{4} a_2 b_2, \frac{1-\lambda}{4} a_1 b_2, \frac{1-\lambda}{4} a_2 b_1 \right).$$

The following averages will be used:

$$\begin{aligned} \overline{v_{B_P, D_R E_S}} &= \frac{1}{2} \left[\overline{v_{B_P, D_R E_S}} + \overline{v_{B_P, E_S D_R}} \right], \\ \overline{\xi_{B_P C_Q, D_R E_S}} &= \frac{1}{2} \left[\overline{\xi_{B_P C_Q, D_R E_S}} + \overline{\xi_{B_P C_Q, E_S D_R}} \right], \\ \overline{\xi_{B_P C_Q, D_R E_S}} &= \frac{1}{2} \left[\overline{\xi_{B_P C_Q, D_R E_S}} + \overline{\xi_{C_Q B_P, D_R E_S}} \right]. \end{aligned}$$

The general method of expanding gametic set measures will be demonstrated with reference to the pedigree of Figure 1, each letter in that figure referring to a group. Digametic measure expansions are considered first, $\psi_{B_A C_A}$ being used as an example. From Figure 1 it can be seen that a gamete $a'b'$ among the output gametes of group C is a parental type from either group G or group H with probability $\frac{1+\lambda}{4}$ in each case, or a recombinant type with a' from group G and b' from group H, or vice versa, each with probability $\frac{1-\lambda}{4}$. Hence the following expansion:

$$\begin{aligned} X(A \varepsilon ab \varepsilon B, A \varepsilon a'b' \varepsilon C) &= \\ \frac{1+\lambda}{4} [X(A \varepsilon ab \varepsilon B, C \varepsilon a'b' \varepsilon G) + X(A \varepsilon ab \varepsilon B, C \varepsilon a'b' \varepsilon H)] + \\ \frac{1-\lambda}{4} [X(A \varepsilon ab \varepsilon B, C \varepsilon a' \varepsilon G, C \varepsilon b' \varepsilon H) + X(A \varepsilon ab \varepsilon B, C \varepsilon a' \varepsilon H, C \varepsilon b' \varepsilon G)], \\ \therefore \psi_{B_A C_A} &= \psi_{B_A, (G \cup H)} = \frac{1+\lambda}{4} [\psi_{B_A G} + \psi_{B_A H}] + \frac{1-\lambda}{2} \psi_{B_A, G \cup H}. \quad (9) \end{aligned}$$

FIGURE 1.—General Mating Scheme.

For an example of the expansion of a trigametic measure, consider $\underline{v}_{B_A, G_C H_C}$. The genes a, b from B are traced back to their possible origins in the previous generation:

$$\begin{aligned} & \mathbf{X}(A \varepsilon ab \varepsilon B, C \varepsilon a' \varepsilon G, C \varepsilon b' \varepsilon H) \\ = & \frac{1+\lambda}{4} [\mathbf{X}(B \varepsilon ab \varepsilon D, C \varepsilon a' \varepsilon G, C \varepsilon b' \varepsilon H) + \mathbf{X}(B \varepsilon ab \varepsilon E, C \varepsilon a' \varepsilon G, C \varepsilon b' \varepsilon H)] \\ & + \frac{1-\lambda}{4} [\mathbf{X}(B \varepsilon a \varepsilon D, B \varepsilon b \varepsilon E, C \varepsilon a' \varepsilon G, C \varepsilon b' \varepsilon H) \\ & + \mathbf{X}(B \varepsilon a \varepsilon E, B \varepsilon b \varepsilon D, C \varepsilon a' \varepsilon G, C \varepsilon b' \varepsilon H)], \\ \therefore \underline{v}_{B_A, G_C H_C} = & \underline{v}_{(D_B E_B), G_C H_C} \\ = & \frac{1+\lambda}{4} [\underline{v}_{D_B, G_C H_C} + \underline{v}_{E_B, G_C H_C}] + \frac{1-\lambda}{2} \underline{v}_{D_B E_B, G_C H_C} . \end{aligned}$$

A similar expansion is obtained for $\underline{v}_{B_A, H_C G_C}$, so that:

$$\begin{aligned} \underline{v}_{B_A, G_C H_C} = & \underline{v}_{(D_B E_B), G_C H_C} \\ = & \frac{1+\lambda}{4} [\underline{v}_{D_B, G_C H_C} + \underline{v}_{E_B, G_C H_C}] + \frac{1-\lambda}{2} \underline{v}_{D_B E_B, G_C H_C} . \end{aligned} \quad (10)$$

Combining equations (9) and (10) finishes the expansion of $\underline{\psi}_{B_A C_A}$ in terms of measures involving the gametes received by groups B and C.

$$\begin{aligned} \underline{\psi}_{B_A C_A} = & \underline{\psi}_{(D_B E_B), (G_C H_C)} \\ = & \left(\frac{1+\lambda}{4} \right)^2 [\underline{\psi}_{D_B G_C} + \underline{\psi}_{D_B H_C} + \underline{\psi}_{E_B G_C} + \underline{\psi}_{E_B H_C}] \\ & + \frac{1-\lambda^2}{8} [\underline{v}_{D_B, G_C H_C} + \underline{v}_{E_B, G_C H_C} + \underline{v}_{G_C, D_B E_B} + \underline{v}_{H_C, D_B E_B}] \\ & + \frac{(1-\lambda)^2}{4} \underline{v}_{D_B E_B, G_C H_C} . \end{aligned} \quad (11)$$

As an example of a quadrigametic measure expansion, consider $\underline{z}_{D_B E_B, G_C H_C}$. The four genes are now on four gametes and each has probability of one half of coming from one of two groups. For example:

$$\begin{aligned} & \mathbf{X}(B \varepsilon a \varepsilon D, B \varepsilon b \varepsilon E, C \varepsilon a' \varepsilon G, C \varepsilon b' \varepsilon H) \\ &= \frac{1}{2} [\mathbf{X}(D \varepsilon a \varepsilon K, B \varepsilon b \varepsilon E, C \varepsilon a' \varepsilon G, C \varepsilon b' \varepsilon H) \\ & \quad + \mathbf{X}(D \varepsilon a \varepsilon L, B \varepsilon b \varepsilon E, C \varepsilon a' \varepsilon G, C \varepsilon b' \varepsilon H)], \\ \therefore \underline{z}_{D_B E_B, G_C H_C} &= \underline{z}_{(K_D) L_D, E_B, G_C H_C} \\ &= \frac{1}{2} [\underline{z}_{K_D E_B, G_C H_C} + \underline{z}_{L_D E_B, G_C H_C}]. \end{aligned} \quad (12)$$

The parental groups of E, G and H may also be brought in to finish this expansion. This method of treating one gene at a time may also be used to finish expanding

$\underline{v}_{B_A, \overline{G_C H_C}}$:

$$\begin{aligned} \underline{v}_{B_A, \overline{G_C H_C}} &= \underline{v}_{(D_B E_B), \overline{(P_G Q_G) H_C}} \\ &= \frac{1+\lambda}{8} \left[\underline{v}_{D_B, \overline{P_G H_C}} + \underline{v}_{D_B, \overline{Q_G H_C}} + \underline{v}_{E_B, \overline{P_G H_C}} + \underline{v}_{E_B, \overline{Q_G H_C}} \right] \\ & \quad + \frac{1-\lambda}{4} \left[\underline{z}_{D_B E_B, \overline{P_G H_C}} + \underline{z}_{D_B E_B, \overline{Q_G H_C}} \right]. \end{aligned} \quad (13)$$

The parental groups of H may also be brought into the expansion.

In these general expansions, no group is considered to contribute more than one set of gametes. Since each gametic set can be identified solely by donor group, the notation is redundant in specifying both donor and recipient group. For mating schemes in which a group may contribute two or more sets of gametes, the redundancy disappears as becomes evident in the next section.

SPECIAL EXPANSIONS

Although the $\mathbf{X}$ measures were defined for distinct genes a, a' and b, b' , no restrictions are placed on the groups or individuals from which the gametes carrying these genes originate. Whenever one group does provide more than one gametic set, so that the group appears twice or more as a donor in the subscript, special expansions are needed. Two or more gametes from the group may have arisen from the same individual, which raises the possibility that they are carrying copies of the same genes and so are automatically identical by descent.

This need to consider the possibility of single individuals providing more than one gamete prohibits the expansion of gametic set measures back directly to gametic set measures of the previous generation. Instead an intermediate stage, that of average individual measures, is used to identify cases of common individuals. The procedure is thus to express a gametic set measure as a linear combination of average individual measures and then expand these latter back to gametic set measures.

The expression in terms of average individual measures depends upon the

probabilities of two or more gametes being drawn from one individual. Verbal definitions of the necessary gametic sampling probabilities are now given.

$P_{B_A}^2, P_{B_A}^{11}$ are the probabilities that two gametes received by group A from group B came from one and two individuals, respectively, in group B.

$P_{B_A}^3, P_{B_A}^{21}, P_{B_A}^{111}$ are the probabilities that three gametes received by group A from group B came from one, two, and three individuals, respectively, in group B.

$P_{B_A}^4, P_{B_A}^{211}, P_{B_A}^{1111}$ are the probabilities that four gametes received by group A from group B came from one, three, and four individuals, respectively, in group B.

$P_{B_A}^{31}$ is the probability that of four gametes received by group A from group B, three were from one individual and the fourth from another individual in group B.

$P_{B_A}^{22}$ is the probability that of four gametes received by group A from group B, two were from one individual and two were from another individual in group B.

The probabilities are expressed in terms of the numbers of gametes, k_i , contributed to the set of gametes by the i th member of the donor group. For example, if group B has N_B members and gives a set of N_A gametes to group A:

$$P_{B_A}^2 = \frac{\sum_{i=1}^{N_B} k_i(k_i - 1)}{N_A(N_A - 1)}$$

Expressions for the other nine probabilities are listed in APPENDIX 1. They are applicable whenever a group, A, receives exactly one set of gametes from a parental group, B. Inspection of these expressions reveals the following six relations:

$$\begin{aligned} P_{B_A}^{11} &= 1 - P_{B_A}^2 & P_{B_A}^{111} &= 1 - 3P_{B_A}^2 + 2P_{B_A}^3 \\ P_{B_A}^{21} &= 3(P_{B_A}^2 - P_{B_A}^3) & P_{B_A}^{211} &= 6P_{B_A}^2 - 12P_{B_A}^3 + 6P_{B_A}^4 - 2P_{B_A}^{22} \\ P_{B_A}^{31} &= 4(P_{B_A}^3 - P_{B_A}^4) & P_{B_A}^{1111} &= 1 - 6P_{B_A}^2 + 8P_{B_A}^3 - 3P_{B_A}^4 + P_{B_A}^{22} \end{aligned}$$

It will thus be necessary to calculate just four probabilities.

