PEDIGREE MATING WITH TWO LINKED LOCI[1]

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MEASURES of inbreeding for linked loci have been defined by several authors, including HALDANE (1949), SCHNELL (1961) and SHIKATA (1962). These measures were defined to give the probability that genes at each of several linked loci were simultaneously identical by descent. A method for determining these quantities for pedigrees of individuals or for systems of mating other than selfing had not been developed.

By introducing trigametic and quadrigametic measures in addition to the usual digametic ones, COCKERHAM and WEIR (1968) were able to evaluate an inbreeding function for all generations of a sib mating system. This paper extends that work to procedures that will accommodate pedigrees of individuals and all pedigree mating systems. Finite populations will be considered elsewhere.

The object of this investigation then is to determine for a disomic individual with a known pedigree, the probability that two linked autosomal loci carry genes identical by descent. At the same time other probability measures are developed. No restriction is placed on the number of alleles per locus.

DEFINITION OF MEASURES

The general measure is defined as in COCKERHAM and WEIR (1968). For any two distinct genes, a, a′ at one locus, and any two distinct genes b, b′ at another locus, a general measure $\mathbf{X}(ab, a'b')$ is given by:

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

The identity sign $\equiv$ means identity by descent.

Now the four genes in the argument of $\mathbf{X}$ may be carried on two, three, or four distinct gametes. In the digametic case, a distinction will be made when the two gametes unite. There are thus four cases to be defined:

$$\mathbf{F}_A = \mathbf{X}(ab \ni A, a'b' \ni A), \tag{2}$$

$$\underline{\theta}_{BC} = \mathbf{X}(ab \in B, a'b' \in C), \tag{3}$$

$$\underline{\gamma}_{B,DE} = \mathbf{X}(ab \in B, a' \in D, b' \in E), \tag{4}$$

$$\underline{\delta}_{BC,DE} = \mathbf{X}(a \in B, b \in C, a' \in D, b' \in E). \tag{5}$$

One digametic measure (2) expresses the fact that ab, a′b′ are on gametes which unite to form

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an individual A, while the other digametic measure (3) is for gametes ab and a′b′, formed by individuals B and C respectively. Individuals B, D, E, form gametes carrying ab, a′, b′ respectively, for the trigametic measure (4), and a, b, a′, b′ are on four distinct gametes, from individuals B, C, D, E, respectively, in (5). The convention of reserving small letters for genes and capitals for individuals will be maintained throughout this discussion. In usual terminology, $\mathbf{F}_A$ is the two locus inbreeding function of individual A and $\underline{\theta}_{BC}$ is the two locus coancestry function of individuals B and C. When A is an offspring of B and C, as in Figure 1, equation (6) holds.

$$\mathbf{F}_A = \underline{\theta}_{BC}\,. \tag{6}$$

All measures are vectors with four components which sum to unity. The first and fourth components of $\mathbf{F}_A$, corresponding to the probabilities of double identity and double non-identity, are termed the two locus inbreeding and panmictic coefficients, respectively, for A. Equation (1) and (2) show that the sum of the first two and the sum of the first and third components of $\mathbf{F}_A$ are just the one locus inbreeding coefficients for the a and b loci, respectively. They are written as $F_{1.A}$ and $F_{.1A}$, or if they have the same value, as F_{1A}. Similarly the sums of the remaining two components may be written as $F_{0.A}$ and $F_{.0A}$, or F_{0A}. Table 1 gives marginal totals for the remaining three measures.

For the two loci being considered, the linkage parameter λ is such that the gametic array produced by an individual with genotype ab/a′b′ is

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

GENERAL EXPANSIONS

The method of determining the inbreeding function $\mathbf{F}$ for some generation of an inbreeding system is first to express $\mathbf{F}$ in terms of the measures for the previous generation. Either the expansions are then carried back to the initial population, or a set of transition equations is solved for $\mathbf{F}$. In either case, the expansions of measures back to the preceding generation must be established.

The general method of expanding each of the measures will be demonstrated with reference to the pedigree of Figure 1.

In the expansions, averages of measures will sometimes be used. The notation is

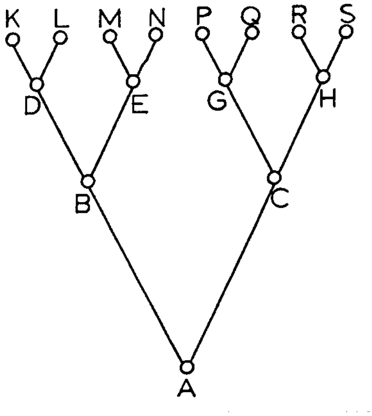

FIGURE 1.—The general pedigree.

TABLE 1

Marginal totals of measures

θ_{11BC}	θ_{10BC}	$\theta_{1.BC}$
θ_{01BC}	θ_{00BC}	$\theta_{0.BC}$
$\theta_{.1BC}$	$\theta_{.0BC}$	1
$\gamma_{11B,DE}$	$\gamma_{10B,DE}$	$\theta_{1.BD}$
$\gamma_{01B,DE}$	$\gamma_{00B,DE}$	$\theta_{0.BD}$
$\theta_{.1BE}$	$\theta_{.0BE}$	1
$\delta_{11BC,DE}$	$\delta_{10BC,DE}$	$\theta_{1.BD}$
$\delta_{01BC,DE}$	$\delta_{00BC,DE}$	$\theta_{0.BD}$
$\theta_{.1CE}$	$\theta_{.0CE}$	1

$$\underline{\gamma}_{B,\overline{DE}} = \tfrac{1}{2}\,(\underline{\gamma}_{B,DE} + \underline{\gamma}_{B,ED}),$$
$$\underline{\delta}_{BC,\overline{DE}} = \tfrac{1}{2}\,(\underline{\delta}_{BC,DE} + \underline{\delta}_{BC,ED}),$$
$$\underline{\delta}_{BC,\overline{DE}} = \tfrac{1}{2}\,(\underline{\delta}_{BC,DE} + \underline{\delta}_{CB,DE}).$$

Digametic measure expansions are considered first, $\underline{\theta}_{BC}$ being used as an example. From Figure 1 it can be seen that a gamete a′b′ from individual C is a parental type from either G or H with probability $\frac{1+\lambda}{4}$ in each case, or a recombinant type with a′ *from* G *and* b′ *from* H, *or vice versa*, each with probability $\frac{1-\lambda}{4}$. Hence the followinг expansion:

$$\mathbf{X}(\text{ab} \,\varepsilon\, \text{B}, \text{a}'\text{b}' \,\varepsilon\, \text{C}) = \frac{1+\lambda}{4}\,[\mathbf{X}(\text{ab} \,\varepsilon\, \text{B}, \text{a}'\text{b}' \,\varepsilon\, \text{G}) + \mathbf{X}(\text{ab} \,\varepsilon\, \text{B}, \text{a}'\text{b}' \,\varepsilon\, \text{H})]$$
$$+ \frac{1-\lambda}{4}\,[\mathbf{X}(\text{ab} \,\varepsilon\, \text{B}, \text{a}' \,\varepsilon\, \text{G}, \text{b}' \,\varepsilon\, \text{H}) + \mathbf{X}(\text{ab} \,\varepsilon\, \text{B}, \text{a}' \,\varepsilon\, \text{H}, \text{b}' \,\varepsilon\, \text{G})],$$
$$\therefore \underline{\theta}_{BC} = \underline{\theta}_{B(GH)} = \frac{1+\lambda}{4}\,[\underline{\theta}_{BG} + \underline{\theta}_{BH}] + \frac{1-\lambda}{2}\,\underline{\gamma}_{B,\overline{GH}}\,. \tag{7}$$

