ONE- AND TWO-LOCUS INBREEDING

FOR

RECURRENT SELECTION

AND

OVERLAPPING GENERATIONS SELECTION

SCHEMES

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ABSTRACT

Inbreeding coefficients at one and two loci are evaluated for recurrent selection and overlapping generations selection schemes. These mating schemes have found great use in plant and animal breeding. The inbreeding coefficients are derived in terms of probability measures that genes are identical by descent. The procedures demonstrated here can be applied to any regular system of mating between individuals or groups of individuals.

For individual mating systems, two digametic individual measures are defined and employed in the derivation of a recurrence formula for the one-locus inbreeding coefficients. Two further classes of individual measures, trigametic and quadrigametic, are required for transition from one generation to the previous one to allow the calculation of the inbreeding coefficients for the two-locus case. This process is illustrated for the case of recurrent selection. For recurrent selection populations with various imposed assumptions, numerical values of the average inbreeding coefficients at the end of the breeding cycles are listed to demonstrate the effects of linkage and population size on the accrual of inbreeding and hence of homozygosity.

For group mating systems, gametic set measures are needed in addition to the average individual measures. Transition equations relating values in successive generations of gametic set measures are established for the calculation of the group inbreeding coefficients. As an illustration of this process, the one- and two-locus inbreeding coefficients for populations with overlapping generations are evaluated. Both monoecious and dioecious populations of diploids are considered and family size is not restricted to being Poisson. Inbreeding effective numbers found by the exact treatment here are compared to various previous approximate results.

ACKNOWLEDGEMENTS

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1   INTRODUCTION

. Since SEWALL WRIGHT (1921) introduced the concept of the inbreeding coefficient F_1 in terms of the correlation between uniting gametes, population geneticists have found great use for such a measure as it summarizes information about the mating system. Later, BARTLETT and HALDANE (1934) using a generation matrix of mating types and MALECOT (1948) using probability arguments succeeded in providing alternative methods of calculating inbreeding coefficients. Of these, MALECOT's definition of the coefficient as the probability of identity by descent of homologous genes within an individual is more widely accepted because it leads to easier application.

The reason for choosing the inbreeding coefficient F_1 as a basis for the analysis of one-locus systems is partly the ease with which it can be calculated. WRIGHT (1922) gave the formula for the inbreeding coefficient of an individual I in a given pedigree as

$$F_{1_I} = \Sigma \; (\tfrac{1}{2})^{n_1 + n_2} (\frac{1 + F_{1_A}}{2})$$

where A denotes an arbitrary common ancestor n_1 and n_2 generations above the two parents of I. The summation extends over all such different pathways and ancestors. For regular systems of mating, MALECOT (1948) showed that recurrence formulas can be established for the evaluation of the inbreeding coefficients. His idea was extended by COCKERHAM (1967) to include matings between groups of individuals.

The applications of the one-locus inbreeding coefficients have been well studied (e.g. KEMPTHORNE 1957). In the first place, it indicates the effect of finite population size or a regular system of mating on a population of breeding individuals, thus allowing different systems to be compared. Secondly, a knowledge of the properties of the initial population together with the inbreeding coefficient allows the evaluation of the mean and the variance of a quantitative trait. The calculation of the covariance between the genotypic values of inbred individuals requires the introduction of the four-gene measures as discussed by WEIR and COCKERHAM (1977).

Many characters of plants and animals exhibit continuous variation as a result of the simultaneous segregation of many genes at many loci affecting the characters. On the other hand, a character controlled by certain loci may be affected by selection practised on other loci. The analysis of characters in these situations necessitates the study of multi-locus theory. While the one-locus quantitative theory involves the dependencies between the action or frequencies of allelic genes caused by dominance or inbreeding, the consideration of the effect of two or more loci involves the further complications of epistasis, linkage and linkage disequilibrium.

As the analysis of one-locus systems requires the knowledge of the inbreeding coefficient F_1, it is natural that an analogous measure, the two-locus inbreeding coefficient F_{11} should be of considerable help in the study of two-locus models. This quantity gives the probability that two linked autosomal loci of a diploid individual carry genes identical by descent. COCKERHAM and WEIR (1968) and WEIR and COCKERHAM (1969a) were able to establish an algorithm by which the two-locus inbreeding coefficient can be calculated and they demonstrated the procedure for sib mating and for any pedigree mating of individuals. The algorithm requires the introduction of trigametic and quadrigametic measures in addition to the usual digametic ones, the one-locus inbreeding and coancestry coefficients needed for the one-locus theory. WEIR and COCKERHAM (1969 b) also used similar arguments in conjunction with those of COCKERHAM (1967) to develop a procedure for the evaluation of two-locus group inbreeding coefficients for systems of matings between groups of individuals.

The two-locus inbreeding coefficient allows an identity disequilibrium to be defined

$$\eta_{11} = F_{11} - (F_1)^2$$

which measures the dependence of two genes at two loci and hence increases with linkage. This quantity is zero for any pedigree mating in the absence of linkage as then the relationship $F_{11} = (F_1)^2$ always holds. For any regular system of mating, it is zero for a non-inbred initial population or when complete double identity is obtained and is positive for all other generations.

The two-locus inbreeding coefficient, though characterizing the effects of linkage and mating system on the identity by descent of two pairs of linked genes, does not by itself provide the expression of joint genotypic frequencies at two loci. To offer complete solutions to two-locus problems, a complete set of four-gene parameters needs to be set up.

A pair of genes is said to be equivalent by descent if both genes descend from genes on one initial gamete. For two genes a, a' at one locus and two genes b, b' at a second locus, a class of individual descent measures was defined which gives the probabilities of the various arrangements of these four genes on gametes in the initial population (COCKERHAM and WEIR 1973, 1977, WEIR and COCKERHAM 1973, 1974). The measures thus relate the structure of any generation to that of an initial population. A set of eight summary components of descent measures was chosen to work with as they are simpler to evaluate and to apply than the original set of measures. General procedures for calculating these summary measures have been established. When the structure of the initial population is known, these summary measures lead to expressions for two-locus genotypic frequencies and various disequilibria functions, and also to the means and variances of quantitative characters (WEIR and COCKERHAM 1977). The last paper also mentioned that some eight-gene descent measures would need to be defined in dealing with the problem of covariances between individuals.

When two genes at each of two loci are simultaneously equivalent by descent, their identity by descent is ensured. Therefore two components of the summary measures are the one-and two-locus inbreeding oefficients. In particular, in the absence of initial linkage disequilibrium, these two coefficients are sufficient to express the two-locus genotypic frequencies, means and variances in terms of the properties of an initial population.