The reciprocals of the four quantities $P_{B_A}^2, P_{B_A}^3, P_{B_A}^4$, and $P_{B_A}^{22}$ are called the *digametic*, *irigametic*, *quadrigametic* and *bi-digametic effective numbers*, respectively, for the gametic set received by group A from group B. The digametic number is the usual "effective population number" (WRIGHT 1931). APPENDIX 1 also lists expected values for these four probabilities in terms of central moments of the k -distribution.

Now the expression of gametic set measures, with repeated donor groups, as average individual measures may proceed. All cases that can arise from the general pedigree of Figure 1 are listed.

$$\psi_{B_A B_A} = P_{B_A}^2 \bar{\psi}_{BB} + P_{B_A}^{11} \bar{\psi}_{BB'} \quad (14)$$

$$\psi_{B_A, C_A C_A} = P_{B_A}^2 \bar{\psi}_{B, CC} + P_{B_A}^{11} \bar{\psi}_{B, CC'} \quad (15)$$

$$\psi_{B_A, \overline{B_A C_A}} = P_{B_A}^2 \bar{\psi}_{B, \overline{BC}} + P_{B_A}^{11} \bar{\psi}_{B, \overline{B'C}} \quad (16)$$

$$\psi_{B_A, B_A B_A} = P_{B_A}^3 \bar{\psi}_{B, BB} + \frac{1}{3} P_{B_A}^{21} (\bar{\psi}_{B, B'B'} + 2\bar{\psi}_{B, \overline{BB'}}) + P_{B_A}^{111} \bar{\psi}_{B, B'B''} \quad (17)$$

$$\bar{\zeta}_{D_B E_{B'} D_B G_C} = P_{D_B}^2 \bar{\delta}_{DE, DG} + P_{D_B}^{11} \bar{\delta}_{DE, D'G} \quad (18)$$

$$\begin{aligned} \bar{\zeta}_{B_A B_{A'} C_A C_A} &= P_{B_A}^2 P_{C_A}^2 \bar{\delta}_{BB, CC} + P_{B_A}^2 P_{C_A}^{11} \bar{\delta}_{BB, CC'} + P_{B_A}^{11} P_{C_A}^2 \bar{\delta}_{BB', CC} \\ &\quad + P_{B_A}^{11} P_{C_A}^{11} \bar{\delta}_{BB', CC'} \end{aligned} \quad (19)$$

$$\begin{aligned} \bar{\zeta}_{B_A C_{A'} B_A C_A} &= P_{B_A}^2 P_{C_A}^2 \bar{\delta}_{BC, BC} + P_{B_A}^2 P_{C_A}^{11} \bar{\delta}_{BC, BC'} + P_{B_A}^{11} P_{C_A}^2 \bar{\delta}_{BC, B'C} \\ &\quad + P_{B_A}^{11} P_{C_A}^{11} \bar{\delta}_{BC, B'C'} \end{aligned} \quad (20)$$

$$\begin{aligned} \bar{\zeta}_{B_A B_{A'} \overline{B_A C_A}} &= P_{B_A}^3 \bar{\delta}_{BB, \overline{BC}} + \frac{1}{3} P_{B_A}^{21} (\bar{\delta}_{BB', \overline{BC}} + 2 \bar{\delta}_{BB, \overline{B'C}}) \\ &\quad + P_{B_A}^{111} \bar{\delta}_{BB', \overline{B'C}} \end{aligned} \quad (21)$$

$$\begin{aligned} \bar{\zeta}_{B_A B_{A'} B_A B_A} &= P_{B_A}^4 \bar{\delta}_{BB, BB} + P_{B_A}^{31} \bar{\delta}_{BB, \overline{BB'}} + \frac{1}{3} P_{B_A}^{22} (2 \bar{\delta}_{BB, B'B'} + \bar{\delta}_{BB', BB'}) \\ &\quad + \frac{1}{3} P_{B_A}^{211} (2 \bar{\delta}_{BB, B'B''} + \bar{\delta}_{BB', BB''}) + P_{B_A}^{1111} \bar{\delta}_{BB', B''B''}. \end{aligned} \quad (22)$$

These equations make use of the equality of some quadrigametric measures:

$$\bar{\delta}_{BC, DE} = \bar{\delta}_{DE, BC} = \bar{\delta}_{BE, DC} = \bar{\delta}_{DC, BE}.$$

In the average individual measures, primes denote distinct individuals. For example $\bar{\theta}_{BB'}$ is the average of all individual digametic measures defined for two distinct members of group B. Gametic set measures without repeated donor subscripts also have individual measure expressions:

$$\bar{\psi}_{B_A C_A} = \bar{\theta}_{BC} \quad (23)$$

$$\bar{\psi}_{B_A' G_C H_C} = \bar{\gamma}_{B, GH} \quad (24)$$

$$\bar{\zeta}_{D_B E_{B'} G_C H_C} = \bar{\delta}_{DE, GH} \quad (25)$$

Having set up these expressions we now proceed to expand the average individual measures back to gametic set measures of the previous generation. For the average individual measures without repeated subscripts the "general expansions" of WEIR and COCKERHAM (1968) are appropriate, provided the expansions are made back to sets of gametes rather than individual gametes. For instance, for $\bar{\theta}_{BC}$:

$$\bar{\theta}_{BC} = \bar{\psi}_{(D_B E_{B'}) (G_C H_C)} \quad (26)$$

The expression of (26) is just the expansion given in equation (11), emphasizing that there is no need for the intermediate stage of individual measures when the gametic set measure is defined on distinct groups.

Average individual measures with repeated subscripts do require special expansions, analogous to those of WEIR and COCKERHAM (1968). That for $\bar{\theta}_{BB}$ will be derived here, and other cases listed in APPENDIX 2. For $\bar{\theta}_{bb}$ the two gametes ab , $a'b'$ from one individual in group B are each traced back to an array of pairs of genes. These arrays are identical, and hold for any member of group B. They are equal to

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

where subscripts denote from which groups the genes came. The pedigree of

TABLE 1
Expansion of $\bar{\theta}_{00BB}$ to gametic set measures

$\bar{\theta}_{00BB}$	$a'b'$			
	$\frac{1+\lambda}{4}$ $a_D b_D$	$\frac{1+\lambda}{4}$ $a_E b_E$	$\frac{1-\lambda}{4}$ $a_D b_E$	$\frac{1-\lambda}{4}$ $a_E b_D$
$\frac{1+\lambda}{4} a_D b_D$	0	$\psi_{00D_B E_B}$	0	0
$\frac{1+\lambda}{4} a_E b_E$	$\psi_{00D_B E_B}$	0	0	0
$\frac{1-\lambda}{4} a_D b_E$	0	0	0	$\psi_{00D_B E_B}$
$\frac{1-\lambda}{4} a_E b_D$	0	0	$\psi_{00D_B E_B}$	0

Figure 1 is still appropriate. These arrays are arranged as headings in a two-way table (Table 1), the body of which carries the probabilities that the marginal gametes are not identical by descent. Collecting all the terms in Table 1 gives

$$\bar{\theta}_{00BB} = \frac{1+\lambda^2}{4} \psi_{00D_B E_B}.$$

The same procedure can be applied to the other three components of $\bar{\theta}_{BB}$ but these will not be needed as all calculations in this paper can be made with the fourth (double non identity) component of each measure. The reason for working with just one component was discussed in COCKERHAM and WEIR (1968). The four components of *any* inbreeding measure $X(ab, a'b')$ can be arranged in a two-by-two array so that the row totals are $\text{Prob}(a \equiv a')$ and $\text{Prob}(a \not\equiv a')$ while the column totals are $\text{Prob}(b \equiv b')$ and $\text{Prob}(b \not\equiv b')$. Only the fourth component, X_{00} , has the property that its expansions can be made to the same (fourth) components of other measures, so that it may be used exclusively. Once having determined X_{00} , substitution of $\lambda = 1$ gives the one-locus panmictic coefficients $X_{01} + X_{00} = \text{Prob}(a \not\equiv a')$ and $X_{10} + X_{00} = \text{Prob}(b \not\equiv b')$ and thus the four marginal totals mentioned above. In other words the whole vector $\mathbf{X}$ is readily found once X_{00} is found. For the remainder of this paper, only the fourth components of measures will be used so that the measures will not have an underline. Generally, *the double zero subscript will be omitted* but is always to be understood.

The basis for determining the two-locus inbreeding function for a group has now been established. The method rests on relating values of a set of gametic set measures in one generation to values in the preceding generation. When every group produces just one output set of gametes, such (general) expansions can be made directly. Otherwise the (special) expansions necessitate an intermediate stage of individual measures.

Choosing the set of gametic set measures proceeds just as for individual mating schemes (WEIR and COCKERHAM 1968) and begins by specifying the inbreeding

function to be determined, and writing it as a gametic set measure. For Figure 1 for example

$$\bar{F}_{00A} = \psi_{00B_A C_A}.$$

This set measure is then expanded (directly or via individual measures) to digametic, trigametic and quadrigametic set measures for the previous generation.

When a specific pedigree of groups is being considered, these measures are themselves expanded back to the preceding generation. The process continues until the panmictic coefficient $\bar{F}_{00A}$ has been expressed entirely in terms of (fourth components of) measures involving the common ancestral groups of the parental groups of A, whereupon numerical values for these measures are substituted.

When there is a constant mating pattern in every generation, recurrence relations for a complete set of measures are established. The two locus panmictic coefficient is necessarily a member of this complete, or smallest, set of measures, any member of which in generation $(t+1)$ can be expanded to members of the set in generation t . The types of measures introduced by the expansion of F_{00}^{t+1} are noted, and transition equations established relating their values in generation $(t+1)$ to measures in generation t . The process continues until no new types of measure are introduced in the expansions. By way of illustration of constant mating patterns this paper considers monoecious and dioecious populations.

Before these two examples can be given, gametic sampling plans must be discussed.

GAMETIC SAMPLING PLANS

Two methods of sampling sets of gametes from a group will be considered: combined and independent sampling. These sampling plans were described by COCKERHAM (1967).

For the *independent sampling plan*, various output gametic sets from a group are drawn independently, so that the probability of any member of the group contributing a random gamete in one output set is not dependent on its contributions to other sets. In the *combined sampling plan* however, a particular gametic output set is a random sample of the total gametic output of a group. Only groups of finite size are being considered.

When the numbers of gametes, k_i , contributed to a set of N_A gametes by the i th of the N_B members of group B are identically, binomially distributed $Bi(N_A, \frac{1}{N_B})$ the gametes are said to have an *equal-chance distribution*. In other words, any member of the group has the same probability of contributing each and every gamete in the set. As there is no restriction on the individual of origin of any output gamete then, there is no difference in the results between combined and independent sampling. APPENDIX 3 lists values of the gametic sampling probabilities for equal chance gamete formation.