For an example of a trigametric measure expansion, consider $\underline{\gamma}_{B,GH}$. The gamete ab from B is replaced by its values in the previous generation.

$$\mathbf{X}(\text{ab} \,\varepsilon\, \text{B}, \text{a}' \,\varepsilon\, \text{G}, \text{b}' \,\varepsilon\, \text{H}) = \frac{1+\lambda}{4}[\mathbf{X}(\text{ab} \,\varepsilon\, \text{D}, \text{a}' \,\varepsilon\, \text{G}, \text{b}' \,\varepsilon\, \text{H}) + \mathbf{X}(\text{ab} \,\varepsilon\, \text{E}, \text{a}' \,\varepsilon\, \text{G}, \text{b}' \,\varepsilon\, \text{H})]$$
$$+ \frac{1-\lambda}{4}\,[\mathbf{X}(\text{a} \,\varepsilon\, \text{D}, \text{b} \,\varepsilon\, \text{E}, \text{a}' \,\varepsilon\, \text{G}, \text{b}' \,\varepsilon\, \text{H}) + \mathbf{X}(\text{a} \,\varepsilon\, \text{E}, \text{b} \,\varepsilon\, \text{D}, \text{a}' \,\varepsilon\, \text{G}, \text{b}' \,\varepsilon\, \text{H})],$$
$$\therefore \underline{\gamma}_{B,GH} = \underline{\gamma}_{(DE),GH} = \frac{1+\lambda}{4}\,[\underline{\gamma}_{D,GH} + \underline{\gamma}_{E,GH}] + \frac{1-\lambda}{2}\,\underline{\delta}_{\overline{DE},GH}. \tag{8}$$

A similar equation is obtained for $\underline{\gamma}_{B,HG}$, so that

$$\underline{\gamma}_{B,\overline{GH}} = \underline{\gamma}_{(DE),\overline{GH}} = \frac{1+\lambda}{4}\,[\underline{\gamma}_{D,\overline{GH}} + \underline{\gamma}_{E,\overline{GH}}] + \frac{1-\lambda}{2}\,\underline{\delta}_{\overline{DE},\overline{GH}}. \tag{9}$$

Combining equations (7) and (9) finishes the expansion for $\underline{\theta}_{BC}$ in terms of measures involving the parents of B and C.

$$\underline{\theta}_{BC} = \underline{\theta}_{(DE)(GH)} = \left(\frac{1+\lambda}{4}\right)^2 [\underline{\theta}_{GD} + \underline{\theta}_{EG} + \underline{\theta}_{DH} + \underline{\theta}_{EH}] +$$
$$\frac{1-\lambda^2}{8} [\underline{\gamma}_{D,\overline{GH}} + \underline{\gamma}_{E,\overline{GH}} + \underline{\gamma}_{G,\overline{DE}} + \underline{\gamma}_{H,\overline{DE}}] + \frac{(1-\lambda)^2}{4} \underline{\delta}_{\overline{DE},\overline{GH}}. \tag{10}$$

As an example of a quadrigametic measure expansion, consider $\underline{\delta}_{DE,GH}$. The four genes are now on separate gametes, so each has probability of one half of coming from one of two individuals. For example

$$\mathbf{X}(\mathrm{a}\varepsilon \mathrm{D}, \mathrm{b}\varepsilon \mathrm{E}, \mathrm{a}'\varepsilon \mathrm{G}, \mathrm{b}'\varepsilon \mathrm{H}) = \tfrac{1}{2} [\mathbf{X}(\mathrm{a}\varepsilon \mathrm{K}, \mathrm{b}\varepsilon \mathrm{E}, \mathrm{a}'\varepsilon \mathrm{G}, \mathrm{b}'\varepsilon \mathrm{H}) +$$
$$\mathbf{X}(\mathrm{a}\varepsilon \mathrm{L}, \mathrm{b}\varepsilon \mathrm{E}, \mathrm{a}'\varepsilon \mathrm{G}, \mathrm{b}'\varepsilon \mathrm{H})],$$

$$\therefore \underline{\delta}_{DE,GH} = \underline{\delta}_{(KL)E,GH} = \tfrac{1}{2} [\underline{\delta}_{KE,GH} + \underline{\delta}_{LE,GH}]. \tag{11}$$

The parents of E, G and H may also be brought in to complete the expansion. This method of treating one gene at a time may also be used to finish expanding $\underline{\gamma}_{B,\overline{GH}}$:

$$\underline{\gamma}_{(DE),\overline{(PQ)H}} = \frac{1+\lambda}{8} [\underline{\gamma}_{D,\overline{PH}} + \underline{\gamma}_{D,\overline{QH}} + \underline{\gamma}_{E,\overline{PH}} + \underline{\gamma}_{E,\overline{QH}}]$$
$$+ \frac{1-\lambda}{4} [\underline{\delta}_{\overline{DE},\overline{PH}} + \underline{\delta}_{\overline{DE},\overline{QH}}]. \tag{12}$$

The parents of H can also be brought into the expansion.

In these general expansions, quadrigametic measures expand back to quadrigametic measures. Trigametic measures expand back to trigametic and quadrigametic measures and digametic expand back to digametic, trigametric and quadrigametic. If the number of letters in the subscript of a measure is termed the order of the measure, these last statements may be restated as: in general expansions, measures expand back to measures with as great as or greater order.

SPECIAL EXPANSIONS

Although the **X** measures are defined for distinct genes, a, a′ and b, b′, no restrictions are placed on the individuals from which these genes originate. Whenever one individual does provide more than one of the distinct gametes for a measure (so that the individual appears more than once in the subscript) special expansions are needed. If the individual provides two genes at one locus, they may be copies of the same gene in that individual and so automatically identical by descent. There is also the fact that genes on any number of gametes produced by one individual can only have been carried on one or two gametes in the previous generation. Thus, when an individual occurs more than once in the subscript of a measure, the expansion includes a measure of a lower order.

One special expansion, that for $\underline{\theta}_{BB}$, will be derived here and the remaining ten special cases listed in the appendix. Details of derivation of those are given by WEIR (1968).

For $\underline{\theta}_{BB}$, the two gametes ab, a′b′ from individual B, are each replaced by their gametic arrays. These arrays are identical and equal to

$$\left(\frac{1+\lambda}{4} \mathrm{a}_E\mathrm{b}_E, \frac{1+\lambda}{4} \mathrm{a}_D\mathrm{b}_D, \frac{1-\lambda}{4} \mathrm{a}_E\mathrm{b}_D, \frac{1-\lambda}{4} \mathrm{a}_D\mathrm{b}_E\right),$$

TABLE 2

Expansion of θ_{11BB}

		ab			
		$\frac{1+\lambda}{4}$	$\frac{1+\lambda}{4}$	$\frac{1-\lambda}{4}$	$\frac{1-\lambda}{4}$
	θ_{11BB}	a_Eb_E	a_Db_D	a_Eb_D	a_Db_E
a′b′	$\frac{1+\lambda}{4}$ a_Eb_E	1	θ_{11ED}	$\theta_{.1ED}$	$\theta_{1.ED}$
	$\frac{1+\lambda}{4}$ a_Db_D	θ_{11ED}	1	$\theta_{1.ED}$	$\theta_{.1ED}$
	$\frac{1-\lambda}{4}$ a_Eb_D	$\theta_{.1ED}$	$\theta_{1.ED}$	1	θ_{11ED}
	$\frac{1-\lambda}{4}$ a_Db_E	$\theta_{1.ED}$	$\theta_{.1ED}$	θ_{11ED}	1

where subscripts indicate from which parents the genes came. These arrays are arranged as headings in a two-way table (Table 2), and the probabilities that the two gametes carry genes identical by descent are entered in the body of the table.