The two-locus inbreeding coefficient thus contains a great deal of information about the two-locus structure of a population as the one-locus coefficient does for the one-locus model. It is the purpose of the present work to illustrate further the evaluation of the two-locus inbreeding coefficients in the cases of recurrent selection

and overlapping generations selection schemes. These are schemes
designed to slow down the rate of inbreeding in selection programmes
and the inbreeding coefficients would give indications of the approach
to homozygosity. The literature appropriate to the two mating schemes
will be reviewed when they are introduced in Chapters 3 and 4.

Techniques developed for population genetics are thus being applied
to quantitative genetics. The mating schemes studied contain the com-
plication that specific rules are stated for the selection of members
of a generation to serve as parents of the next generation. An indication
of the complexity is the fact that this thesis offers the first exact
and correct evaluation of even the one-locus inbreeding coefficients.

Just as inbreeding measures summarize information about mating
systems, effective numbers can be defined and summarize the behaviour
of inbreeding measures. Such effective numbers will be discussed when
appropriate throughout the thesis.

2 REVIEW OF ONE- AND TWO-LOCUS INBREEDING MEASURES

2.1 One-Locus Individual Measures

For inbreeding at one locus, the identity status of pairs of genes
a, a' at the locus is needed. A probability measure $\underline{X}$ with two compo-
nents according to the identity relations is defined as :

$$\underline{X}(a,a') = \begin{bmatrix} X_1(a,a') \\ X_0(a,a') \end{bmatrix} = \begin{bmatrix} \text{Prob } (a \equiv a') \\ \text{Prob } (a \not\equiv a') \end{bmatrix}$$

where the equivalence sign $\equiv$ means identity by descent. No restriction
is placed on the number of alleles.

$\underline{X}$ is a digametic measure as a and a' must be carried on two distinct
gametes. When dealing with individual mating schemes, two types of the
measure need to be distinguished according to whether or not the two
gametes unite and these two are sufficient for the establishment of
recurrence relations for the evaluation of the one-locus inbreeding
coefficient :

$\underline{F}_I = \underline{X}(a,a'$: a,a' are on two gametes uniting to form
individual I)

$\underline{\theta}_{JK} = \underline{X}(a,a'$: a,a' are on two gametes taken from
individuals J and K respectively).

Evidently, F_{1_I} is the inbreeding coefficient of I,

F_{0_I} is the panmictic coefficient of I,

$\theta_{1_{JK}}$ is the coancestry coefficient of J and K,

and $F_{1_I} = \theta_{1_{JK}}$ if I is the offspring of J and K.

2.2 One-Locus Group Measures

. To study systems of matings between groups of individuals, let
I, J, K denote individuals belonging to groups i, j and k respectively.
The coancestry between groups j and k is determined by the identity
status of genes on two gametes taken randomly from the two gametic
output sets provided by groups j and k respectively. It is referred
to as a gametic set measure. To take account of the gametic sampling
scheme, it is necessary to specify the groups that receive the gametes.

$$\underline{\Psi}_{j_p k_q} = \underline{X}(a,a' : \text{a is on one gamete in the gametic set that}$$
$$\text{group p receives from group j and a' is on}$$
$$\text{one gamete in the gametic set that group q}$$
$$\text{receives from group k}).$$

The inbreeding function of group i, $\underline{F}_i$, is given by the average
coancestry between its parental groups, j and k say

$$\underline{F}_i = \underline{\Psi}_{j_i k_i}$$

averages taken over all such pairs of gametes. Recurrence relations are
then established between values in successive generations of a complete
set of digametic set measures for the evaluation of $\underline{F}_i$.

A difficulty arises when one group acts as a donor of both gametes
for a gametic set measure, for example $\underline{\Psi}_{j_p j_q}$. The two gametes taken
from the same group may have come from the same individual and there is
a possibility of the two genes being automatically identical by descent.
This situation prohibits the expansion of gametic set measures back
directly to gametic set measures of the previous generation. Individual
measures need to be defined to identify cases that the two gametes of
interest have come from the same or two distinct individuals :

$$\underline{\theta}_{J_j K_k} = \underline{X}(a,a' : \text{a is on a gamete taken from individual J in}$$
$$\text{group j and a' is on a gamete from individual}$$
$$\text{K in group k}).$$

Primes are used to denote distinct individuals. For example, the average individual coancestry function for two distinct members of group j is written as $\theta_{J_j J'_j}$. The procedure is thus to express a gametic set measure as a linear combination of individual measures by using the gametic sampling probabilities, and then to expand these individual measures back to gametic set measures of the previous generation (WEIR and COCKERHAM 1969b).

2.3   Two-Locus Individual Measures

The following work serves as an extension of Section 2.1 and is based on the work of WEIR and COCKERHAM (1969a). For two loci with genes a and b respectively, the identity status of two pairs of genes, a, a' and b, b' is needed. The usual procedure is to define a four component vector for these gene pairs as

$$\underline{X}(ab,a'b') = \begin{bmatrix} X_{11}(ab,a'b') \\ X_{10}(ab,a'b') \\ X_{01}(ab,a'b') \\ X_{00}(ab,a'b') \end{bmatrix} = \begin{bmatrix} \text{Prob}(a\equiv a',\ b\equiv b') \\ \text{Prob}(a\equiv a',\ b\not\equiv b') \\ \text{Prob}(a\not\equiv a',\ b\equiv b') \\ \text{Prob}(a\not\equiv a',\ b\not\equiv b') \end{bmatrix}$$

To evaluate such two-locus inbreeding measures, it is necessary to distinguish the cases where the pairs of genes are carried on two, three or four gametes. There are two digametic measures, just as there are in the one-locus case :

$$\underline{F}_I = \underline{X}(ab,a'b' : ab,a'b' \text{ are on the two gametes uniting to form individual I}),$$

$$\underline{\theta}_{JK} = \underline{X}(ab,a'b' : ab,a'b' \text{ are on two gametes taken from individuals J and K, respectively}).$$

The trigametic and quadrigametic measures are written as $\underline{\gamma}$ and $\underline{\delta}$, respectively :

$$\underline{\gamma}_{I;JK} = \underline{X}(ab,a'b' : ab,\ a'b' \text{ are on three gametes taken from individuals I, J, and K, respectively}),$$

$$\underline{\delta}_{IJ;KL} = \underline{X}(ab,a'b' : a,b,a',b' \text{ are on four gametes taken from}$$
$$\text{individuals } I, J, K \text{ and } L, \text{ respectively}).$$

The four components of each measure sum to unity. The first and fourth component of $\underline{F}_I$, giving the probabilities of double identity and double non-identity by descent are termed the two-locus inbreeding and panmictic coefficients respectively for individual I.