The results of the two sampling schemes generally differ whenever there is a restriction on the number of gametes contributed by each individual. This paper considers the situation of every member of a group being constrained to provide

FIGURE 2.—Monoecious Mating Scheme.

exactly two gametes for the next generation. For independent sampling this means that every individual in a group, B, contributes exactly one gamete to each of two gametic sets, while for combined sampling it means that two gametic sets are formed at random from a pool of $2N_B$ gametes. For combined sampling with two gametes per parent the values of the sampling probabilities are given in APPENDIX 3, but for independent sampling they will be listed as needed in the text.

MONOECIOUS POPULATIONS

The monoecious mating scheme is shown in Figure 2, where A and B are the groups of individuals comprising generations $t+1$ and t respectively. Although two gametic sets are involved, the number of male and female gametes must be the same. Each generation has the same size, N .

There are nine possible gametic set measures and they are now listed together with an abbreviated notation. In order that gametic sets can be identified, the donor group is subscripted by m or f for male or female set rather than by recipient group. The double zero subscript is to be understood throughout.

$$\begin{array}{ll}
 \Theta_1^{t+1} = \psi_{B_m B_f} & \Delta_1^{t+1} = \zeta_{B_m B_m, B_f B_f} \\
 \Theta_2^{t+1} = \psi_{B_m B_m} = \psi_{B_f B_f} & \Delta_2^{t+1} = \zeta_{B_m B_f, B_m B_f} = \zeta_{B_f B_m, B_f B_m} \\
 \Gamma_1^{t+1} = v_{B_m, B_f B_f} = v_{B_f, B_m B_m} & \Delta_3^{t+1} = \zeta_{B_m B_m, B_m B_f} = \zeta_{B_f B_f, B_f B_m} \\
 \Gamma_2^{t+1} = v_{B_m, B_m B_f} = v_{B_f, B_f B_m} & \Delta_4^{t+1} = \zeta_{B_m B_m, B_m B_m} = \zeta_{B_f B_f, B_f B_f} \\
 \Gamma_3^{t+1} = v_{B_m, B_m B_m} = v_{B_f, B_f B_f} &
 \end{array}$$

In a monoecious population there is no difference between, say, $\psi_{B_m B_m}$ and $\psi_{B_f B_f}$. They have the common value Θ_2^{t+1} .

The two-locus panmictic coefficient for group A is expressed as a gametic set measure,

$$\bar{F}_{00}^{t+1} = \bar{F}_{00A} = \psi_{B_m B_f} = \Theta_1^{t+1},$$

and this set measure is now to be expressed as a linear combination of average individual measures.

Consider first the equal-chance gamete formation scheme and/or the combined sampling plan. In these cases, each of the $2N$ gametes sampled from group B may have originated from any member of the group, regardless of whether the gamete is male or female. There can be no distinction then between either of the digametic

measures Θ_1 , Θ_2 or between any of the trigametic measures Γ_1 , Γ_2 , Γ_3 or between any of the quadrigametic measures Δ_1 , Δ_2 , Δ_3 , and Δ_4 . The three distinct gametic set measures will be labelled Θ , Γ , and Δ . Their expressions as average individual measures are just those given in equations (14), (17), and (22), respectively. The expansions of individual measures back to gametic set measures of the previous generation may be deduced by modifying the table of APPENDIX 4. By adding together the first two, the next three, and the remaining four columns, the expansions of each individual measure to Θ , Γ , and Δ , respectively, can be read.

The expansion of $\bar{\theta}_{BB'}$ (and hence of Θ) showed that both Γ and Δ were needed in the complete set of measures. All of the individual measures thus introduced can themselves be expanded back to some or all of Θ , Γ , Δ .

Equations (14), (17), and (22) may be combined with the modified table of APPENDIX 4 to provide the transition equations for the complete set of gametic measures.

For the equal-chance gamete formation scheme, substitution of the probabilities of APPENDIX 3 with $N_B = N$ gives:

$$\begin{bmatrix} \Theta \\ \Gamma \\ \Delta \end{bmatrix}^{t+1} = \begin{bmatrix} \frac{(1+\lambda)^2}{4} - \frac{\lambda}{2N} & \frac{(N-1)(1-\lambda^2)}{2N} & \frac{(N-1)(1-\lambda)^2}{4N} \\ \frac{1+\lambda}{4N} - \frac{\lambda}{4N^2} & \frac{(N-1)(N+1+\lambda(N-2))}{2N^2} & \frac{(N-1)(2N-3)(1-\lambda)}{4N^2} \\ \frac{2N-1}{4N^3} & \frac{(N-1)(2N-1)}{N^3} & \frac{(N-1)(2N-1)(2N-3)}{4N^3} \end{bmatrix} \begin{bmatrix} \Theta \\ \Gamma \\ \Delta \end{bmatrix}^t \quad (27)$$

When $\lambda = 1$ this should reduce to the one locus panmictic coefficient equation. Setting $\lambda = 1$ and writing $\bar{F}_0$ for Θ does indeed lead to:

$$\bar{F}_0^{t+1} = \frac{2N-1}{2N} \bar{F}_0^t, \quad (28)$$

which is just as given by WRIGHT (1931).

For combined sampling with two gametes per parent the probabilities follow from APPENDIX 3 by setting $N_B = N$ and $N_A = 2N$. The transition matrix is:

$$\begin{bmatrix} \Theta \\ \Gamma \\ \Delta \end{bmatrix}^{t+1} = \begin{bmatrix} \frac{(1+\lambda)^2}{4} - \frac{\lambda}{2(2N-1)} & \frac{(1-\lambda^2)(N-1)}{2N-1} & \frac{(1-\lambda)^2(N-1)}{2(2N-1)} \\ \frac{1+\lambda}{4(2N-1)} & \frac{1}{2} + \frac{\lambda(N-2)}{2N-1} & \frac{(1-\lambda)(4N-7)}{4(2N-1)} \\ \frac{1}{2(2N-1)(2N-3)} & \frac{4N-7}{(2N-1)(2N-3)} & \frac{16N^2-56N+51}{4(2N-1)(2N-3)} \end{bmatrix} \begin{bmatrix} \Theta \\ \Gamma \\ \Delta \end{bmatrix}^t \quad (29)$$

The usual (KIMURA and CROW 1963) one-locus equation follows from setting $\lambda = 1$:

$$\bar{F}_0^{t+1} = \frac{4N-3}{4N-2} \bar{F}_0^t. \quad (30)$$

Now consider the independent sampling scheme with two gametes, one male and one female, per parent. Each of the nine gametic set measures are now differ-

ent. For example, the two digametic measures have quite different expressions in terms of individual measures:

$$\bar{F}_{00}^{t+1} = \Theta_1^{t+1} = \frac{1}{N} \bar{\theta}_{BB} + \frac{N-1}{N} \bar{\theta}_{BB'}, \quad (31)$$

$$\Theta_2^{t+1} = \bar{\theta}_{BB'}; \quad (32)$$

While a male and a female gamete may come from one individual, with this sampling scheme two male or two female gametes cannot. Expanding $\bar{\theta}_{BB}$ and $\bar{\theta}_{BB'}$ to gametic set measures introduces Θ_2 , Γ_2 , Δ_1 and Δ_2 . These in turn are expressed as individual measures which, when expanded, involve the whole nine set measures. The complete set is thus of order nine. The expressions of each of the rest of the nine in terms of average individual measures for this independent sampling scheme with two gametes per parent are now listed, and the expansion of the ten individual measures needed, back to gametic set measures shown in the table of APPENDIX 4. (None of the ten measures involves three gametes from one individual so that row three in the table is not needed.)

$$\Gamma_1^{t+1} = \frac{2}{N} \gamma_{B, BB'} + \frac{N-2}{N} \gamma_{B, B'B''} \quad (33)$$

$$\Gamma_2^{t+1} = \frac{1}{N} \gamma_{B, BB'} + \frac{1}{N} \gamma_{B, B'B'} + \frac{N-2}{N} \gamma_{B, B'B''} \quad (34)$$

$$\Gamma_3^{t+1} = \bar{\gamma}_{B, B'B''} \quad (35)$$

$$\begin{aligned} \Delta_1^{t+1} = \frac{1}{N(N-1)} [\bar{\delta}_{BB', BB'} + \bar{\delta}_{BB, B'B'} + 2(N-2) \bar{\delta}_{BB', BB''} \\ + 2(N-2) \bar{\delta}_{BB, B'B''} + (N-2)(N-3) \bar{\delta}_{BB', B''B''}] \end{aligned} \quad (36)$$

$$\begin{aligned} \Delta_2^{t+1} = \frac{1}{N(N-1)} [2 \bar{\delta}_{BB, B'B'} + 4(N-2) \bar{\delta}_{BB, B'B''} \\ + (N-2)(N-3) \bar{\delta}_{BB', B''B''}] \end{aligned} \quad (37)$$

$$\Delta_3^{t+1} = \frac{2}{N} \bar{\delta}_{BB, B'B''} + \frac{1}{N} \bar{\delta}_{BB', BB''} + \frac{N-3}{N} \bar{\delta}_{BB', B''B''} \quad (38)$$

$$\Delta_4^{t+1} = \bar{\delta}_{BB', B''B''} \quad (39)$$

Combining equations (31)—(39) with the table of APPENDIX 4 gives the transition equation

$$\mathbf{u}_{t+1} = \Omega_1 \mathbf{u}_t,$$

where $\mathbf{u}'_t = [\Theta_1, \Theta_2, \Gamma_1, \Gamma_2, \Gamma_3, \Delta_1, \Delta_2, \Delta_3, \Delta_4]^t$ and Ω_1 is shown in equation (40).