Collecting all the terms from Table 2 gives

$$\theta_{11BB} = \frac{1+\lambda^2}{4} + \frac{1+\lambda^2}{4}\,\theta_{11ED} + \frac{1-\lambda^2}{4}\,\theta_{1.ED} + \frac{1-\lambda^2}{4}\,\theta_{.1ED}$$

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

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

$$= \theta_{11ED} + \tfrac{1}{2}\,\theta_{10ED} + \tfrac{1}{2}\,\theta_{01ED} + \frac{1+\lambda^2}{4}\,\theta_{00ED}\ .$$

Applying the same procedure for the other three components of θ_{BB} leads to the following equation:

$$\underline{\theta}_{BB} = \begin{bmatrix} 1 & \tfrac{1}{2} & \tfrac{1}{2} & \frac{1+\lambda^2}{4} \\ 0 & \tfrac{1}{2} & 0 & \frac{1-\lambda^2}{4} \\ 0 & 0 & \tfrac{1}{2} & \frac{1-\lambda^2}{4} \\ 0 & 0 & 0 & \frac{1+\lambda^2}{4} \end{bmatrix} \underline{\theta}_{ED}$$

$$= \Phi(\lambda)\,\mathbf{F}_B, \qquad (13)$$

where $\Phi(\lambda)$ denotes the 4 × 4 matrix. Note that $\mathbf{F}_B$ is of lower order than $\underline{\theta}_{BB}$.

SPECIFIC PEDIGREE

First to be considered are pedigrees of specific individuals. It is required to determine the inbreeding function of some specified individual when the common ancestors of its parents are of known relationship and degree in inbreeding.

The inbreeding function of the individual is expanded back to digametic, trigametic and quadrigametic measures involving its parents. These measures in turn are 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 common ancestors, whereupon the numerical values for these measures are substituted.

As an example, consider the pedigree of Figure 2. For the one locus coefficients direct application of WRIGHT's general formula gives

$$F_{1C} = (\tfrac{1}{2})^3[1+F_{1G}] + (\tfrac{1}{2})^3[1+F_{1H}],$$

$$F_{1A} = (\tfrac{1}{2})^2[1+F_{1C}] + (\tfrac{1}{2})^3[1+F_{1D}] + (\tfrac{1}{2})^5[1+F_{1H}] + (\tfrac{1}{2})^5[1+F_{1G}],$$

which assumes that G and H are unrelated and thus F_{1D} is zero. (If G and H are related, $\theta_{1GH} = F_{1D}$ is not zero and F_{1C} must have $\tfrac{1}{2}$ F_{1D} added to it while F_{1A} must have $(\tfrac{1}{2})^3F_{1D}$ added.) If further, G and H are non-inbred

$$F_{1C} = \tfrac{1}{4},\ F_{1A} = \tfrac{1}{2}.$$

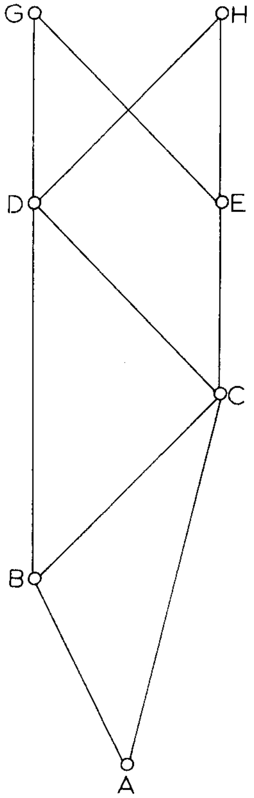

FIGURE 2.—Specific pedigree.

The two locus inbreeding function $\mathbf{F}_A$ is expanded back until it is expressed entirely in terms of measures involving only the common ancestors C, D, H and G. There will be need for the special expansions listed in the appendix. From (6)

$$\mathbf{F}_A = \underline{\theta}_{BC} ,$$

which, from (7)

$$= \frac{1+\lambda}{4} \underline{\theta}_{CC} + \frac{1+\lambda}{4} \underline{\theta}_{DC} + \frac{1-\lambda}{2} \underline{\gamma}_{C,\overline{DC}} .$$

This expansion also illustrates the general rule that the first stage of an expansion is to the parents of the youngest individual in the subscript. Using the expansion in equations (13), (7) and (36) for $\underline{\theta}_{CC}$, $\underline{\theta}_{DC}$ and $\underline{\gamma}_{C,\overline{DC}}$ gives

$$\mathbf{F}_A = \left[\frac{1+\lambda}{4} \Phi(\lambda) + \left(\frac{1+\lambda}{4}\right)^2 \mathbf{I} + \frac{1-\lambda}{8} \Phi(i)\right] \mathbf{F}_C + \left[\left(\frac{1+\lambda}{4}\right)^2 \mathbf{I} + \frac{1-\lambda}{8} \Phi(i)\right] \Phi(\lambda) \mathbf{F}_D$$
$$+ \frac{(1-\lambda)(2+\lambda)}{8} \mathbf{I}\, \underline{\gamma}_{D,\overline{DE}} + \frac{1-\lambda}{8} \mathbf{I}\, \underline{\gamma}_{E,DD} ,$$

where $\mathbf{I}$ is the 4 × 4 unit matrix, and $\underline{\theta}_{DE}$ is written as $\mathbf{F}_C$. The expansions of equations (36) and (33) are now used to expand $\underline{\gamma}_{D,\overline{DE}}$ and $\underline{\gamma}_{E,DD}$ to measures involving the parents of D, while general expansions suffice for the parents of E. They lead to

$$\mathbf{F}_A = \left[\frac{1+\lambda}{4} \Phi(\lambda) + \left(\frac{1+\lambda}{4}\right)^2 \mathbf{I} + \frac{1-\lambda}{8} \Phi(i)\right] \mathbf{F}_C + \left[\left(\frac{1+\lambda}{4}\right)^2 \mathbf{I} + \frac{1-\lambda}{8} \Phi(i)\right] \Phi(\lambda) \mathbf{F}_D$$
$$+ \frac{(1-\lambda)(2+\lambda)}{16} \mathbf{I} \left[\underline{\gamma}_{D,\overline{DG}} + \underline{\gamma}_{D,\overline{DH}}\right] + \frac{1-\lambda^2}{32} \mathbf{I} \left[\underline{\gamma}_{G,DD} + \underline{\gamma}_{H,DD}\right]$$
$$+ \frac{(1-\lambda)^2}{16} \mathbf{I}\, \underline{\delta}_{DD,\overline{GH}} .$$