One locus measures may be found by summing appropriate components of two-locus measures as shown in Table 2.1.

Table 2.1   Relationship between One- and Two-locus Measures

F_{11_I}	F_{10_I}	$F_{1\cdot_I}=F_{1_I}$
F_{01_I}	F_{00_I}	$F_{0\cdot_I}=F_{0_I}$
$F_{\cdot 1_I}=F_{1_I}$ $F_{\cdot 0_I}=F_{0_I}$		1
$\theta_{11_{JK}}$	$\theta_{10_{JK}}$	$\theta_{1\cdot_{JK}}=\theta_{1_{JK}}$
$\theta_{01_{JK}}$	$\theta_{00_{JK}}$	$\theta_{0\cdot_{JK}}=\theta_{0_{JK}}$
$\theta_{\cdot 1_{JK}}=\theta_{1_{JK}}$ $\theta_{\cdot 0_{JK}}=\theta_{0_{JK}}$		1
$\gamma_{11_{I;JK}}$	$\gamma_{10_{I;JK}}$	$\theta_{1\cdot_{IJ}}=\theta_{1_{IJ}}$
$\gamma_{01_{I;JK}}$	$\gamma_{00_{I;JK}}$	$\theta_{0\cdot_{IJ}}=\theta_{0_{IJ}}$
$\theta_{\cdot 1_{IK}}=\theta_{1_{IK}}$ $\theta_{\cdot 0_{IK}}=\theta_{0_{IK}}$		1

Table 2.1   (continued)

$\delta_{11IJ;KL}$	$\delta_{10IJ;KL}$	$\theta_{1\cdot IK}=\theta_{1IK}$
$\delta_{01IJ;KL}$	$\delta_{00IJ;KL}$	$\theta_{0\cdot IK}=\theta_{0IK}$
$\theta_{\cdot 1JL}=\theta_{1JL}$	$\theta_{\cdot 0JL}=\theta_{0JL}$	1

For example, the one-locus coefficient of an individual I is given by

$$F_{1I} = F_{11I} + F_{10I} = F_{11I} + F_{01I}$$

with the assumption that both loci are equally inbred. Once the one-locus coefficients are known, the tables demonstrate that only one component of each of the two-locus measures need be calculated in order to determine all the measures. For convenience, the component X_{00} for double non-identity is usually chosen to work with.

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

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

2.4   Two-Locus Group Measures

In analysing group mating systems at two loci, WEIR and COCKERHAM (1969b) have defined three classes of gametic set measures :

$\psi_{j_p k_q}$ = $\underline{X}$(ab,a'b' : ab are on one gamete in the gametic set that group p receives from group j and a'b' are on one gamete in the gametic set that group q receives from group k),

$\nu_{i_p;j_q k_r}$ = $\underline{X}$(ab,a'b' : ab is on one gamete in the gametic set that group p receives from group i, a' is on one gamete in the gametic set that group q receives from group j and b' is on one gamete in the gametic set that group r receives from group k),

$$\underline{\zeta}_{i_p j_q; k_r \ell_s} = \underline{X}(ab,a'b' : a,b,a',b' \text{ are on four gametes in the}$$
gametic sets that groups p,q,r,s

. receive from groups i,j,k,ℓ, respectively).

The procedure for the evaluation of the two-locus group inbreeding function $\underline{F}_i$ is to first express it as the coancestry function between the parental groups, j and k say,

$$\underline{F}_i = \underline{\psi}_{j_i k_i}$$

and then to establish recurrence relations for a complete set of gametic set measures for the calculation of $\underline{\psi}_{j_i k_i}$.

Just as in the one-locus case, whenever a group appears more than once as a donor in the subscript of a gametic set measure, the expansion procedure requires an intermediate stage of individual measures. Let I,J,K,L denote members of group i,j,k,ℓ, respectively, three types of individual measures are distinguished :

$$\underline{\theta}_{J_j K_k} = \underline{X}(ab,a'b' : ab, a'b' \text{ are on two gametes taken from}$$
individuals J, K in groups j and k, respectively),

$$\underline{\gamma}_{I_i; J_j K_k} = \underline{X}(ab,a'b' : ab, a',b' \text{ are on three gametes taken}$$
from individuals I,J,K in groups i,j and k, respectively),

$$\underline{\delta}_{I_i J_j; K_k L_\ell} = \underline{X}(ab,a'b' : a,b,a',b' \text{ are on four gametes taken}$$
from individuals I,J,K,L in groups $i,$ j,k and ℓ, respectively).

3 ONE- AND TWO-LOCUS INBREEDING FOR RECURRENT SELECTION

3.1 Introduction

With the inbreeding measures defined generally, and the machinery developed by COCKERHAM and WEIR (1968) for the calculation of the two-locus inbreeding coefficients, in this Chapter a one- and two-locus analysis of inbreeding for a population undergoing recurrent selection is presented.

The use of recurrent selection (RS) procedures in plant breeding is now well established. As PENNY, et al (1963) point out in their review, the recombination or crossing phase in an RS programme slows the rapid approach to homozygosity which limits selection under selfing systems. To monitor the level of homozygosity in RS programme, it is convenient to calculate inbreeding coefficients. These coefficients indicate identity by descent and so do not give a complete description of homozygosity. They do provide lower bounds, however, (CAIN and HINKELMANN, 1970) and the algebra needed to establish recurrence equations for inbreeding coefficients may also be applied directly to measures of homozygosity.

A one-locus coefficient was calculated by SPRAGUE, et al (1952) and a quite detailed discussion of one- and two-locus coefficients was given by CAIN and HINKELMANN (1970, 1972). These last two papers contain some errors and do not seem to follow the most natural development of inbreeding measures. One difficulty with the papers of CAIN and HINKELMANN is that they are based on the approach of SHIKATA (e.g., SHIKATA, 1965) which is of limited application (e.g., WEIR, 1971).

3.2 Mating and Selection Schemes

The population consists of diploid individuals capable of both selfing and intercrossing. There is no restriction on the number of alleles at each of the loci studied. A constant number of progeny per individual is assumed and possible viability effects are ignored. The development will be based on one progeny per mating (self or intercross).