$$a_1 = \left[\begin{array}{cccccccc} \frac{1+\lambda}{4N} + \frac{(1+\lambda)^2(N-1)}{8N} & \frac{(1+\lambda)^2(N-1)}{8N} & 0 & \frac{(1+\lambda)^2(N-1)}{2N} & 0 & \frac{(1-\lambda)^2(N-1)}{8N} & \frac{(1-\lambda)^2(N-1)}{8N} & 0 \\ \frac{(1+\lambda)^2}{8} & \frac{(1+\lambda)^2}{8} & 0 & \frac{1-\lambda^2}{2} & 0 & \frac{(1-\lambda)^2}{8} & \frac{(1-\lambda)^2}{8} & 0 \\ 0 & 0 & \frac{1}{4N} + \frac{(1+\lambda)(N-2)}{8N} & \frac{1}{2N} + \frac{(1+\lambda)(N-2)}{4N} & \frac{(1+\lambda)(N-2)}{8N} & \frac{(1-\lambda)(N-2)}{8N} & \frac{(1-\lambda)(N-2)}{4N} & 0 \\ \frac{1+\lambda}{8N} & \frac{1+\lambda}{8N} & \frac{1}{4N} + \frac{(1+\lambda)(N-2)}{8N} & \frac{3}{4N} + \frac{(1+\lambda)(N-2)}{4N} & \frac{(1+\lambda)(N-2)}{8N} & \frac{(1-\lambda)(N-1)}{8N} & \frac{(1-\lambda)(N-2)}{4N} & 0 \\ 0 & 0 & \frac{1+\lambda}{8} & \frac{1-\lambda}{4} & \frac{1+\lambda}{8} & \frac{1-\lambda}{8} & \frac{1-\lambda}{4} & 0 \\ \frac{1}{8N(N-1)} & \frac{1}{8N(N-1)} & \frac{N-2}{4N(N-1)} & \frac{1}{2N} & \frac{N-2}{4N(N-1)} & \frac{N^2-3N+3}{8N(N-1)} & \frac{N-2}{2N} & \frac{(N-2)(N-3)}{8N(N-1)} \\ \frac{1}{4N(N-1)} & \frac{1}{4N(N-1)} & \frac{N-2}{2N(N-1)} & \frac{1}{N} & \frac{N-2}{2N(N-1)} & \frac{N^2-3N+3}{4N(N-1)} & \frac{N-2}{2N} & \frac{(N-2)(N-3)}{8N(N-1)} \\ 0 & 0 & \frac{1}{4N} & \frac{1}{2N} & \frac{1}{4N} & \frac{N-1}{8N} & \frac{2N-3}{8N} & \frac{N-3}{8N} \\ 0 & 0 & 0 & 0 & 0 & \frac{1}{8} & \frac{1}{2} & \frac{1}{8} \end{array} \right] \quad (40)$$

When $\lambda = 1$ there are just two transition equations needed to determine Θ_1 :

$$\Theta_1^{t+1} = \frac{1}{2} \Theta_1^t + \frac{N-1}{2N} \Theta_2^t, \quad \Theta_2^{t+1} = \frac{1}{2} \Theta_1^t + \frac{1}{2} \Theta_2^t.$$

Solving these for the one-locus panmictic coefficient $\bar{F}_0 = \Theta_1$ gives:

$$\bar{F}_0^{t+1} = \bar{F}_0^t - \frac{1}{4N} \bar{F}_0^{t-1} \quad (41)$$

as given by COCKERHAM (1967).

The use of the transition matrix in determining the two-locus panmictic coefficient for an inbreeding system was discussed in WEIR and COCKERHAM (1968). For various values of the linkage parameter λ and population size N , successive powers of the matrix are computed numerically. Postmultiplying such matrices by the initial vector of set measures provides the vectors (and hence $\bar{F}_{00}$) in successive generations. If the one-locus coefficient is calculated at the same time, using the recurrence relations shown above for $\lambda = 1$, the whole inbreeding function can be found:

$$\bar{\mathbf{F}} = \begin{bmatrix} 1 & -2\bar{F}_0 + \bar{F}_{00} \\ \bar{F}_0 - \bar{F}_{00} \\ \bar{F}_0 - \bar{F}_{00} \\ \bar{F}_{00} \end{bmatrix}.$$

The largest eigenvalue of the transition matrix gives the limiting rate of decrease of double non identity (WEIR 1968). In practice this rate is found by taking

FIGURE 3.—Values of $\bar{F}_{11}$ for a monoecious mating scheme with equal chance gamete formation.

TABLE 2

Largest eigenvalues of transition matrices for monoecious populations with equal chance gamete formation

Linkage parameter, λ	Population size, N		
	4	8	16
0.0	.76956	.87959	.93858
0.2	.77119	.87992	.93863
0.4	.77485	.88070	.93877
0.6	.78361	.88277	.93915
0.8	.80759	.89037	.94085
0.9	.83353	.90329	.94411
1.0	.87500	.93750	.96875

the ratio of successive values of $\bar{F}_{00}^t$ and noting the limiting value as t becomes large. One minus the largest eigenvalue is termed the *rate of inbreeding*.

Some numerical calculations were performed for monoecious populations assuming non inbred initial populations—so that the initial vectors were composed entirely of 1's.

For equal-chance gamete formation the values of $\bar{F}_{11}$, the probability of double identity, are shown in Figure 3 and the largest eigenvalues of the transition matrix are shown in Table 2. For two gametes per parent the largest eigenvalues are given in Table 3 for both combined and independent sampling; but only for combined sampling are values of $\bar{F}_{11}$ given, Figure 4, since differences between the two are not easily distinguished graphically.

FIGURE 4.—Values of $\bar{F}_{11}$ for a monoecious mating scheme with combined sampling and two gametes per parent.

TABLE 3

Largest eigenvalues of transition matrices for monoecious populations with two gametes per parent for combined sampling and independent sampling (in parentheses) of gametic sets

Linkage parameter, λ	Population size, N		
	4	8	16
0.0	.86231 (.87067)	.93455 (.93646)	.96800 (.96850)
0.2	.86249 (.87085)	.93447 (.93648)	.96800 (.96850)
0.4	.86326 (.87161)	.93456 (.93658)	.96802 (.96851)
0.6	.86588 (.87413)	.93493 (.93694)	.96807 (.96856)
0.8	.87607 (.88385)	.93684 (.93879)	.96837 (.96886)
0.9	.89213 (.89898)	.94152 (.94340)	.96938 (.96988)
1.0	.92857 (.93301)	.96667 (.96771)	.98387 (.98412)

DIOECIOUS MATING

The mating scheme for dioecious populations is shown in Figure 5, where groups are labelled with m or f for males or females. Population size is assumed constant at N_m males and N_f females per generation. When $N_m = N_f = 1$ the system is full-sib mating, which was studied by COCKERHAM and WEIR (1968).

In this section equal-chance gamete formation and combined sampling with two gametes per parent will be considered, but the treatment of independent sampling with two gametes per parent is outlined briefly in APPENDIX 5. As in the monoecious case, several of the possible gametic set measures have the same value. The nine distinct gametic set measures, with an abbreviated notation, are now listed. For these measures, subscripts refer to donor groups.

$$\begin{aligned}
 \Theta_1^t &= \psi_{mf}^t & \Delta_1^t &= \zeta_{mm, ff}^t \\
 \Theta_2^t &= \frac{1}{2} (\psi_{mm}^t + \psi_{ff}^t) & \Delta_2^t &= \zeta_{mf, mf}^t \\
 \Gamma_1^t &= \frac{1}{2} (v_{m, ff}^t + v_{f, mm}^t) & \Delta_3^t &= \frac{1}{2} (\zeta_{mm, mf}^t + \zeta_{ff, mf}^t) \\
 \Gamma_2^t &= \frac{1}{2} (v_{m, mf}^t + v_{f, fm}^t) & \Delta_4^t &= \frac{1}{2} (\zeta_{mm, mm}^t + \zeta_{ff, ff}^t) \\
 \Gamma_3^t &= \frac{1}{2} (v_{m, mm}^t + v_{f, ff}^t)
 \end{aligned}$$

FIGURE 5.—Dioecious mating scheme.

Because there may be different numbers of males and females, the gametic sampling probabilities for the two groups can be different so that it is not possible to equate such measures as ψ_{mm}^t and ψ_{ff}^t . However, each has a very similar expression in terms of average individual measures so it is convenient to work with their average. Each locus is expected to be equally inbred, so that $\xi_{mf, mf}^t$ represents the common value of that measure and the equal quantity $\xi_{fm, fm}^t$.

Once again the inbreeding function of a generation, male or female group, is expressed as a gametic set measure:

$$\bar{F}_{00}^{t+1} = \bar{F}_{00m}^{t+1} = \bar{F}_{00f}^{t+1} = \psi_{mf}^{t+1} = \Theta_1^{t+1}.$$

In expressing Θ_1 as a combination of individual measures, and expanding these back to gametic set measures it is found that the complete set of gametic set measures is just the nine listed above. While the expressions of the nine gametic set measures in terms of average individual measures could be deduced from equations (14)—(23) they will be given here to illustrate the averaging of set measures with similar expressions.

From (23):

$$\Theta_1^t = \bar{\theta}_{mf}^t. \quad (42)$$

From (14):

$$\Theta_2^t = \frac{1}{2} (P_m^2 \bar{\theta}_{mm}^t + P_f^2 \bar{\theta}_{ff}^t) + \frac{1}{2} (P_m^{11} \bar{\theta}_{mm'}^t + P_f^{11} \bar{\theta}_{ff'}^t),$$

but $\bar{\theta}_{mm}^t = \bar{\theta}_{ff}^t$ and $\bar{\theta}_{mm'}^t = \bar{\theta}_{ff'}^t$, so that setting $P^2 = \frac{1}{2}(P_m^2 + P_f^2)$ and

$$P^{11} = \frac{1}{2} (P_m^{11} + P_f^{11})$$

$$\Theta_2^t = P^2 \bar{\theta}_{mm}^t + P^{11} \bar{\theta}_{mm'}^t. \quad (43)$$

Note that for equal chance gamete formation, and/or combined sampling, the recipient group for a set of gametes need not appear in the sampling probabilities. Proceeding in the same manner, and defining these further average probabilities;

$$P^3 = \frac{1}{2} (P_m^3 + P_f^3)$$

$$P^{21} = \frac{1}{2} (P_m^{21} + P_f^{21})$$

$$P^{111} = \frac{1}{2} (P_m^{111} + P_f^{111})$$

$$P^{22} = \frac{1}{2} (P_m^{22} + P_f^{22})$$

$$P^{211} = \frac{1}{2} (P_m^{211} + P_f^{211})$$

$$P^{31} = \frac{1}{2} (P_m^{31} + P_f^{31})$$

$$P^{2,2} = P_m^2 P_f^2$$

$$P^{1111} = \frac{1}{2} (P_m^{1111} + P_f^{1111})$$

$$P^{11,11} = P_m^{11} P_f^{11}$$

$$P^{2,11} = P_m^2 P_f^{11} + P_m^{11} P_f^2$$

the remaining expressions are obtained.