As a final step the tri- and quadrigametic measures involving D are expanded back to measures involving G and H. The final expansion, with $\underline{\theta}_{GH}$ written as $\mathbf{F}_D$ is

$$\mathbf{F}_A = \left[\frac{1+\lambda}{4} \Phi(\lambda) + \left(\frac{1+\lambda}{4}\right)^2 \mathbf{I} + \frac{1-\lambda}{8} \Phi(i)\right] \mathbf{F}_C$$
$$+ \left[\frac{(1-\lambda)(2+\lambda)}{64} \Phi(i)\Phi(\lambda) + \frac{1-\lambda^2}{128} \Phi(\lambda)\right] (\mathbf{F}_G + \mathbf{F}_H)$$
$$+ \left(\frac{4-3\lambda-\lambda^2}{64}\right) \mathbf{I} \left[\underline{\gamma}_{G,\overline{GH}} + \underline{\gamma}_{H,\overline{GH}}\right]$$
$$+ \left[\frac{1-\lambda^2}{64} \mathbf{I} + \frac{(1-\lambda)(2+\lambda)}{32} \Phi(i) + \left(\frac{1+\lambda}{4}\right)^2 \Phi(\lambda) + \frac{1-\lambda}{8} \Phi(i)\Phi(\lambda)\right] \mathbf{F}_D$$
$$+ \frac{(1-\lambda)(2+\lambda)}{64} \mathbf{I} \left[\underline{\gamma}_{G,HH} + \underline{\gamma}_{H,GG}\right] + \frac{(1-\lambda)^2}{32} \mathbf{I}\, \underline{\delta}_{\overline{GH},\overline{GH}} .$$

If G and H are assumed to be non-inbred and unrelated

$$\mathbf{F}_G = \mathbf{F}_H = \mathbf{F}_D = [0,0,0,1]' .$$

The inbreeding function of C, the offspring of non-inbred full sibs, which can be evaluated by an expansion similar to that above, is

$$\mathbf{F}_C = \begin{bmatrix} (2+3\lambda^2+2\lambda^3+\lambda^4)/32 \\ (6-3\lambda^2-2\lambda^3-\lambda^4)/32 \\ (6-3\lambda^2-2\lambda^3-\lambda^4)/32 \\ (18+3\lambda^2+2\lambda^3+\lambda^4)/32 \end{bmatrix} \qquad (14)$$

This follows from combining values of the locus coefficient F_{1C} (which equals $F_{11C}+F_{10C}$ or $F_{11C}+F_{01C}$) found above and of F_{11C} given by previous authors (HALDANE 1949). For the trigametic measures $\gamma_{G,HH}$ and $\gamma_{H,GG}$ there is no chance of identical genes, so

$$\underline{\gamma}_{G,HH} = \underline{\gamma}_{H,GG} = [0,0,0,1]'\,.$$

The measures $\underline{\gamma}_{G,\overline{GH}}$ and $\underline{\gamma}_{H,\overline{HG}}$ however do involve two genes at one locus from the same individual, so that

$$\underline{\gamma}_{G,\overline{HG}} = \underline{\gamma}_{H,\overline{GH}} = [0, 1/4, 1/4, 1/2]'\,.$$

The quadrigametic measure $\underline{\delta}_{\overline{GH},\overline{GH}}$ is the average of the four measures $\delta_{GH,GH}$, $\underline{\delta}_{GH,HG}$, $\underline{\delta}_{HG,GH}$ and $\underline{\delta}_{HG,HG}$, and has the value

$$\underline{\delta}_{\overline{GH},\overline{GH}} = [1/8, 1/8, 1/8, 5/8]'\,.$$

Substituting the values of the measures for the common ancestors into the complete expansion of $\mathbf{F}_A$ yields

$$\mathbf{F}_A = \begin{bmatrix} (128+10\lambda+36\lambda^2+47\lambda^3+20\lambda^4+10\lambda^5+4\lambda^6+\lambda^7)/512 \\ (128-10\lambda-36\lambda^2-47\lambda^3-20\lambda^4-10\lambda^5-4\lambda^6-\lambda^7)/512 \\ (128-10\lambda-36\lambda^2-47\lambda^3-20\lambda^4-10\lambda^5-4\lambda^6-\lambda^7)/512 \\ (128+10\lambda+36\lambda^2+47\lambda^3+20\lambda^4+10\lambda^5+4\lambda^6+\lambda^7)/512 \end{bmatrix}\,. \qquad (15)$$

For complete linkage ($\lambda = 1$), $F_{11A} = F_{1A} = 1/2$, while for free recombination ($\lambda = 0$), $F_{11A} = F^2_{1A} = 1/4$.

PEDIGREE SYSTEMS OF MATING

When there is a constant mating pattern for every generation, the above approach is neither practicable for long pedigrees nor necessary. Instead, recurrence relations for various measures are established.

As noted in COCKERHAM and WEIR (1968), the fact that the marginal totals in Table 1 can be found from the one locus inbreeding and panmictic coefficients, means that only one component of the two locus inbreeding function needs to be found. For convenience the two locus panmictic coefficient and corresponding (fourth) components of other measures are used.

Because of the recurring nature of the pedigree systems, a new notation is introduced. Instead of being subscripted according to individual, measures are superscripted according to generation. Subscripts refer to individuals providing gametes in the argument of the measures while superscripts refer to the generation formed by the gametes.

The object is to find a set of simultaneous transition equations between values in successive generations of a minimal set of (fourth components of) measures. The two locus panmictic coefficient is necessarily a member of this smallest, or complete, set of measures. Any member of a complete set of measures in gener-

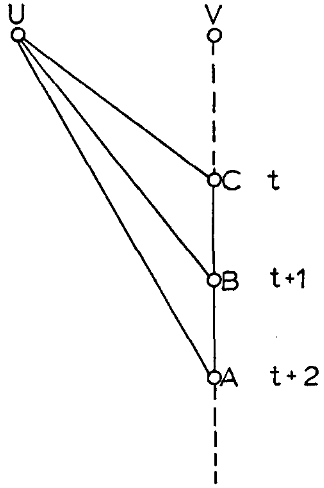

FIGURE 3.—Backcrossing to the same parent pedigree.

ation $(t+1)$ can be expressed in terms of 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 $(t+1)$ to values of measures in generation t. This process is continued until there are just enough (s) equations. The complete set of measures, 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 s simultaneous transition equations are used for its determination. If s is sufficiently small this can be done directly. Consider for example the parent offspring pedigree of Figure 3 where each mating is a backcrossing to the same parent.