Initially N non-inbred and unrelated individuals are drawn from a source population and selfed. The resulting N offspring are crossed in ·all possible pairs and then another selfing phase entered. The population size would quickly become unmanageable of course for there would be M = N(N-1)/2 individuals at the end of the first intercross phase, M(M-1)/2 at the end of the second, and so on.

Selection will be supposed to be practised by selecting N individuals at the end of each selfing phase. The basis for this selection will not be discussed, but note (CAIN and HINKELMANN, 1970) that this treatment includes such schemes as simple RS, reciprocal RS and RS for general and specific combining ability. The calculations made will include all of the M individuals at the end of each intercross phase. Selection will be supposed to be at random, so that it is necessary to make use of sampling probabilities. Any mating scheme in which there is no choice of mates is expressly excluded from consideration here, but may be analysed by other methods (e.g., WEIR and COCKERHAM, 1969a). Most of the discussion will be for the case where N individuals are chosen quite at random from the M at the end of each selfing phase, and so would be appropriate for a control population. Following CAIN and HINKELMANN (1970), two schemes of random selection with constraints will be considered. These are the so called "minimum" and "maximum" inbreeding schemes. In the former case, each of the selected individuals contributes exactly two gametes to the next group of selected individuals. In the latter case, one of the selected individuals contributes N-1 gametes, two contribute two gametes while the remaining N-3 individuals each contributes exactly one gamete to the next group of selected individuals. The mating and selection schemes are illustrated for N = 4 in Figure 3.1. Random selection is when the four individuals selected in generation 1 of a cycle are selected without regard to gametic contributions in the previous cycle.

The quantities to be determined are the average inbreeding coefficients for the intercross and selfed populations, so that all members of these populations must be considered whether or not they contribute to succeeding generations.
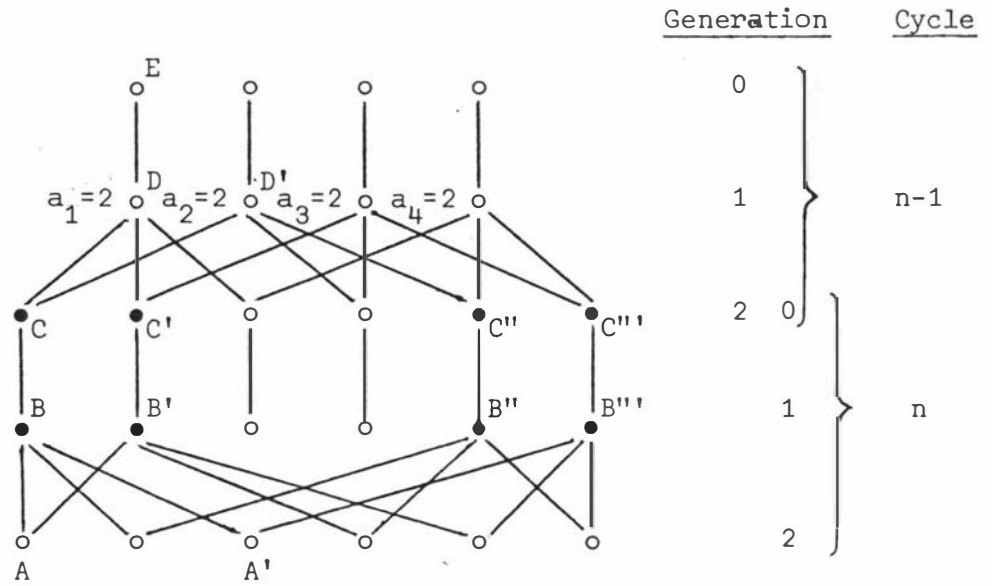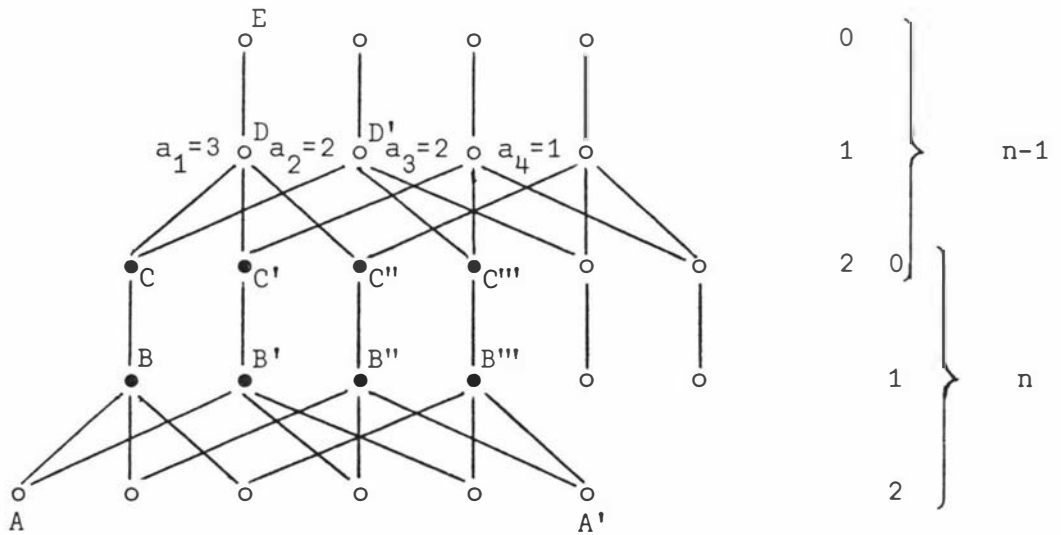
Figure 3.1.   Mating and selection schemes for N = 4.   Selected
                individuals are shown as solid circles.

3.3   One-Locus Case

·   The inbreeding coefficient of a random one of the M members, say
A, of generation 2 (intercrossed generation) of cycle n can be written
as F_{1A} or as $F_{1(2,n)}$.   As not all members of this generation have the
same pedigree, F_{1A} is an average measure. F_{1A} is first expressed as
$\theta_{1BB'}$, the coancestry of two of the N distinct individuals B and B'
chosen at random from generation 1 (selected selfed generation) of
cycle n.   The process of tracing gametes back in time continues until
a set of transition equations is established which allow the calcula-
tion of F_{1A} and of F_{1B}.