From (15):

$$\Gamma_1^t = P^2 \bar{\gamma}_{m,ff}^t + P^{11} \bar{\gamma}_{m,ff'}^t. \quad (44)$$

From (16):

$$\Gamma_2^t = P^2 \bar{\gamma}_{m, mf}^t + P^{11} \bar{\gamma}_{m, m'f}^t. \quad (45)$$

From (17):

$$\Gamma_3^t = P^3 \bar{\gamma}_{m, mm}^t + \frac{1}{3} P^{21} (\bar{\gamma}_{m, m'm'}^t + 2 \bar{\gamma}_{m, mm'}^t) + P^{111} \bar{\gamma}_{m, m'm''}^t. \quad (46)$$

From (19):

$$\Delta_1^t = P^{2,2} \bar{\delta}_{mm, ff}^t + P^{2,11} \bar{\delta}_{mm', ff}^t + P^{11,11} \bar{\delta}_{mm', ff'}^t. \quad (47)$$

From (20):

$$\Delta_2^t = P^{2,2} \bar{\delta}_{mf, mf}^t + P^{2,11} \bar{\delta}_{mf, m'f}^t + P^{11,11} \bar{\delta}_{mf, m'f'}^t. \quad (48)$$

From (21):

$$\Delta_3^t = P^3 \bar{\delta}_{mm, mf}^t + \frac{1}{3} P^{21} (\bar{\delta}_{mm', mf}^t + 2 \bar{\delta}_{mm, m'f}^t) + P^{111} \bar{\delta}_{mm', m'f}^t. \quad (49)$$

From (22):

$$\begin{aligned} \Delta_4^t = & P^4 \bar{\delta}_{mm, mm}^t + P^{31} \bar{\delta}_{mm, mm'}^t + \frac{1}{3} P^{22} (2 \bar{\delta}_{mm, m'm'}^t + \bar{\delta}_{mm', mm}^t) \\ & + \frac{1}{3} P^{211} (2 \bar{\delta}_{mm, m'm''}^t + \bar{\delta}_{mm', mm''}^t) + P^{1111} \bar{\delta}_{mm', m''m''}^t. \end{aligned} \quad (50)$$

The expansions of each of the twenty-eight individual measures back to gametic set measures are all contained in the table of APPENDIX 4. Many of them have the same expansion. Each of $\bar{\theta}_{mf}^{t+1}$ and $\bar{\theta}_{mm'}^{t+1}$, for example involve gametes from distinct individuals and so have a common expansion—that of $\bar{\theta}_{BB'}^{t+1}$. The other equivalences in expansion are

$\bar{\gamma}_{m, mm}^{t+1}, \bar{\delta}_{mm, mm}^{t+1}$	as	$\bar{\gamma}_{B, BB}^{t+1}, \bar{\delta}_{BB, BB}^{t+1}$
$\bar{\gamma}_{m, mf}^{t+1}, \bar{\gamma}_{m, mm'}^{t+1}, \bar{\delta}_{mm, mm'}^{t+1}, \bar{\delta}_{mm, mf}^{t+1}$	as	$\bar{\gamma}_{B, BB'}^{t+1}, \bar{\delta}_{BB, BB'}^{t+1}$
$\bar{\gamma}_{m, ff'}^{t+1}, \bar{\gamma}_{m, m'f'}^{t+1}, \bar{\gamma}_{m, m'm''}^{t+1}$	as	$\bar{\gamma}_{B, B'B''}^{t+1}$
$\bar{\delta}_{mm, ff}^{t+1}, \bar{\delta}_{mm, m'm'}^{t+1}$	as	$\bar{\delta}_{BB, B'B'}^{t+1}$
$\bar{\delta}_{mf, mf}^{t+1}, \bar{\delta}_{mm', mm'}^{t+1}$	as	$\bar{\delta}_{BB', BB'}^{t+1}$
$\bar{\delta}_{mm', ff}^{t+1}, \bar{\delta}_{mm, m'f}^{t+1}, \bar{\delta}_{mm, m'm''}^{t+1}$	as	$\bar{\delta}_{BB, B'B''}^{t+1}$
$\bar{\delta}_{mf, m'f}^{t+1}, \bar{\delta}_{mm', mf}^{t+1}, \bar{\delta}_{mm', mm''}^{t+1}$	as	$\bar{\delta}_{BB', BB''}^{t+1}$
$\bar{\delta}_{mm', ff'}^{t+1}, \bar{\delta}_{mf, m'f'}^{t+1}, \bar{\delta}_{mm', m''f}^{t+1}, \bar{\delta}_{mm', m''m''}^{t+1}$	as	$\bar{\delta}_{BB', B''B''}^{t+1}$

Combining equations (42)–(50) with the table of APPENDIX 4 provides the transition equation

$$\mathbf{v}_{t+1} = \Omega_2 \mathbf{v}_t$$

where $\mathbf{v}_t' = [\Theta_1, \Theta_2, \Gamma_1, \Gamma_2, \Gamma_3, \Delta_1, \Delta_2, \Delta_3, \Delta_4]^t$ and Ω_2 is displayed in equation (51).

[illegible]

Substituting $\lambda = 1$ into (51) shows that just two equations are necessary to determine the panmictic coefficient. They are

$$\begin{aligned}\Theta_1^{t+1} &= \frac{1}{2} \Theta_1^t + \frac{1}{2} \Theta_2^t \\ \Theta_2^{t+1} &= \frac{1}{2} \Theta_1^t + \frac{1}{2} P^{11} \Theta_2^t.\end{aligned}$$

Eliminating Θ_2 gives the usual (WRIGHT 1931) one-locus equation which, with $\bar{F}_0$ written for Θ_1 , is

$$\bar{F}_0^{t+1} = \bar{F}_0^t + \frac{1}{4} P^2 (\bar{F}_0^{t-1} - 2\bar{F}_0^t),$$

so that $2/P^2$ is the "overall (digametic) effective number" N_e .

Another check on the matrix is to set $N_m = N_f = 1$. This implies that $P^2 = P^{2,2} = 1$ and that the other P 's are zero. These values substituted into (51) show that $\Theta_1, \Theta_2, \Gamma_1, \Gamma_2, \Delta_1, \Delta_2$ are sufficient to determine Θ_1 and that, as expected, the matrix is that given by COCKERHAM and WEIR (1968) for sib mating.

Some numerical calculations were performed for dioecious populations. Values of the largest eigenvalues of the transition matrices are given in Table 4 for equal-chance gamete formation and in Table 5 for two gametes per parent with combined and independent sampling. The eigenvalues for independent sampling and two gametes per parent are for the matrix of APPENDIX 5. The results for $\bar{F}_{11}$ are not shown graphically since they are so similar to those for monoecious populations.

The appropriate values of the sampling probabilities are found in APPENDIX 3, and for equal chance gamete formation:

$$N_e = 2/P^2 = 4N_mN_f/(N_m+N_f)$$

as given by WRIGHT (1931). Table 4 shows two cases where different numbers of males and females give the same values of N_e . These combinations are: $N_m = N_f = 4$ and $N_m = 3, N_f = 6$ which both give $N_e = 8$, and $N_m = 5, N_f = 6$ and

TABLE 4
Largest eigenvalues of transition matrices for dioecious populations with equal chance gamete formation

Population size			Linkage parameter, λ						
N_m	N_f	N_e	0.0	0.2	0.4	0.6	0.8	0.9	1.0
1	2	2.667	.71747	.71881	.72305	.73439	.76570	.79789	.84650
2	2	4.000	.79404	.79479	.79692	.80287	.82204	.84639	.89034
2	4	5.333	.83791	.83843	.83975	.84336	.85597	.87700	.91496
3	3	6.000	.85365	.85403	.85504	.85789	.86830	.88484	.92356
4	4	8.000	.88660	.88682	.88738	.88897	.89524	.90683	.94139
3	6	8.000	.88658	.88682	.88740	.88902	.89530	.90686	.94139
4	6	9.600	.90394	.90409	.90447	.90555	.90997	.91889	.95062
5	6	10.909	.91463	.91474	.91502	.91583	.91925	.92655	.95626
3	30	10.909	.91458	.91475	.91510	.91600	.91949	.92672	.95626
8	8	16.000	.94044	.94049	.94060	.94093	.94242	.94613	.96973

TABLE 5

Largest eigenvalues of transition matrices for dioecious populations with two gametes per parent with combined sampling and independent sampling (in parenthesis) of gametic sets

$$N_m = N_f = N/2$$

Linkage parameter, λ	Population size, N					
	4		8		16	
0.0	.85299	(.85617)	.93231	(.93324)	.96749	(.96773)
0.2	.85315	(.85676)	.93232	(.93332)	.96749	(.96774)
0.4	.85395	(.85810)	.93242	(.93349)	.96751	(.96776)
0.6	.85668	(.86152)	.93280	(.93398)	.96756	(.96783)
0.8	.86742	(.87304)	.93475	(.93612)	.96786	(.96818)
0.9	.88445	(.89005)	.93960	(.94111)	.96888	(.96925)
1.0	.92356	(.92732)	.96556	(.96655)	.98361	(.98386)

$N_m = 3$, $N_f = 30$ which both give $N_e = 10.909$. For $\lambda = 1$, the one locus case, the largest eigenvalues must be equal for each pair because of the equal digametic effective numbers. The eigenvalues stay close for other linkage values but the relation is not a simple one, and must depend on the trigametic, quadrigametic and bi-digametic effective numbers (which are different for the different N_m , N_f pairs).

All the eigenvalues shown for two gametes per parent with combined and independent sampling are for equal numbers ($N/2$) of males and females.

DISCUSSION

By defining averages of, and gametic set counterparts for, the individual inbreeding measures of WEIR and COCKERHAM (1968) it is possible to determine two locus inbreeding functions for matings among finite groups. With these functions determined, the effects of linkage on the probability of two loci carrying genes identical by descent can be discussed.

Figures 3 and 4 illustrate the inbreeding process for monoecious populations. The effects are similar in nature for dioecious populations, and for pedigree systems of mating (WEIR and COCKERHAM 1968). The maximum effect of linkage occurs of course for $\lambda = 1$, in which case $\bar{F}_{11}(1) = \bar{F}_1$, and the effect, $\bar{F}_{11}(1) - \bar{F}_{11}(0)$, increases with time and has a maximum near the generation in which $\bar{F}_{11}(1) = \bar{F}_1 = 0.5$ and then decreases to zero at complete double identity. In general the effect $\bar{F}_{11}(\lambda) - \bar{F}_{11}(0)$ decreases rapidly as a polynomial function of λ and has a maximum in a much earlier generation as λ decreases.

An interesting but relatively unimportant difference occurs between finite populations and pedigree systems of mating. It was demonstrated for individual pedigrees, and thus pedigree systems of mating, that $F_{11}(0) = F_1^2$ (WEIR and COCKERHAM 1968). For finite populations $\bar{F}_{11}(0) > \bar{F}_1^2$. (This is demonstrated in the next paragraph.) Sampling among parents for gametes and/or the inclusion of random elements in the uniting of gametes leads to a correlation in identity by descent even between unlinked loci because genes at both loci are of necessity

included in each gamete. This combined sampling and union of genes at both loci provides another kind of information.

All individuals in a particular group do have specific pedigrees, which are not generally the same. For the r th individual, $F_{11r}(0) = F_{1r}^2$ as shown in WEIR and COCKERHAM (1968). Note that these two quantities are expected values over all individuals with the same pedigree. The coefficients $\bar{F}_{11}$ and $\bar{F}_1$, on the other hand, are averages over all the possible pedigrees members of the group might have—i.e.,

$$\bar{F}_{11}(0) = E[F_{11r}(0)] = E[(F_{1r})^2]$$

$$\bar{F}_1 = E[F_{1r}] .$$

Thus,

$$\bar{F}_{11}(0) - \bar{F}_1^2 = \sigma_{F_1}^2$$

where $\sigma_{F_1}^2$ is the variance among the inbreeding coefficients of individuals for one of the loci; the two inbreeding coefficients of individuals being perfectly correlated. Since the expected value of a quantity squared exceeds the square of the expected value of the quantity, $\bar{F}_{11}(0) > \bar{F}_1^2$.