In that figure, individuals A, B, C are in generations $t+2$, $t+1$, t respectively. The initial pair U and V are not related and their offspring is in generation 0. The case where they are also non-inbred will be considered first. Expanding the two locus panmictic coefficient for A gives

$$F_{00A} = \theta_{00BU} = \frac{1+\lambda}{4}\left[\theta_{00UU} + \theta_{00CU}\right] + \frac{1-\lambda}{2}\gamma_{00U,\overline{CU}}\,. \tag{16}$$

From equation (13)

$$\theta_{00UU} = \frac{1+\lambda^2}{4}$$

because $\mathbf{F}_U = [0, 0, 0, 1]'$ when U is non-inbred. Equation (16) can thus be written as in (17) where ϕ^{t+1} is an abbreviation for $\gamma_{00C,\overline{CU}}$.

$$F_{00}^{t+2} = \frac{(1+\lambda)(1+\lambda^2)}{16} + \frac{1+\lambda}{4}F_{00}^{t+1} + \frac{1-\lambda}{2}\phi^{t+1}\,. \tag{17}$$

Now an expansion must be given for the additional measure $\gamma_{00C,\overline{CU}} = \phi^{t+1}$ introduced in (16). Expanding to the parents of B gives

$$\gamma_{00U,\overline{BU}} = \tfrac{1}{2}\,\gamma_{00U,UU} + \tfrac{1}{2}\,\gamma_{00U,\overline{CU}}\,. \tag{18}$$

From the appendix, equation (31),

$$\gamma_{00U,UU} = \tfrac{1}{4}\,,$$

since U is non-bred, and this value substituted into (18) gives

$$\phi^{t+2} = \tfrac{1}{8} + \tfrac{1}{2}\,\phi^{t+1}\,. \tag{19}$$

Eliminating ϕ from (17) and (19) provides the recurrence relation for the two locus panmictic coefficient:

$$F_{00}^{t+2} = \frac{3+\lambda}{4} F_{00}^{t+1} - \frac{1+\lambda}{8} F_{00}^{t} + \frac{3-\lambda+\lambda^2+\lambda^3}{32}\,. \tag{20}$$

As U and V were unrelated their offspring is non-inbred, so that $F_{00}^{0} = 1$. The first value of ϕ is $\phi^0 = \gamma_{00U,\overline{VU}}$ which is equal to $\tfrac{1}{2}$. Equation (17) then gives the other initial value required for (20): $F_{00}^{1} = \dfrac{9+\lambda+\lambda^2+\lambda^3}{16}$. Substitution of $\lambda = 1$ into (17) gives the usual (JENNINGS 1916) one locus equation:

$$F_0^{t+2} = \tfrac{1}{4} + \tfrac{1}{2} F_0^{t+1}, \quad F_0^1 = \tfrac{3}{4}\,. \tag{21}$$

Combining values found from equations (20) and (21) enables the following inbreeding functions to be found:

$$\mathbf{F}^0 = [0, 0, 0, 1]'$$

$$\mathbf{F}^1 = \begin{bmatrix} (1+\lambda+\lambda^2+\lambda^3)/16 \\ (3-\lambda-\lambda^2-\lambda^3)/16 \\ (3-\lambda-\lambda^2-\lambda^3)/16 \\ (9+\lambda+\lambda^2+\lambda^3)/16 \end{bmatrix}$$

$$\mathbf{F}^2 = \begin{bmatrix} (\ 9+2\lambda+6\lambda^2+6\lambda^3+\lambda^4)/64 \\ (15-2\lambda-6\lambda^2-6\lambda^3-\lambda^4)/64 \\ (15-2\lambda-6\lambda^2-6\lambda^3-\lambda^4)/64 \\ (25+2\lambda+6\lambda^2+6\lambda^3+\lambda^4)/64 \end{bmatrix}$$

$$\cdot \quad \cdot \quad \cdot \quad \cdot$$

$$\mathbf{F}^\infty = \begin{bmatrix} (3-\lambda+\lambda^2+\lambda^3)/4(3-\lambda) \\ (3-\lambda-\lambda^2-\lambda^3)/4(3-\lambda) \\ (3-\lambda-\lambda^2-\lambda^3)/4(3-\lambda) \\ (3-\lambda+\lambda^2+\lambda^3)/4(3-\lambda) \end{bmatrix}$$

In all generations $F_{00} = F_0$ if $\lambda = 1$ and $F_{00} = F_0^2$ if $\lambda = 0$.

A more practical case may now be considered. This mating scheme is often used when U and V are unrelated but each is completely inbred. Equation (16) still holds, but because any two genes at one locus from U must now be identical, $\theta_{00UU} = \gamma_{00U,\overline{CU}} = 0$. The recurrence formula for F_{00} thus follows immediately from (16):

$$F_{00}^{t+2} = \frac{1+\lambda}{4} F_{00}^{t+1}\,. \tag{22}$$

Substituting $\lambda = 1$ gives the equation for the one locus panmictic coefficient, which, together with (22) leads to the recurrence relation for the whole vector **F**.

$$\mathbf{F}^{t+1} = \begin{bmatrix} 1 & \frac{1}{2} & \frac{1}{2} & \frac{1+\lambda}{4} \\ 0 & \frac{1}{2} & 0 & \frac{1+\lambda}{4} \\ 0 & 0 & \frac{1}{2} & \frac{1+\lambda}{4} \\ 0 & 0 & 0 & \frac{1+\lambda}{4} \end{bmatrix} \mathbf{F}^{t}, \qquad \boldsymbol{F}^{0} = \begin{bmatrix} 0 \\ 0 \\ 0 \\ 1 \end{bmatrix} \qquad (23)$$

This system is very similar to selfing, for which the appropriate transition equation (Shikata 1962; Narain 1965) follows from equation (13):

$$\mathbf{F}^{t+1} = \Phi(\lambda)\mathbf{F}^{t}\,.$$

The matrix $\Phi(\lambda)$ differs from that in equation (23) only by having each λ replaced by λ^2, so that the two systems differ only when linkage is neither complete nor zero. The matrix in equation (23) may be written as $\Phi(\sqrt{\lambda})$.

Numerical values of $\mathbf{F}_{11}$ for backcrossing to the same parent for each of the two initial conditions are shown in Figure 4. The curves for initial double identity also represent a selfing system, i.e., the curves for $\lambda = 0.8$ and $\lambda = 0.5$ are also selfing curves for $\lambda = 0.89$ and $\lambda = 0.71$. The boundary curves ($\lambda = 0$, $\lambda = 1$) for initial identity and selfing are the same. For the system with initial non-identity, which does not tend to complete identity, the values at the right of each curve indicate the limiting value of F_{11}. This example has illustrated the procedure for systems with a small complete set of measures.

For complete sets of larger order, matrix techniques must be used to solve the

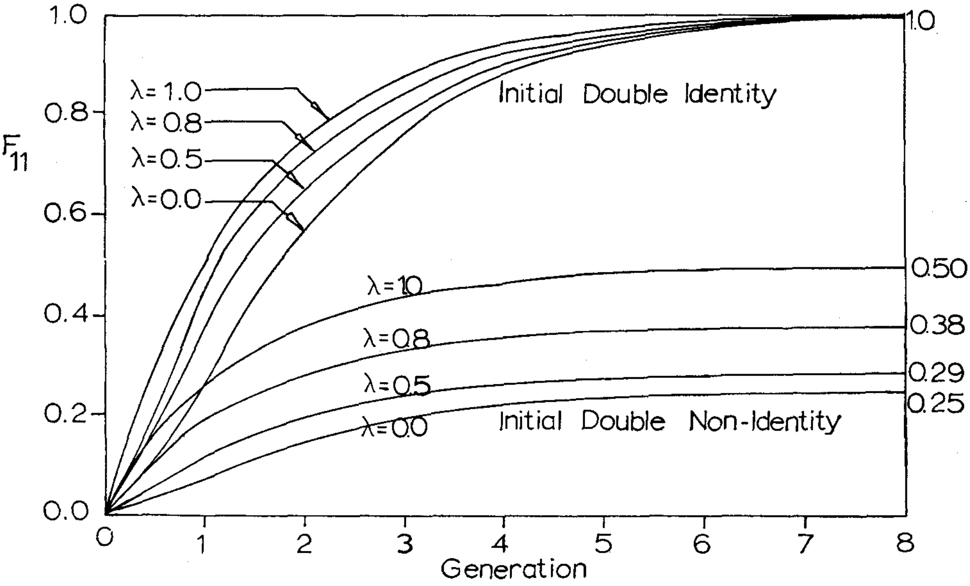

FIGURE 4.—F_{11} for backcrossing to the same parent.