3.3.1   Sampling Probabilities for One-Locus Case

If C and C' are the parents of B and B', respectively, they are
distinct members of the selected intercross population (generation 2
of cycle n-1) and

$$F_{1A} = \theta_{1BB'} = \theta_{1CC'} \quad .$$
(3.3.1)

The selected intercross population refers to the parents of the
selected selfed population. Further expansion back in time requires
account to be taken of whether C and C' have a common parent, with
probability P_{211}, or whether they have four distinct parents, with
probability P_{1111}. For both schemes in Figure 3.1, individual A has
grandparents C, C' with a common parent D, while the grandparents of
individual A' do not have a common parent. In general, when a set of
2m gametes received by m members of generation 2 of cycle n is consi-
dered, $P_{t_1 t_2 \ldots t_r}$ is the probability that these gametes are from r
individuals in generation 1 of cycle n and that the ith of these
individuals contributed t_i of the gametes. This requires that the
t_i sum to 2m.

The four gametes received by distinct individuals C, C' necessarily
come from three or four individuals unless N, the selected population
size, is equal to 2. This provides

$$P_{211} + P_{1111} = 1, N \geq 3; \quad P_{22} = 1, N = 2.$$

For the unrestricted random sampling scheme, $N \geq 3$, the sampling probabilities may be taken to refer to four gametes uniting to form any two of the M crossed offspring in generation 2 of a cycle. The number of such pairs of offspring is $\binom{M}{2}$ and, since selection is random, the number of ways in which three distinct parents can be chosen for a pair is $\binom{N}{3}$. Finally, the number of ways in which one of the three parents can be chosen to contribute two gametes, and become the common parent to the pair of individuals, is $\binom{3}{1}$ so that

$$P_{211} = \binom{N}{3}\binom{3}{1} \Big/ \binom{M}{2} = \frac{4}{N+1} \quad , \quad P_{1111} = \frac{N-3}{N+1} \, , \, N \geq 3 \quad . \tag{3.3.2}$$

For the restricted random selection schemes, as in CAIN and HINKELMANN (1970), let a_i denote the number of gametes contributed by the ith selected individual to the next generation of selected individuals. These a_i must satisfy

$$1 \leq a_i \leq N - 1 \quad , \quad \sum_{i=1}^{N} a_i = 2N$$

and may be regarded as the number of gametes the ith selected selfed individual contributes to the following generation of selected intercrossed individuals. Now P_{211} can be regarded as the probability that a pair of individuals from the selected intercross population have a common parent in the preceding selected self population. There are $\binom{N}{2}$ such pairs of individuals and $\sum_i a_i(a_i-1)/2$ pairs of gametes from a single parent, so that

$$P_{211} = \sum_i a_i(a_i-1)/N(N-1) \quad . \tag{3.3.3}$$

Figure 3.1 shows the a_i's for the case $N = 4$. For minimum inbreeding, $a_i = 2$ for $i = 1,2,...N$ so that

$$P_{211} = 2/(N-1) \quad , \quad N \geq 3$$

while for maximum inbreeding it is appropriate to write $a_1 = N-1$, $a_2 = a_3 = 2$, $a_i = 1$ for $i = 4,5,...N$ and hence

$$P_{211} = (N^2 - 3N + 6)/N(N-1) \quad , \quad N \geq 4 \quad . \tag{3.3.4}$$

Note that, as expected, P_{211} for unrestricted random selection is greater than that for minimum inbreeding and less than that for maximum inbreeding for all $N \geq 4$.

3.3.2   Recurrence Formulae for $N \geq 4$ for One-Locus Case

If primes are used to denote distinct random individuals, equation (3.3.1) can be expressed as

$$\theta_{1CC'} = P_{211}(\theta_{1DD} + 3\theta_{1DD'})/4 + P_{1111}\theta_{1DD'} \, . \qquad (3.3.5)$$

From the usual result for the coancestry of an individual with itself

$$\theta_{1DD} = (1 + F_{1D})/2$$
$$F_{1D} = \theta_{1EE} = (1 + F_{1E})/2 \qquad\qquad (3.3.6)$$

and these expressions may be substituted into (3.3.5) which, with $\theta_{1DD'}$ written as F_{1C}, gives

$$F_{1A} = 3P_{211}/16 + (3P_{211} + 4P_{1111})F_{1C}/4 + P_{211}F_{1E}/16. \qquad (3.3.7)$$

Recall that D, D' are any two of the selected selfed individuals, while C in F_{1C} refers to any of the M offspring obtained by crossing these.

In general then, the average inbreeding for the whole of the intercross generation follows from (3.3.7) as

$$
\begin{aligned}
F_{1(2,n)} = {} & 3P_{211}/16 + (1-P_{211}/4)F_{1(2,n-1)} \\
& + P_{211}F_{1(2,n-2)}/16
\end{aligned}
\qquad (3.3.8)
$$

and that for the whole of the selfed generation follows from (3.3.6) as

$$F_{1(1,n)} = (1 + F_{1(2,n-1)})/2 \, . \qquad\qquad (3.3.9)$$

While any initial conditions at all may be accommodated, it is usual to take $F_{1(2,0)} = F_{1(2,1)} = 0$, where $F_{1(2,0)}$ is for the initial N individuals.

For unrestricted random selection, substitution of P_{211} from (3.3.2) into (3.3.8) gives

$$F_{1(2,n)} = \frac{3}{4(N+1)} + \frac{N}{N+1} F_{1(2,n-1)} + \frac{1}{4(N+1)} F_{1(2,n-2)} \qquad (3.3.10)$$

which corrects equations (3.1), (3.2) of CAIN and HINKELMANN (1970).

For restricted random selection, if P_{211} from (3.3.3) is substituted into (3.3.8), a result is obtained similar to that in equation (6.1) of CAIN and HINKELMANN (1970), who refer to this case as effective directional selection.

In the maximum inbreeding case there is the unusual result that average inbreeding increases with population size. This is because, for $N \geq 6$, P_{211} is an increasing function of N. As N increases, there is a greater chance that any two members of the selected intercross generation have a common parent. This extreme case is less likely to occur by chance under unrestricted random selection as N increases, however.

3.3.3   Recurrence Formulae for $N < 4$ for One-Locus Case

For a population to be maintained at size less than four, there can be no selection since $M \leq N$ and the situation is really outside the scope of this Chapter. For N=1 the system becomes the simple selfing case with no scope for intercrossing. For N = 3 each individual always contributes exactly two gametes to succeeding generations, and, from either (3.3.2) or (3.3.3), $P_{211} = 1$. Equation (3.3.8) does reduce to

$$F_{1(2,n)} = \frac{3}{16} + \frac{3}{4} F_{1(2,n-1)} + \frac{1}{16} F_{1(2,n-2)} \qquad (3.3.11)$$

as given in (6.1) of CAIN and HINKELMANN (1970).