The identity disequilibrium function $\eta_{11}(\lambda)$, $\bar{F}_{11}(\lambda) - \bar{F}_1^2$, may be divided into two parts

$$\eta_{11}(\lambda) = \eta'_{11}(\lambda) + \sigma_{F_1}^2$$

so that

$$\bar{F}_{11}(\lambda) - \bar{F}_1^2 = [\bar{F}_{11}(\lambda) - \bar{F}_{11}(0)] + [\bar{F}_{11}(0) - \bar{F}_1^2]$$

where $\eta'_{11}(\lambda)$ shows the effects of linkage and $\sigma_{F_1}^2$ the correlated effects involved in sampling and uniting of the genes.

The variance $\sigma_{F_1}^2$ is too small to allow $\bar{F}_{11}(0)$ and $\bar{F}_1^2$ to be distinguished graphically, and after a few generations it is essentially zero. It decreases as $N > 1$ increases, decreases as the digametic effective population number increases, and decreases with the avoidance of mating relatives. Hence $\eta'_{11}(\lambda)$ can be approximated closely by $\eta_{11}(\lambda)$ which accounts for the maximum η'_{11} occurring at the same time as does $\eta_{11}(1) = \bar{F}_1(1 - \bar{F}_1)$, ($\bar{F}_1 = 0.5$).

As for asymptotic rates of inbreeding, i.e. one minus the largest eigenvalue, under consideration are the rates for the range $\bar{F}_{11}(1) = \bar{F}_1$ to $\bar{F}_{11}(0) \approx \bar{F}_1^2$, the rates for intermediate values of λ always ranking the same as λ . Thus the effects of population size, avoidance of the mating of relatives, reduction of the gametic variance and type of sampling of gametic sets on the asymptotic rate for $\bar{F}_{11}$ will be qualitatively the same as for $\bar{F}_1$ and $\bar{F}_1^2$ and quantitatively between the effects on $\bar{F}_1$ and $\bar{F}_1^2$ dependent upon the value of λ . These effects may be summarized and some verified from the tables of asymptotic rates. The avoidance of mating relatives increases the generation of onset of inbreeding to the degree of avoidance. With equal chance gamete formation avoidance decreases the inbreeding in every generation and thus the asymptotic rate. This result is principally because of the

concomitant reduction in gametic variance, which, when further reduced for any system, reduces all rates. With two gametes per parent—i.e., no gametic variance, and combined sampling of gametic sets, the avoidance of mating relatives, while increasing the inbreeding in the generation of onset, reduces the early rate and increases the asymptotic rate. Further, the substitution of independent for combined sampling of gametic sets increases the initial inbreeding and reduces the asymptotic rate.

SUMMARY

Inbreeding systems involving matings between finite groups are studied when two linked, autosomal loci of a diploid organism are considered. The digametic, trigametic, and quadrigametic inbreeding measures used in an earlier paper (WEIR and COCKERHAM 1968) for individuals are extended to apply to groups of individuals and to sets of gametes.—Transition equations relating values in successive generations of gametic set measures are established. For a general pedigree, when each group provides only one set of gametes, these equations may be found directly, otherwise gametic set measures must first be expressed as linear combinations of average individual measures and then these expanded back to gametic set measures. While such expansions are independent of the distribution of gametes from parents, the expression of set measures as individual measures does depend on gametic distributions. The transition matrix is employed to give numerical values of the average probability of double identity by descent for members of a group, and for the limiting rate of loss of double non identity.—An identity disequilibrium function with two components, one for the correlated effects of sampling and union of gametes in finite populations, and one for the effects of linkage, is defined.—The procedures are illustrated for monoecious and dioecious populations.

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APPENDIX 1

Expressions and expected values for sampling probabilities

If the *i*th member of group B contributes k_i gametes to an output set of N_A gametes received

by group A, the gametic sampling probabilities have the following expressions. All summations are over the integers 1 to N_B (the number of members of group B).

$$\begin{aligned}
 P_{B_A}^2 &= \frac{\sum_i k_i (k_i - 1)}{N_A (N_A - 1)} & P_{B_A}^4 &= \frac{\sum_i k_i (k_i - 1) (k_i - 2) (k_i - 3)}{N_A (N_A - 1) (N_A - 2) (N_A - 3)} \\
 P_{B_A}^{11} &= \frac{\sum_i k_i (N_A - k_i)}{N_A (N_A - 1)} & P_{B_A}^{31} &= \frac{4 \sum_i k_i (k_i - 1) (k_i - 2) (N_A - k_i)}{N_A (N_A - 1) (N_A - 2) (N_A - 3)} \\
 P_{B_A}^3 &= \frac{\sum_i k_i (k_i - 1) (k_i - 2)}{N_A (N_A - 1) (N_A - 2)} & P_{B_A}^{22} &= \frac{3 \sum_{i \neq j} k_i (k_i - 1) k_j (k_j - 1)}{N_A (N_A - 1) (N_A - 2) (N_A - 3)} \\
 P_{B_A}^{21} &= \frac{3 \sum_i k_i (k_i - 1) (N_A - k_i)}{N_A (N_A - 1) (N_A - 2)} & P_{B_A}^{211} &= \frac{6 \sum_{i \neq j} k_i (k_i - 1) k_j (N_A - k_i - k_j)}{N_A (N_A - 1) (N_A - 2) (N_A - 3)} \\
 P_{B_A}^{111} &= \frac{\sum_{i \neq j} k_i k_j (N_A - k_i - k_j)}{N_A (N_A - 1) (N_A - 2)} & P_{B_A}^{1111} &= \frac{\sum_{i \neq j \neq l} k_i k_j k_l (N_A - k_i - k_j - k_l)}{N_A (N_A - 1) (N_A - 2) (N_A - 3)}
 \end{aligned}$$

When the k_i are identically distributed, the expected values of the probabilities can be expressed in terms of these central moments:

$$\begin{aligned}
 \sigma_{B_A}^2 &= E[\sum_i (k_i - \bar{k}_{B_A})^2 / N_B] & m_{4B_A} &= E[\sum_i (k_i - \bar{k}_{B_A})^4 / N_B] \\
 m_{3B_A} &= E[\sum_i (k_i - \bar{k}_{B_A})^3 / N_B] & m_{22B_A} &= E[\sum_i \sum_j (k_i - \bar{k}_{B_A})^2 (k_j - \bar{k}_{B_A})^2 / N_B]
 \end{aligned}$$

Note that expectations are being taken over all possible sets of N_A gametes provided by group B, where $\bar{k}_{B_A} = N_A / N_B$. The expected values of the four probabilities that need evaluating follow.

$$\begin{aligned}
 P_{B_A}^2 &= \frac{\sigma_{B_A}^2 + \bar{k}_{B_A} (\bar{k}_{B_A} - 1)}{\bar{k}_{B_A} (N_A - 1)} \\
 P_{B_A}^3 &= \frac{m_{3B_A} + 3(\bar{k}_{B_A} - 1) \sigma_{B_A}^2 + \bar{k}_{B_A} (\bar{k}_{B_A} - 1) (\bar{k}_{B_A} - 2)}{\bar{k}_{B_A} (N_A - 1) (N_A - 2)} \\
 P_{B_A}^4 &= \frac{m_{4B_A} + 2(2\bar{k}_{B_A} - 3) m_{3B_A} + (6\bar{k}_{B_A}^2 - 18\bar{k}_{B_A} + 11) \sigma_{B_A}^2 + \bar{k}_{B_A} (\bar{k}_{B_A} - 1) (\bar{k}_{B_A} - 2) (\bar{k}_{B_A} - 3)}{\bar{k}_{B_A} (N_A - 1) (N_A - 2) (N_A - 3)} \\
 P_{B_A}^{22} &= \{ 3(N_B - 1) m_{22B_A} + 6(1 - 2\bar{k}_{B_A}) m_{3B_A} + 3[2N_B \bar{k}_{B_A} (\bar{k}_{B_A} - 1) - (6\bar{k}_{B_A}^2 - 6\bar{k}_{B_A} + 1)] \sigma_{B_A}^2 \\
 &\quad + 3(N_B - 1) \bar{k}_{B_A}^2 (\bar{k}_{B_A} - 1)^2 \} / [\bar{k}_{B_A} (N_A - 1) (N_A - 2) (N_A - 3)]
 \end{aligned}$$

APPENDIX 2

Expansions of average individual measures with repeated subscripts

This appendix corresponds to the one in WEIR and COCKERHAM (1968). Each of the average individual measures with repeated subscripts listed in equations (14) — (22) is expanded back to gametic set measures of the previous generation. All expansions refer to the pedigree of Figure 1, and only the fourth components of measures are used.

$$\begin{aligned}
\bar{\gamma}_{B, BB} &= \frac{1}{4} \psi_{D_B E_B} = \frac{1}{4} \bar{F}_B \\
\bar{\delta}_{BB, BB} &= \bar{\gamma}_{B, BB} \\
\bar{\gamma}_{C, BB} &= \bar{\gamma}_{C, (DE)(DE)} = \frac{1}{4} [\psi_{C_B D_B} + \psi_{C_B E_B}] + \frac{1}{2} \nu_{C_B, D_B E_B} \\
\bar{\delta}_{BB, GH} &= \bar{\delta}_{(DE)(DE), GH} = \frac{1}{4} [\nu_{D_B, G_C H_C} + \nu_{E_B, G_C H_C}] + \frac{1}{2} \xi_{D_B E_B, G_C H_C} \\
\bar{\delta}_{BB, CC} &= \bar{\delta}_{BB, (GH)(GH)} = \frac{1}{4} [\nu_{G_C, B_A B_A} + \nu_{H_C, B_A B_A}] + \frac{1}{2} \xi_{B_A B_A, G_C H_C} \\
\bar{\gamma}_{B, BC} &= \bar{\gamma}_{(DE), (DE)C} = \frac{1}{4} [\nu_{D_B, C_A E_B} + \nu_{E_B, C_A D_B}] \\
\bar{\delta}_{BB, BC} &= \bar{\gamma}_{B, BC} \\
\bar{\delta}_{BC, BC} &= \bar{\xi}_{D_B G_C, E_B H_C} \\
\bar{\delta}_{BG, BH} &= \bar{\delta}_{(DE)G, (DE)H} = \frac{1}{2} \xi_{D_B H_C, E_B G_C} \\
\bar{\delta}_{GB, HB} &= \bar{\delta}_{G(DE), H(DE)} = \frac{1}{2} \xi_{H_C D_B, G_C E_B}
\end{aligned}$$