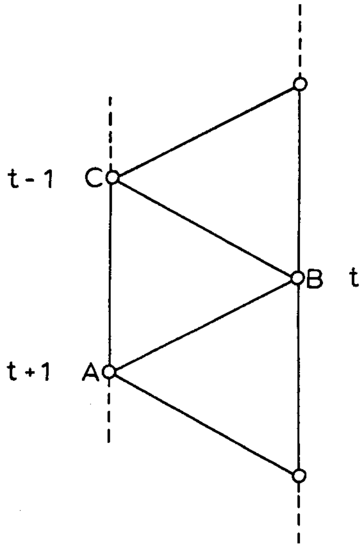

FIGURE 5.—Mating to the younger parent pedigree.

simultaneous transition equations for F_{00}. The s transition equations are written in the form:

$$\mathbf{u}_{t+1} = \Omega \, \mathbf{u}_t \, , \tag{24}$$

where $\mathbf{u}'_t$ is the s-vector $[F_{00}, X_{00_1}, \ldots, X_{00_{s-1}}]^t$ of measures in the complete set, and Ω is an s × s transition matrix. Since the minimal equation f(x) of the transition matrix is the equation of lowest order satisfied by the matrix itself, the simplest recurrence relation for F_{00} must follow from that equation (COCKERHAM and WEIR 1968). In particular, it is the first component of the vector equation

$$f(\Omega) \, \mathbf{u}_t = \mathbf{O}.$$

When f(x) has factors, that factor g(x), of smallest order, such that $g(\Omega)\mathbf{u}_t$ has zero first component gives the required simplest recurrence relation.

The procedure was demonstrated for sib mating (s = 6) by COCKERHAM and WEIR (1968), and will be used here to treat parent offspring mating where each mating is to the younger parent as in Figure 5, where A belongs to generation $(t+1)$.

Once again, the first step is to expand F_{00A}.

$$F_{00A} = \theta_{00CB,} = \frac{1+\lambda}{4}\,[\theta_{00CC} + \theta_{00CD}] + \frac{1-\lambda}{2}\,\gamma_{00C,\overline{CD}}$$

i.e.

$$F_{00}^{t+1} = \frac{1+\lambda}{4}\,[\phi^t + F^t_{00}] + \frac{1-\lambda}{2}\,\alpha^t \, . \tag{25}$$

Note the introduction of the abbreviation α^t for $\gamma_{00C,\overline{CD}}$. Other abbreviations will be introduced in the following equations without comment. The two additional measures introduced here must be expanded, using the special expansions. From equation (13):

$$\theta_{00BB} = \frac{1+\lambda^2}{4} F_{00B} ,$$

i.e.
$$\phi^{t+1} = \frac{1+\lambda^2}{4} F^t_{00} . \qquad (26)$$

From the appendix, equation (36):

$$\gamma_{00B,\overline{BC}} = \tfrac{1}{4} \left(\gamma_{00C,\overline{CD}} + \gamma_{00D,CC}\right),$$

i.e.
$$\alpha^{t+1} = \tfrac{1}{4} \left(\alpha^t + \beta^t\right). \qquad (27)$$

From the appendix, equation (33):

$$\gamma_{00C,BB} = \tfrac{1}{4} \left(\theta_{00CC} + \theta_{00CD}\right) + \tfrac{1}{2} \gamma_{00C,\overline{CD}} ,$$

i.e.
$$\beta^{t+1} = \tfrac{1}{4} \left(\phi^t + F^t_{00}\right) + \tfrac{1}{2} \alpha^t . \qquad (28)$$

The complete set (F_{00}, ϕ, α, β) is thus of order 4, and the transition equation is

$$\begin{bmatrix} F_{00} \\ \phi \\ \alpha \\ \beta \end{bmatrix}^{t+1} = \begin{bmatrix} \frac{1+\lambda}{4} & \frac{1+\lambda}{4} & \frac{1-\lambda}{2} & 0 \\ \frac{1+\lambda^2}{4} & 0 & 0 & 0 \\ 0 & 0 & \tfrac{1}{4} & \tfrac{1}{4} \\ \tfrac{1}{4} & \tfrac{1}{4} & \tfrac{1}{2} & 0 \end{bmatrix} \begin{bmatrix} F_{00} \\ \phi \\ \alpha \\ \beta \end{bmatrix}^{t} . \qquad (29)$$

From the characteristic equation of the transition matrix, the following recurrence formula is found:

$$F^{t+4}_{00} = \frac{2+\lambda}{4} F^{t+3}_{00} + \frac{2+\lambda^2+\lambda^3}{16} F^{t+2}_{00} - \frac{1+5\lambda+\lambda^2+\lambda^3}{64} F^{t+1}_{00} - \frac{\lambda(1+\lambda^2)}{64} F^t_{00} . \qquad (30)$$

When $\lambda = 1$, the usual one locus equation (JENNINGS 1916) is found:

$$F^{t+2}_{00} = \tfrac{1}{2} F^{t+1}_{00} + \tfrac{1}{4} F^t_{00} ,$$

so that $F^t_{00} = F^t_0$. When $\lambda = 0$, the equation is that found for sib mating by COCKERHAM and WEIR (1968):

$$F^{t+1}_{00} = \tfrac{1}{2} F^{t+2}_{00} + \tfrac{1}{8} F^{t+1}_{00} - \frac{1}{64} F^t_{00} ,$$

so that $F^t_{00} = (F^t_0)^2$. Mating to the younger parent and full sib mating thus differ only when linkage is neither complete nor zero. Figure 6 gives curves for F_{11} for various linkage values.

DISCUSSION

A method has been presented which enables the determination of the two locus inbreeding function in the presence of linkage. Various probability measures are defined for two, three, or four gametes, and the method rests upon relating values of these measures for the offspring to their values for the parents.