To maintain a population of size N = 2, it would be necessary for the pair of individuals in each intercrossing phase to leave two offspring instead of one. The system then reduces to one of alternating selfing and full sib mating, for which the appropriate recurrence

formula is

$$F_{1(2,n)} = \frac{3}{8} + \frac{1}{2} F_{1(2,n-1)} + \frac{1}{8} F_{1(2,n-2)}. \qquad (3.3.12)$$

Equation (3.3.9) is still to be used in conjunction with (3.3.11) and (3.3.12).

3.4   Two-Locus Case

For inbreeding at two loci, the identity status of two pairs of genes , a,a' at one locus and b,b' at another locus needs to be considered. The four genes may be carried on two, three or four distinct gametes and hence, in addition to the digametic measures sufficient for the one-locus analysis, two further classes of measures, trigametic and quadrigametic, are required for transition from one cycle to the previous one to allow the calculation of the two-locus inbreeding function.

From Table 2.1, it is evident that, to determine the four components of the inbreeding function, the only information needed is one of the components in addition to the one-locus coefficients, as for example, $F_{11} = F_{00} + 2F_1 - 1$. It will be convenient to work with the two-locus panmictic coefficient, and the corresponding (fourth) components of other measures.

For further convenience the following average measures are defined :

$$\underline{\gamma}_{I;\overline{JK}} = (\underline{\gamma}_{I;JK} + \underline{\gamma}_{I;KJ})/2 \quad ,$$

$$\underline{\delta}_{IJ;\overline{KL}} = (\underline{\delta}_{IJ;KL} + \underline{\delta}_{IJ;LK})/2 \quad ,$$

$$\underline{\delta}_{\overline{IJ};\overline{KL}} = (\underline{\delta}_{IJ;KL} + \underline{\delta}_{IJ;LK} + \underline{\delta}_{JI;KL} + \underline{\delta}_{JI;LK})/4 \quad .$$

Expansions of two-locus measures make use of the linkage parameter λ which was defined on Page 9. The one-locus situation corresponds to

$\lambda=1$, for then the two loci are completely linked and a and b are transmitted as one gene. Independent transmission of a and b occurs when $\lambda=0$.

3.4.1   Selfing Phase Expansions for Two-Locus Case

The general method of calculating $\underline{F}$ for any generation follows that for the one-locus coefficient F_1. Starting with a random member A of generation 2 of cycle n, $\underline{F}_A$ is expressed as the two-locus coancestry coefficient of its distinct parents

$$\underline{F}_A = \underline{\theta}_{BB'} \quad \text{and} \quad F_{00A} = \theta_{00BB'} \tag{3.4.1}$$

The tracing of the genes received by A back through the selfing phase is now more complicated since the four genes may be carried on two, three or four gametes in that phase. In particular, if individual B receives gametes $a_C b_C$, $a'_C b'_C$ from its single parent C and transmits gamete $a_B b_B$ to individual A, then $a_B b_B$ is traced back to the array

$$\frac{1+\lambda}{4} a_C b_C + \frac{1+\lambda}{4} a'_C b'_C + \frac{1-\lambda}{4} a'_C b_C + \frac{1-\lambda}{4} a_C b'_C$$

and similarly for the gamete transmitted from B' to A. The two arrays may be written as the margins of a two way table, as in Table 3.1, and the value of $\theta_{00BB'}$ in each of the sixteen cases written in the body of the table.

Collecting terms in this table shows that

$$\theta_{00BB'} = \frac{(1+\lambda)^2}{4} \theta_{00CC'} + \frac{1-\lambda^2}{2} \gamma_{00C;C'C'}$$
$$+ \frac{(1-\lambda)^2}{4} \delta_{00CC;C'C'} \tag{3.4.2}$$

where, once again, primes are used to denote distinct rather than particular individuals.

Table 3.1   Expansion of $\theta_{00BB'}$

	$a_B b_B$			
$\theta_{00BB'}$	$\dfrac{1+\lambda}{4}$ $a_C b_C$	$\dfrac{1+\lambda}{4}$ $a'_C b'_C$	$\dfrac{1-\lambda}{4}$ $a_C b'_C$	$\dfrac{1-\lambda}{4}$ $a'_C b_C$
$\dfrac{1+\lambda}{4}$ $a_{C'} b_{C'}$	$\theta_{00CC'}$	$\theta_{00CC'}$	$\gamma_{00C';CC}$	$\gamma_{00C';CC}$
$\dfrac{1+\lambda}{4}$ $a'_{C'} b'_{C'}$	$\theta_{00CC'}$	$\theta_{00CC'}$	$\gamma_{00C';CC}$	$\gamma_{00C';CC}$
$a_{B'} b_{B'}$ $\dfrac{1-\lambda}{4}$ $a_{C'} b'_{C'}$	$\gamma_{00C;C'C'}$	$\gamma_{00C;C'C'}$	$\delta_{00CC;C'C'}$	$\delta_{00CC;C'C'}$
$\dfrac{1-\lambda}{4}$ $a'_{C'} b_{C'}$	$\gamma_{00C;C'C'}$	$\gamma_{00C;C'C'}$	$\delta_{00CC;C'C'}$	$\delta_{00CC;C'C'}$

Further expansion, now through the intercross phase, will require the use of sampling probabilities as previously, followed by expansions through another selfing phase. These selfing expansions will evidently be for genes received by two, three or four individuals (in generation 1 of cycle n-1).

For the other digametic measure θ_{00BB}, double non-identity is preserved only if the four genes on the two gametes from B descend from four distinct genes on the two gametes received by B from its single parent C. This occurs with probability $(1+\lambda^2)/4$ and hence

$$\theta_{00BB} = \frac{1+\lambda^2}{4} \theta_{00CC} .$$ (3.4.3)

When genes a',b', or when all four genes a,b,a',b', are on separate gametes from B, double non-identity is preserved with probability 1/4 and

$$\gamma_{00B;BB} = \frac{1}{4} \theta_{00CC} ,$$ (3.4.4)

$$\delta_{00BB;BB} = \frac{1}{4} \theta_{00CC} .$$ (3.4.5)

The argument for the expansion of $\gamma_{00B;B'B'}$ is the same as that for θ_{00BB}, except that the frequencies for the gametic array of a'b' are all equal to 1/4. Since genes a',b' are on separate gametes, linkage cannot affect these frequencies. The appropriate expansion is then

$$\gamma_{00B;B'B'} = \frac{1+\lambda}{4} \theta_{00CC'} + \frac{1}{2} \gamma_{00C;C'C'}$$
$$+ \frac{1-\lambda}{4} \delta_{00CC;C'C'} .$$ (3.4.6)