APPENDIX 3

Numerical values of sampling probabilities

For an equal chance gamete formation scheme, the k_i for the N_A gametes in a set provided by group B are identically binomially distributed $B_i(N_A, 1/N_B)$. The required central moments of this distribution are

$$\begin{aligned}
\sigma_{B_A}^2 &= N_A(N_B-1)/N_B^2 & m_{4B_A} &= 3N_A^2(N_B-1)^2/N_B^4 + N_A(N_B-1)(N_B^2-6N_B+6)/N_B^4 \\
m_{3B_A} &= N_A(N_B-1)(N_B-2)/N_B^3 & m_{22B_A} &= N_A^2(N_B^2-2N_B+3)/N_B^4 - N_A(N_B^2-4N_B+6)/N_B^4
\end{aligned}$$

The four sampling probabilities are thus given by

$$\begin{aligned}
P_{B_A}^2 &= \frac{1}{N_B} & P_{B_A}^3 &= \frac{1}{N_B^2} \\
P_{B_A}^4 &= \frac{1}{N_B^3} & P_{B_A}^{22} &= \frac{3(N_B-1)}{N_B^3}
\end{aligned}$$

If each member of group B is constrained to provide exactly N_A/N_B gametes, then all the central moments of the k_i distribution are zero. The sampling probabilities are thus

$$\begin{aligned}
P_{B_A}^2 &= \frac{\bar{k}_{B_A}-1}{N_A-1} & P_{B_A}^3 &= \frac{(\bar{k}_{B_A}-1)(\bar{k}_{B_A}-2)}{(N_A-1)(N_A-2)} \\
P_{B_A}^4 &= \frac{(\bar{k}_{B_A}-1)(\bar{k}_{B_A}-2)(\bar{k}_{B_A}-3)}{(N_A-1)(N_A-2)(N_A-3)} & P_{B_A}^{22} &= \frac{3(\bar{k}_{B_A}-1)^2 \bar{k}_{B_A}(N_B-1)}{(N_A-1)(N_A-2)(N_A-3)}
\end{aligned}$$

With constant population size, when combined sampling is considered, each parent contributes two gametes, so that $\bar{k}_{B_A} = 2$.

APPENDIX 4
Expansion of individual measures in terms of gametic set measures

	θ_1^t	θ_2^t	Γ_1^t	Γ_2^t	Γ_3^t	Δ_1^t	Δ_2^t	Δ_3^t	Δ_4^t
$\bar{\theta}_{BB}^{t+1}$	$\frac{1+\lambda^2}{4}$	0	0	0	0	0	0	0	0
$\bar{\theta}_{BB'}^{t+1}$	$\frac{(1+\lambda)^2}{8}$	$\frac{(1+\lambda)^2}{8}$	0	$\frac{1-\lambda^2}{2}$	0	$\frac{(1-\lambda)^2}{8}$	$\frac{(1-\lambda)^2}{8}$	0	0
$\bar{\gamma}_{B, BB'}^{t+1} \bar{\delta}_{BB, BB}^{t+1}$	$\frac{1}{4}$	0	0	0	0	0	0	0	0
$\bar{\gamma}_{B, B'B'}^{t+1}$	$\frac{1+\lambda}{8}$	$\frac{1+\lambda}{8}$	0	$\frac{1}{2}$	0	$\frac{1-\lambda}{8}$	$\frac{1-\lambda}{8}$	0	0
$\bar{\gamma}_{B, BB'}^{t+1} \bar{\delta}_{BB, BB'}^{t+1}$	0	0	$\frac{1}{4}$	$\frac{1}{4}$	0	0	0	0	0
$\bar{\gamma}_{B, B'B'}^{t+1}$	0	0	$\frac{1+\lambda}{8}$	$\frac{1+\lambda}{4}$	$\frac{1+\lambda}{8}$	$\frac{1-\lambda}{8}$	$\frac{1-\lambda}{8}$	$\frac{1-\lambda}{4}$	0
$\bar{\delta}_{BB, B'B'}^{t+1}$	$\frac{1}{8}$	$\frac{1}{8}$	0	$\frac{1}{2}$	0	$\frac{1}{8}$	$\frac{1}{8}$	0	0
$\bar{\delta}_{BB', BB'}^{t+1}$	0	0	0	0	0	$\frac{1}{4}$	0	0	0
$\bar{\delta}_{BB', B'B''}^{t+1}$	0	0	$\frac{1}{8}$	$\frac{1}{4}$	$\frac{1}{8}$	$\frac{1}{8}$	$\frac{1}{8}$	$\frac{1}{4}$	0
$\bar{\delta}_{BB', BB''}^{t+1}$	0	0	0	0	0	$\frac{1}{4}$	0	$\frac{1}{4}$	0
$\bar{\delta}_{BB', B''B''}^{t+1}$	0	0	0	0	0	$\frac{1}{4}$	$\frac{1}{8}$	$\frac{1}{4}$	$\frac{1}{8}$

APPENDIX 5

Diocious system with independent sampling

Independent sampling, and reduced gametic variance prevents equality of many of the gametic set measures. The simplest situation is when the numbers of males and females are held constant and equal each generation. For this situation the measures together with an abbreviated notation are now listed.

$$\begin{aligned}
 \theta_{11}^t &= \psi_{m,f}^t & \Delta_{12}^t &= \frac{1}{2} (\zeta_{m_m m_m, f_m f_m}^t + \zeta_{m_m m_m, f_f f_f}^t) \\
 \theta_{21}^t &= \psi_{m_m m_f}^t & \Delta_{13}^t &= \frac{1}{2} (\zeta_{m_m m_m, f_m f_f}^t + \zeta_{m_f m_f, f_m f_f}^t) \\
 \theta_{22}^t &= \frac{1}{2} (\psi_{m_m m_m}^t + \psi_{m_f m_f}^t) & \Delta_{21}^t &= \zeta_{m_m f_m, m_f f_f}^t \\
 \Gamma_{11}^t &= \nu_{m, f_m f_f}^t & \Delta_{22}^t &= \frac{1}{2} (\zeta_{m_m f_m, m_m f_m}^t + \zeta_{m_f f_f, m_f f_f}^t) \\
 \Gamma_{12}^t &= \frac{1}{2} (\nu_{m, f_m f_m}^t + \nu_{m, f_f f_f}^t) & \Delta_{23}^t &= \frac{1}{2} (\zeta_{m_m f_m, m_m f_f}^t + \zeta_{m_f f_f, m_f f_m}^t) \\
 \Gamma_{21}^t &= \nu_{m_m, m_f f_f}^t & \Delta_{31}^t &= \frac{1}{2} (\zeta_{m_m m_m, m_m f_f}^t + \zeta_{m_f m_f, m_f f_f}^t) \\
 \Gamma_{22}^t &= \frac{1}{2} (\nu_{m_m, m_m f_f}^t + \nu_{m_f, m_f f_f}^t) & \Delta_{32}^t &= \frac{1}{2} (\zeta_{m_m m_m, m_f f_f}^t + \zeta_{m_f m_f, m_m f_f}^t) \\
 \Gamma_{31}^t &= \frac{1}{2} (\nu_{m_m, m_m m_m}^t + \nu_{m_f, m_f m_f}^t) & \Delta_{33}^t &= \frac{1}{2} (\zeta_{m_m m_f, m_m f_f}^t + \zeta_{m_f m_m, m_f f_f}^t) \\
 \Gamma_{32}^t &= \frac{1}{2} (\nu_{m_m, m_m m_f}^t + \nu_{m_f, m_m m_f}^t) & \Delta_{41}^t &= \frac{1}{2} (\zeta_{m_m m_m, m_m m_m}^t + \zeta_{m_f m_f, m_f m_f}^t) \\
 \Gamma_{33}^t &= \frac{1}{2} (\nu_{m_f, m_m m_m}^t + \nu_{m_m, m_f m_f}^t) & \Delta_{42}^t &= \frac{1}{2} (\zeta_{m_m m_m, m_m m_f}^t + \zeta_{m_f m_f, m_f m_m}^t) \\
 \Delta_{11}^t &= \zeta_{m_m m_f, f_m f_f}^t & \Delta_{43}^t &= \zeta_{m_m m_m, m_f m_f}^t \\
 & & \Delta_{44}^t &= \zeta_{m_m m_f, m_m m_f}^t
 \end{aligned}$$

Each of these gametic set measures represents the average of itself and that measure obtained by replacing m by f and f by m in all positions of the subscripts.

As in the monocious case, these measures are expressed in terms of (57) individual measures, which in turn are expanded back to gametic set measures of the previous generation. Because of equal numbers of each sex, there are just 28 distinct individual measures and expansions (WEIR 1968). The resulting transition matrix, Ω_3 , is now given. Because of its size it is partitioned into four sub-matrices:

$$\Omega_3 = \begin{array}{c} 23 \times 23 \\ \left[\begin{array}{cc|cc} \Omega_4 & & \Omega_5 & \\ 10 \times 10 & & 10 \times 13 & \\ \hline & \Omega_6 & & \Omega_7 \\ 13 \times 10 & & 13 \times 13 & \end{array} \right] \end{array}$$

For convenience, the appropriate gametic set measures are listed along the sides of each of the sub-matrices.