All possible types of expansions of the measures have been listed, and they fall into two classes according to whether the gametes all come from different individuals or not. If distinct individuals are involved the measures expand back to measures of equal or smaller order. For specific pedigrees, the inbreeding function of an individual is expanded back until it has been expressed in terms of measures involving the common ancestors of its parents. For pedigree systems of

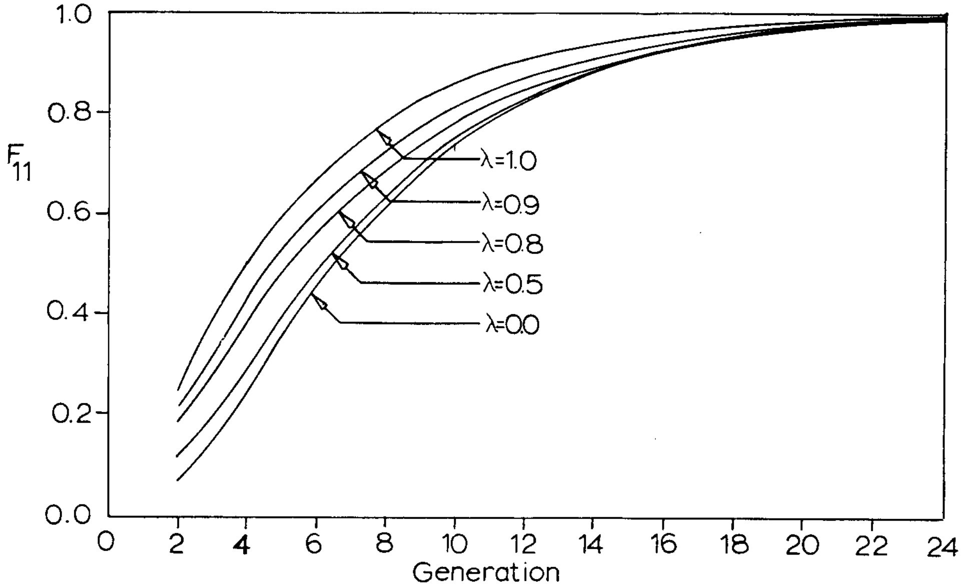

FIGURE 6.—F_{11} for mating to the younger parent.

mating a set of transition equations for the fourth components of a complete set of measures is derived and written in matrix form.

Calculating even the first few powers of the transition matrix to provide algebraic expressions for F_{00} (and hence $\mathbf{F}$), or calculating the minimal equation of the matrix to give a recurrence relation for F_{00}, is practicable only for small matrices. A more useful analysis is provided by numerical values of the inbreeding function for various linkage values.

The limiting behavior of an inbreeding system, as regards the loss of double non-identity, is characterized by the largest eigenvalue of the transition matrix. As this eigenvalue satisfies the factor of the minimal equation furnishing the recurrence formula for F_{00}, it must be the limiting value of the ratio of successive values of F_{00}. One minus this limiting rate of loss of double non-identity may be termed the rate of inbreeding. If the largest eigenvalue for a certain amount of linkage is written as $\mu(\lambda)$, and $\nu(\lambda)$ is any other eigenvalue, then for t sufficiently large for $[\nu(\lambda)/\mu(\lambda)]^t$ to be negligible: $F_{00}^{t+1} = \mu(\lambda)F_{00}^{t}$, and $F_{0}^{t+1} = \mu(1)F_{0}^{t}$. Using the relations $F_0 = F_{00} + F_{01} = F_{00} + F_{10}$ and $F_{11} = 1 - F_{10} - F_{01} - F_{00}$ the following equation is obtained.

$$\mathbf{F}^{t+1} = \begin{bmatrix} 1 & 1-\mu(1) & 1-\mu(1) & 1+\mu(\lambda)-2\mu(1) \\ 0 & \mu(1) & 0 & \mu(1)-\mu(\lambda) \\ 0 & 0 & \mu(1) & \mu(1)-\mu(\lambda) \\ 0 & 0 & 0 & \mu(\lambda) \end{bmatrix} \mathbf{F}^{t}$$

It can be shown that $\mu(\lambda)$ is a monotone increasing function of λ (WEIR 1968).

TABLE 3

Largest eigenvalue of transition matrix for mating to the younger parent

λ	$\mu(\lambda)$
0.0	.65451*
0.1	.65613
0.2	.65919*
0.3	.66407
0.4	.67131
0.5	.68161
0.6	.69587*
0.7	.71508*
0.8	.74013*
0.9	.77148*
1.0	.80902*

* Values also found by BENNETT (1954)

Table 3 gives values of $\mu(\lambda)$ for mating to the younger parent, where asterisks denote values found previously by BENNETT (1954). While his approach was different, the largest eigenvalue of his 8 × 8 matrix also gave the limiting rate of decrease of double non-identity.

To characterize the effects of linkage on the identity by descent of two pairs of linked genes, an identity disequilibrium function (COCKERHAM and WEIR 1968) is defined. This function has four components, each with the same numerical value:

$$\eta^t_{ij} = F^t_{ij} - F^t_i F^t_j \qquad i, j = 0, 1$$

$$\eta^t_{11} = -\eta^t_{10} = -\eta^t_{01} = \eta^t_{00} \;.$$

For a non-inbred initial population, $\eta^0_{ij} = 0$ and if complete double identity is obtained finally, $\eta^\infty_{ij} = 0$. For all other generations η_{11} is positive, so that

$$\text{Prob}(a \equiv a', b \equiv b') > \text{Prob}(a \equiv a')\ \text{Prob}(b \equiv b'),$$

as noted by HALDANE (1949).

For selfing the maximum disequilibrium for any value of λ occurs in the first generation, for sib mating (COCKERHAM and WEIR 1968) in one of the first three generations, and for mating to the younger parent in one of the first four generations (Table 4). For backcrossing to the same parent and initial double identity, the maximum identity disequilibrium is always in the first generation, but for initial double non-identity the generation ranges from the first ($\lambda = 0.1$) to an infinitely distant one ($\lambda = 1.0$).

In general, any pedigree has no identity disequilibrium for zero linkage and a disequilibrium value of

$$\eta_{11} = F_1(1 - F_1)$$

for complete linkage, which has a maximum of 0.25 at $F_1 = 0.5$. Other linkage values give disequilibria between these two bounds. The family of F_{11} curves for any pedigree system of mating is bounded by the curves for F_1 and F_1^2 which

TABLE 4

Maximum value of identity disequilibrium and generation of attainment for mating to the younger parent

Linkage parameter	Maximum identity disequilibrium	Generation
0.0	.0	0
0.1	.0069	2
0.2	.0155	2
0.3	.0261	2
0.4	.0390	2
0.5	.0550	2
0.6	.0748	3
0.7	.1037	3
0.8	.1394	3
0.9	.1883	4
1.0	.2500	4

converge as F_1 approaches unity. Thus, the generation of maximum identity disequilibrium varies from zero for $\lambda = 0$ to the generation for which $F_1 = 0.5$ for $\lambda = 1$, which in the latter case increases with the number of individuals in the system of mating. However, linkage effects do not increase linearly with the amount of linkage, for F^t_{00} and $\mu(\lambda)$ (and hence $\mathbf{F}^t$ and η^t_{ij}) are polynomials in λ. As can be seen from Figures 4 and 6 and Tables 3 and 4, linkage effects are appreciable only once λ is about 0.7, after which they increase rapidly.

Now that a way for treating inbreeding with two linked loci has been established, it is clear how greater numbers of linked loci may be accommodated. For each additional locus considered only one component of the n locus inbreeding function needs to be determined since appropriate marginal total of the 2^n components are equal to the inbreeding functions for smaller numbers of loci. Enumeration for specific pedigrees would be impracticable for very large n unless a computer was used for specified values of λ. For systems of mating, transition equations for a complete set of measures could be established, but again numerical methods would be needed to solve them.