When genes a and b are also on separate gametes, linkage does not affect the gametic arrays of either ab or a'b'. The expansion for $\delta_{00BB,B'B'}$ is then obtained from (3.4.6) by removing λ

$$\delta_{00BB;B'B'} = \frac{1}{4} \theta_{00CC'} + \frac{1}{2} \gamma_{00C;C'C'} + \frac{1}{4} \delta_{00CC;C'C'} .$$ (3.4.7)

To preserve double non-identity in expanding $\gamma_{00B;BB'}$, genes a and a' must be traced back to genes on distinct gametes received by B from C so that

$$\gamma_{00B;BB'} = \frac{1}{2} \gamma_{00C;CC'} .$$ (3.4.8)

By symmetry the expansion for $\gamma_{00B;B'B}$ is

$$\gamma_{00B;B'B} = \frac{1}{2} \gamma_{00C;C'C} .$$ (3.4.9)

Combining equations (3.4.8) and (3.4.9) leads to the expansion of the following average measure

$$\gamma_{00B;\overline{BB'}} = \frac{1}{2} \gamma_{00C;\overline{CC'}} \cdot \tag{3.4.10}$$

Consider the expansion of $\gamma_{00B;B'B''}$, the gamete carrying ab may be a parental type or a recombinant type with probabilities $(1+\lambda)/2$ or $(1-\lambda)/2$ respectively. Therefore

$$\gamma_{00B;B'B''} = \frac{1+\lambda}{2} \gamma_{00C;C'C''} + \frac{1-\lambda}{2} \delta_{00CC;C'C''} \cdot \tag{3.4.11}$$

When genes a,b are carried on separate gametes, λ may be removed from equation (3.4.11) giving

$$\delta_{00BB;B'B''} = \frac{1}{2} \gamma_{00C;C'C''} + \frac{1}{2} \delta_{00CC;C'C''} \cdot \tag{3.4.12}$$

For $\delta_{00BB';BB''}$, genes a and a' must be traced back to genes on two gametes received by B to preserve double non-identity. This occurs with probability 1/2 since a and a' are on separate gametes and hence

$$\delta_{00BB';BB''} = \frac{1}{2} \delta_{00CC';CC''} \cdot \tag{3.4.13}$$

By symmetry

$$\delta_{00B'B;B''B} = \frac{1}{2} \delta_{00C'C;C''C} \cdot \tag{3.4.14}$$

When the same argument is also applied to genes b and b', the following expansion is obtained

$$\delta_{00BB';BB'} = \frac{1}{4} \delta_{00CC';CC'} \cdot \tag{3.4.15}$$

Equations (3.4.12) – (3.4.14) provide the expansion of the average quadrigametic measure

$$\delta_{00\overline{BB'};\overline{BB''}} = \frac{1}{4} \gamma_{00C;C'C''} + \frac{1}{2} \delta_{00\overline{CC'};\overline{CC''}} \cdot \tag{3.4.16}$$

Finally

$$\delta_{00BB';B''B'''} = \delta_{00CC';C''C'''} \cdot \tag{3.4.17}$$

These equations may be manipulated more easily in matrix form. For the selfed generation of cycle n, the twelve measures needed can be written as a vector $\underline{u}_{(1,n)}$

$$\underline{u}'_{(1,n)} = [\theta_{00BB} \; , \; \theta_{00BB'} \; , \; \gamma_{00B;BB} \; , \; \gamma_{00B;B'B'} \; , \; \gamma_{00B;\overline{BB'}} \; ,$$

$$\gamma_{00B;B'B''} \; , \; \delta_{00BB;BB} \; , \; \delta_{00BB;B'B'} \; , \; \delta_{00BB';BB'} \; ,$$

$$\delta_{00BB;B'B''} \; , \; \delta_{00\overline{BB'};\overline{BB''}} \; , \; \delta_{00BB';B''B'''} \;]$$

and the ten measures needed for the intercross generation of cycle n-1 are written as $\underline{v}_{(2,n-1)}$ or as $\underline{v}_{(0,n)}$

$$\underline{v}'_{(2,n-1)} = [\theta_{00CC} \; , \; \theta_{00CC'} \; , \; \gamma_{00C;C'C'} \; , \; \gamma_{00C;\overline{CC'}} \; , \; \gamma_{00C;C'C''} \; ,$$

$$\delta_{00CC;C'C'} \; , \; \delta_{00CC';CC'} \; , \; \delta_{00CC;C'C''} \; , \; \delta_{00\overline{CC'};\overline{CC''}} \; ,$$

$$\delta_{00CC';C''C'''} \;] \; .$$

Equations (3.4.2) - (3.4.7), (3.4.10) - (3.4.12) and (3.4.15) - (3.4.17) become

$$\underline{u}_{(1,n)} = \Psi\underline{v}_{(2,n-1)} = \Psi\underline{v}_{(0,n)} \tag{3.4.18}$$

where the 12 x 10 matrix Ψ has elements defined by those equations.

3.4.2   Sampling Probabilities for Two-Locus Case

The previous section showed that account must be taken of gametes received by two, three or four individuals in generation 1 of a cycle. The four genes of interest on these gametes can be traced back to genes on up to four gametes received by individuals in generation 2 of the previous cycle. Sampling probabilities are needed for these intercross gametes. To take proper account of the restrictions on mating in the intercross phase, sampling probabilities are defined for all $2m$ gametes received by m individuals (m = 2,3,4). Appropriate sums of these probabilities are then taken to give the required probabilities for up to four gametes. The sampling probabilities are given in Table 3.2.