For complete linkage, just the three measures Θ_{11} , Θ_{21} , Θ_{22} are necessary and the transition equation for the (one-locus) panmictic coefficient is seen to be

$$\bar{F}_0^{t+3} = \bar{F}_0^{t+2} - \frac{1}{4N} \bar{F}_0^t$$

as given by COCKERHAM (1967). For a population of size $N=2$, the necessary complete set of measures is Θ_{11} , Θ_{21} , Γ_{11} , Γ_{21} , Δ_{11} , Δ_{21} and the matrix reduces to that for sib mating (COCKERHAM and WEIR 1968).

$$\Omega_4 =$$

Θ_{11}^{t+1}	Θ_{11}^t	Θ_{21}^t	Θ_{22}^t	Γ_{11}^t	Γ_{12}^t	Γ_{21}^t	Γ_{22}^t	Γ_{31}^t	Γ_{32}^t	Γ_{33}^t
Θ_{11}^{t+1}	$\frac{(1+\lambda)^2}{8}$	$\frac{(1+\lambda)^2}{8}$	0	0	0	$\frac{1-\lambda^2}{2}$	0	0	0	0
Θ_{21}^{t+1}	$\frac{1+\lambda^2}{2N} + \frac{(1+\lambda)^2 N-2}{8N}$	0	$\frac{(1+\lambda)^2 N-2}{8N}$	0	0	0	$\frac{1-\lambda^2 N-2}{2N}$	0	0	0
Θ_{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
Γ_{11}^{t+1}	$\frac{1+\lambda}{4N}$	$\frac{1+\lambda}{4N}$	0	0	$\frac{1+\lambda N-2}{8N} + \frac{1}{N}$	$\frac{1+\lambda N-2}{4N}$	0	0	0	$\frac{1+\lambda N-2}{8N}$
Γ_{12}^{t+1}	0	0	0	0	$\frac{1+\lambda}{8}$	$\frac{1+\lambda}{4}$	0	0	0	$\frac{1+\lambda}{8}$
Γ_{21}^{t+1}	0	0	0	$\frac{1}{2N} + \frac{1+\lambda N-2}{8N}$	0	$\frac{1}{2N} + \frac{1+\lambda N-2}{8N}$	$\frac{1+\lambda N-2}{8N}$	0	$\frac{1+\lambda N-2}{8N}$	0
Γ_{22}^{t+1}	0	0	0	$\frac{1+\lambda}{8}$	0	$\frac{1+\lambda}{8}$	$\frac{1+\lambda}{8}$	0	$\frac{1+\lambda}{8}$	0
Γ_{31}^{t+1}	0	0	0	0	$\frac{1+\lambda}{8}$	0	$\frac{1+\lambda}{4}$	$\frac{1+\lambda}{8}$	0	0
Γ_{32}^{t+1}	$\frac{1+\lambda}{4N}$	0	$\frac{1+\lambda}{4N}$	0	$\frac{1}{2N} + \frac{1+\lambda N-4}{8N}$	0	$\frac{3}{2N} + \frac{1+\lambda N-4}{4N}$	$\frac{1+\lambda N-4}{8N}$	0	0
Γ_{33}^{t+1}	0	0	0	0	$\frac{1}{N} + \frac{1+\lambda N-4}{8N}$	0	$\frac{1}{N} + \frac{1+\lambda N-4}{4N}$	$\frac{1+\lambda N-4}{8N}$	0	0

$$\Omega_5 = \begin{bmatrix} \Theta_{11}^{t+1} & \frac{\Delta_{11}^t}{(1-\lambda)^2} & \Delta_{12}^t & \Delta_{13}^t & \frac{\Delta_{21}^t}{(1-\lambda)^2} & \Delta_{22}^t & \Delta_{23}^t & \Delta_{31}^t & \frac{\Delta_{32}^t}{\frac{1-\lambda}{4} \frac{N}{N-2}} & \Delta_{33}^t & \Delta_{41}^t & \Delta_{42}^t & \Delta_{43}^t & \Delta_{44}^t \\ \Theta_{21}^{t+1} & 0 & \frac{(1-\lambda)^2 N-2}{8} \frac{N}{N} & 0 & 0 & \frac{(1-\lambda)^2 N-2}{8} \frac{N}{N} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ \Theta_{22}^{t+1} & 0 & \frac{(1-\lambda)^2}{8} & 0 & 0 & \frac{(1-\lambda)^2}{8} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ \Gamma_{11}^{t+1} & \frac{1-\lambda}{8} & 0 & 0 & \frac{1-\lambda}{8} & 0 & 0 & 0 & \frac{1-\lambda}{4} \frac{N}{N-2} & 0 & 0 & 0 & 0 & 0 \\ \Gamma_{12}^{t+1} & \frac{1-\lambda}{8} & 0 & 0 & \frac{1-\lambda}{8} & 0 & 0 & 0 & \frac{1-\lambda}{4} & 0 & 0 & 0 & 0 & 0 \\ \Gamma_{21}^{t+1} & 0 & 0 & \frac{1-\lambda}{8} \frac{N-2}{N} & 0 & 0 & \frac{1-\lambda}{8} \frac{N}{N-2} & 0 & \frac{1-\lambda}{8} \frac{N}{N-2} & \frac{1-\lambda}{8} \frac{N-2}{N} & 0 & 0 & 0 & 0 \\ \Gamma_{22}^{t+1} & 0 & 0 & \frac{1-\lambda}{8} & 0 & 0 & \frac{1-\lambda}{8} & 0 & \frac{1-\lambda}{8} & \frac{1-\lambda}{8} & 0 & 0 & 0 & 0 \\ \Gamma_{31}^{t+1} & 0 & \frac{1-\lambda}{8} & 0 & 0 & \frac{1-\lambda}{8} & 0 & \frac{1-\lambda}{4} & 0 & 0 & 0 & 0 & 0 & 0 \\ \Gamma_{32}^{t+1} & 0 & \frac{1-\lambda}{8} \frac{N-2}{N} & 0 & 0 & \frac{1-\lambda}{8} \frac{N}{N} & 0 & \frac{1-\lambda}{4} \frac{N-4}{N} & 0 & 0 & 0 & 0 & 0 & 0 \\ \Gamma_{33}^{t+1} & 0 & \frac{1-\lambda}{8} \frac{N-4}{N} & 0 & 0 & \frac{1-\lambda}{8} \frac{N-4}{N} & 0 & \frac{1-\lambda}{4} \frac{N-4}{N} & 0 & 0 & 0 & 0 & 0 & 0 \end{bmatrix}$$

	Θ_{31}^t	Θ_{21}^t	Θ_{22}^t	Γ_{11}^t	Γ_{12}^t	Γ_{21}^t	Γ_{22}^t	Γ_{31}^t	Γ_{32}^t	Γ_{33}^t
Δ_{11}^{t+1}	$\frac{1}{2N^2}$	$\frac{1}{2N^2}$	0	0	$\frac{N-2}{2N^2}$	$\frac{1}{N}$	0	0	0	$\frac{N-2}{2N^2}$
Δ_{12}^{t+1}	0	0	0	0	0	0	0	0	0	0
Δ_{13}^{t+1}	0	0	0	0	$\frac{1}{4N}$	$\frac{1}{2N}$	0	0	0	$\frac{1}{4N}$
Δ_{21}^{t+1}	0	0	0	0	0	0	0	0	0	0
Δ_{22}^{t+1}	0	0	0	0	0	0	0	0	0	0
Δ_{23}^{t+1}	0	0	0	0	0	0	0	0	0	0
$\Omega_6 = \Delta_{31}^{t+1}$	0	0	0	0	0	0	0	0	0	0
Δ_{32}^{t+1}	0	0	0	$\frac{1}{4N}$	0	$\frac{1}{4N}$	$\frac{1}{4N}$	0	$\frac{1}{4N}$	0
Δ_{33}^{t+1}	0	0	0	$\frac{1}{2N}$	0	$\frac{1}{2N}$	$\frac{1}{2N}$	0	$\frac{1}{2N}$	0
Δ_{41}^{t+1}	0	0	0	0	0	0	0	0	0	0
Δ_{42}^{t+1}	0	0	0	0	$\frac{1}{2N}$	0	$\frac{1}{N}$	$\frac{1}{2N}$	0	0
Δ_{43}^{t+1}	$\frac{1}{2N(N-2)}$	0	$\frac{1}{2N(N-2)}$	0	$\frac{N-4}{2N(N-2)}$	0	$\frac{1}{N}$	$\frac{N-4}{2N(N-2)}$	0	0
Δ_{44}^{t+1}	$\frac{1}{N(N-2)}$	0	$\frac{1}{N(N-2)}$	0	$\frac{N-4}{N(N-2)}$	0	2	$\frac{N-4}{N(N-2)}$	0	0

Δ_{i+1}^t	Δ_{11}^t	Δ_{12}^t	Δ_{13}^t	Δ_{21}^t	Δ_{22}^t	Δ_{23}^t	Δ_{31}^t	Δ_{32}^t	Δ_{33}^t	Δ_{41}^t	Δ_{42}^t	Δ_{43}^t	Δ_{44}^t
Δ_{11}^{t+1}	$\frac{1}{8}$	$\frac{(N-2)^2}{8N^2}$	0	$\frac{1}{8}$	0	0	0	$\frac{N-2}{2N}$	0	0	0	$\frac{(N-2)^2}{8N^2}$	0
Δ_{12}^{t+1}	$\frac{1}{8}$	$\frac{1}{8}$	0	$\frac{1}{8}$	0	0	0	$\frac{1}{2}$	0	0	0	$\frac{1}{8}$	0
Δ_{13}^{t+1}	$\frac{1}{8}$	$\frac{N-2}{8N}$	0	$\frac{1}{8}$	0	0	0	$\frac{N-1}{2N}$	0	0	0	$\frac{N-2}{8N}$	0
Δ_{21}^{t+1}	$\frac{1}{4}$	0	0	0	$\frac{(N-2)^2}{8N^2}$	0	0	0	$\frac{N-2}{2N}$	0	0	0	$\frac{(N-2)^2}{8N}$
Δ_{22}^{t+1}	$\frac{1}{4}$	0	0	0	$\frac{1}{8}$	0	0	0	$\frac{1}{2}$	0	0	0	$\frac{1}{8}$
Δ_{23}^{t+1}	$\frac{1}{4}$	0	0	0	$\frac{N-2}{8N}$	0	0	0	$\frac{N-1}{2N}$	0	0	0	$\frac{N-2}{8N}$
Δ_{31}^{t+1}	0	0	$\frac{1}{4}$	0	0	$\frac{1}{8}$	$\frac{1}{8}$	$\frac{1}{4}$	$\frac{1}{8}$	0	$\frac{1}{8}$	0	0
Δ_{32}^{t+1}	0	0	$\frac{N-1}{4N}$	0	0	$\frac{N-2}{8N}$	$\frac{N-4}{8N}$	$\frac{N-1}{4N}$	$\frac{N-2}{8N}$	0	$\frac{N-4}{8N}$	0	0
Δ_{33}^{t+1}	0	0	$\frac{N-2}{4N}$	0	0	$\frac{1}{8}$	$\frac{N-4}{8N}$	$\frac{N-2}{4N}$	$\frac{1}{8}$	0	$\frac{N-4}{8N}$	0	0
Δ_{41}^{t+1}	0	$\frac{1}{4}$	0	0	$\frac{1}{8}$	0	$\frac{1}{2}$	0	0	$\frac{1}{8}$	0	0	0
Δ_{42}^{t+1}	0	$\frac{N-2}{4N}$	0	0	$\frac{N-2}{8N}$	0	$\frac{N-3}{2N}$	0	0	$\frac{N-6}{8N}$	0	0	0
Δ_{43}^{t+1}	0	$\frac{N^2-4N+6}{4N(N-2)}$	0	0	$\frac{N^2-6N+12}{8N(N-2)}$	0	$\frac{N-4}{2N}$	0	0	$\frac{(N-4)(N-6)}{8N(N-2)}$	0	0	0
Δ_{44}^{t+1}	0	$\frac{N^2-6N+12}{4N(N-2)}$	0	0	$\frac{1}{8}$	0	$\frac{N-4}{2N}$	0	0	$\frac{(N-4)(N-6)}{8N(N-2)}$	0	0	0

$$\Omega_i = \Delta_{31}^{t+1}$$