Identity disequilibrium functions could be defined to express the effects of linkage on the inbreeding functions. Consider the three locus case for example. The eight components of the inbreeding function for the a, b, c loci are written as F_{ijk} $(i, j, k = 0, 1)$. Disequilibrium could be measured by $F_{ijk} - F_iF_jF_k$, but this includes two locus disequilibrium effects. If only the b and c loci were linked for example, this function would be $F_iF_{jk} - F_iF_jF_k = F_i\eta_{\mathrm{bc}_{jk}}$. Hence the following quantity is defined to measure that three locus identity disequilibrium not accounted for by two locus disequilibria:

$$\eta_{\mathrm{abc}_{ijk}} = F_{ijk} - F_iF_jF_k - F_i\eta_{\mathrm{bc}_{jk}} - F_j\eta_{\mathrm{ca}_{ki}} - F_k\eta_{\mathrm{ab}_{ij}}\,.$$

Once again there is only one numerical value, for, dropping the abc subscript:

$$\eta_{111} = -\eta_{011} = -\eta_{101} = -\eta_{110} = \eta_{100} = \eta_{010} = \eta_{001} = -\eta_{000}.$$

The maximum three locus disequilibrium must occur when the three loci are completely linked. In this case $F_{111} = F_{.11} = F_{1.1} = F_{11.} = F_1$ and

$$\eta_{111} = F_1(1 - F_1)(1 - 2F_1),$$

which is positive until $F_1 = 0.5$ and negative thereafter. It is large relative to F_{111} only when F_1 is small, and in this region is also comparable to $3F_1\eta_{11}$. As linkage decreases η_{111} rapidly decreases for it involves polynomials in linkage parameters.

There would seem to be little point though in deriving empirical results for more than two loci. For n loci, the family of curves for the n locus inbreeding coefficient is bounded above by F_1 and below by F_1^n and these bounds converge as F_1 approaches unity. The inbreeding coefficients are monotonic functions of the linkage parameters so that linkage increases the probability of identity at all loci. Similarly the n locus panmictic coefficient increases from F_0^n to F_0, so that linkage also increases the probability of non-identity at all loci.

In summary then, the primary effects of linkage can be summarized in terms of two loci effects except in the cases of extreme linkage when one locus results are good approximations. The effects of linkage on inbreeding functions are to increase the frequencies of the classes of all identity or non-identity at the expense of all other classes.

SUMMARY

A method for determining the two locus inbreeding function for pedigrees of individuals is discussed, and illustrated for a specific pedigree and two forms of parent offspring mating.—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 just the two locus inbreeding function.—For specific pedigrees the two locus inbreeding function of an individual is expressed in terms of functions involving just the common ancestors of its parents. For pedigree systems of mating, simultaneous transition equations for a complete set of functions, which includes the inbreeding function, are established. A minimal equation of the transition equation yields the recurrence formula for the two locus panmictic coefficient, while the largest eigenvalue of the matrix gives the limiting rate of loss of double non-identity for the system.—Some general conclusions regarding the effects of linkage on inbreeding are drawn.

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APPENDIX

SPECIAL EXPANSIONS OF MEASURES

All these expansions refer to the pedigree in Figure 1.

$$\underline{\gamma}_{B,BB} = \begin{bmatrix} 1 & \tfrac{1}{2} & \tfrac{1}{2} & \tfrac{1}{4} \\ 0 & \tfrac{1}{2} & 0 & \tfrac{1}{4} \\ 0 & 0 & \tfrac{1}{2} & \tfrac{1}{4} \\ 0 & 0 & 0 & \tfrac{1}{4} \end{bmatrix} \mathbf{F}_B \tag{31}$$

$$= \Phi(0)\,\mathbf{F}_B$$

$$\underline{\delta}_{BB,BB} = \underline{\gamma}_{B,BB} \tag{32}$$

$$\begin{aligned} \underline{\gamma}_{C,BB} &= \underline{\gamma}_{C,(DE)(DE)} \\ &= \tfrac{1}{4}\,[\underline{\theta}_{CD} + \underline{\theta}_{CE}] + \tfrac{1}{2}\,\underline{\gamma}_{C,\overline{DE}} \end{aligned} \tag{33}$$

$$\begin{aligned} \underline{\delta}_{BB,\overline{GH}} &= \underline{\delta}_{(DE)(DE),\overline{GH}} \\ &= \tfrac{1}{4}\,[\underline{\gamma}_{D,\overline{GH}} + \underline{\gamma}_{E,\overline{GH}}] + \tfrac{1}{2}\,\underline{\delta}_{\overline{DE},\overline{GH}} \end{aligned} \tag{34}$$

$$\begin{aligned} \underline{\delta}_{BB,CC} &= \underline{\delta}_{BB,(GH)(GH)} \\ &= \tfrac{1}{4}\,[\underline{\gamma}_{G,BB} + \underline{\gamma}_{H,BB}] + \tfrac{1}{2}\,\underline{\delta}_{BB,\overline{GH}} \end{aligned} \tag{35}$$

$$\underline{\gamma}_{B,\overline{BC}} = \underline{\gamma}_{(DE),\overline{(DE)C}}$$

$$= \begin{bmatrix} \tfrac{1}{4} & \tfrac{1}{8} & \tfrac{1}{8} & 0 \\ 0 & \tfrac{1}{8} & 0 & \tfrac{1}{8} \\ 0 & 0 & \tfrac{1}{8} & \tfrac{1}{8} \\ 0 & 0 & 0 & 0 \end{bmatrix} [\underline{\theta}_{CD} + \underline{\theta}_{CE}] + \tfrac{1}{4}\,[\underline{\gamma}_{D,\overline{CE}} + \underline{\gamma}_{E,\overline{CD}}]$$

$$= \tfrac{1}{4}\Phi(i)\,[\underline{\theta}_{CD} + \underline{\theta}_{CE}] + \tfrac{1}{4}\,[\underline{\gamma}_{D,\overline{CE}} + \underline{\gamma}_{E,\overline{CD}}] \text{ where } i^2 = -1. \tag{36}$$

$$\underline{\delta}_{BB,\overline{BC}} = \underline{\gamma}_{B,\overline{BC}} \tag{37}$$

$$\underline{\delta}_{BC,BC} = \begin{bmatrix} \tfrac{1}{2} & \tfrac{1}{2} & \tfrac{1}{4} & \tfrac{1}{4} \\ 0 & 0 & 0 & 0 \\ 0 & 0 & \tfrac{1}{4} & \tfrac{1}{4} \\ 0 & 0 & 0 & 0 \end{bmatrix} \mathbf{F}_B + \begin{bmatrix} \tfrac{1}{2} & \tfrac{1}{4} & \tfrac{1}{2} & \tfrac{1}{4} \\ 0 & \tfrac{1}{4} & 0 & \tfrac{1}{4} \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \end{bmatrix} \mathbf{F}_C + \underline{\delta}_{DG,EH} \tag{38}$$

$$\underline{\delta}_{BG,BH} = \underline{\delta}_{(DE)G,(DE)H}$$

$$= \begin{bmatrix} \tfrac{1}{2} & 0 & \tfrac{1}{2} & 0 \\ 0 & \tfrac{1}{2} & 0 & \tfrac{1}{2} \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \end{bmatrix} \mathbf{F}_C + \tfrac{1}{2}\,\underline{\delta}_{DH,EG} \tag{39}$$

$$\underline{\delta}_{GB,HB} = \underline{\delta}_{G(DE),H(DE)}$$

$$= \begin{bmatrix} \tfrac{1}{2} & \tfrac{1}{2} & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & \tfrac{1}{2} & \tfrac{1}{2} \\ 0 & 0 & 0 & 0 \end{bmatrix} \mathbf{F}_C + \tfrac{1}{2}\,\underline{\delta}_{HD,GE} \tag{40}$$