Table 3.2 Gametic Sampling Probabilities[†]

Numbers of			Selection Scheme		
Gametes (2m)	Parents (r)	Symbol	Unrestricted*	Minimum** Inbreeding	Maximum*** Inbreeding
4	3	P_{211}	$\binom{3}{1}$	1	$(N^2-3N+6)/2$
	4	P_{1111}	$\binom{3}{1}$	$\frac{1}{2}\binom{N-3}{1}$	$\binom{N-3}{1}$
6	3	P_{222}	1	0	1
	4	P_{2211}	$\binom{4}{2}\binom{2}{1}$	1	$2\binom{N-3}{1}$
	4	P_{3111}	$\binom{4}{1}$	0	$\binom{N-1}{3}$
	5	P_{21111}	$\binom{5}{1}\binom{4}{2}$	$\binom{N-4}{1}$	$\binom{N-3}{2}$
	6	P_{111111}	$\binom{5}{1}\binom{3}{1}$	$\frac{1}{3}\binom{N-4}{2}$	0
8	4	P_{2222}	$\binom{3}{1}$	0(1 if N=4)	0
	4	P_{3221}	$\binom{4}{1}\binom{3}{1}$	0	$\binom{N-3}{1}$
	5	$P_{22211(i)}$	$\binom{5}{3}$	0	0
	5	$P_{22211(ii)}$	$\binom{5}{3}\binom{3}{1}\binom{2}{1}$	1	0
	5	P_{32111}	$\binom{5}{1}\binom{4}{1}\binom{3}{1}$	0	$2\binom{N-3}{2}$
	5	P_{41111}	$\binom{5}{1}$	0	$\binom{N-1}{4}$
	6	P_{311111}	$\binom{6}{1}\binom{5}{3}$	0	$\binom{N-3}{3}$
	6	$P_{221111(i)}$	$\binom{6}{2}\binom{4}{1}\binom{3}{1}$	$\binom{N-5}{1}$	0
	6	$P_{221111(ii)}$	$\binom{6}{2}\binom{4}{2}$	$\frac{1}{2}\binom{N-5}{1}$	0
	7	$P_{2111111}$	$\binom{7}{1}\binom{6}{2}\binom{3}{1}$	$\binom{N-5}{2}$	0

Table 3.2 (continued)

Numbers of			Selection Scheme		
Gametes (2m)	Parents (r)	Symbol	Unrestricted*	Minimum** Inbreeding	Maximum*** Inbreeding
8		$P_{11111111}$	$\binom{7}{1}\binom{5}{1}\binom{3}{1}$	$\frac{1}{4}\binom{N-5}{3}$	0

* divide by $\binom{M}{m}/\binom{N}{r}$

** divide by $\binom{N}{m}/N$

*** divide by $\binom{N}{m}$

†Assumes that $N \geq r$ in any line and that $N \geq 4$.

The derivation of the sampling probabilities in Table 3.2 is illustrated by reference to P_{21111}, the probability that the six gametes received by three of the N selected members of the intercross generation descend from five members of the selected self generation in the previous cycle in such a way that one of the five gives two gametes. For the unrestricted random selection case, the six gametes considered are received by any three of the M members of the whole intercross generation so that P_{21111} will have a denominator of $\binom{M}{3}$. For the numerator , note that there are $\binom{N}{5}$ ways of choosing the five members of the self generation and $\binom{5}{1}$ ways of choosing one of them to give two gametes. There are then $\binom{4}{2}$ ways of choosing two from the remaining four individuals to provide the gametes which unite with the two from the first individual chosen and so

$$P_{21111} = \binom{5}{1}\binom{4}{2}\binom{N}{5}/\binom{M}{3} \qquad N \geq 5$$

$$= 0 . \qquad N < 5$$

Although expressions were provided by CAIN and HINKELMANN (1970), it is not possible to express the probabilities for the restricted selection schemes in terms of a_i, the numbers of gametes contributed to the selected intercross individuals by the ith selected selfed individual. When the probabilities involve a choice of more than one member of the self generation (in contrast to the one needed for P_{211} in the one-locus case), knowledge of the mating pattern between members of this generation is needed. Such knowledge is not provided by the a_i.

A restriction not mentioned by CAIN and HINKELMANN is made in the case of minimum inbreeding. It will be assumed that the minimum inbreeding scheme, in the intercross phase, is equivalent to circular mating (KIMURA and CROW, 1963b) for N individuals. This means, for example, that it is not possible to select two sets of N/2 offspring that have disjoint sets of N/2 parents.

The sampling probabilities P_{21111} for the two restricted selection schemes will be derived with reference to the three selected intercross individuals as indicated by solid circles in Figure 3.2. In each case, these three individuals receive six gametes satisfying the definition of P_{21111}.

N selected
intercross
individuals

Minimum Inbreeding

N selected
intercross
individuals

Maximum Inbreeding
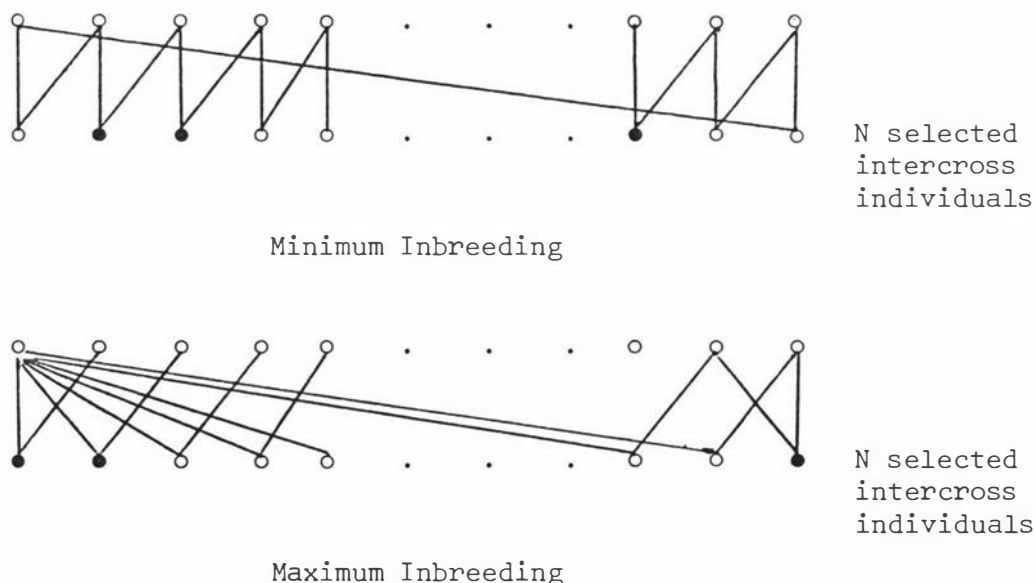
Figure 3.2.   Mating in intercross phase for minimum and
maximum inbreeding.

For either restricted selection scheme three intercross indi-
viduals can be chosen in $\binom{N}{3}$ ways. In the minimum inbreeding case
two of these three can be chosen to have a common parent in N ways.
The third can be chosen not to have a parent in common with either
of the first two in (N-4) ways so that

$$P_{21111} = N(N-4)/\binom{N}{3} \qquad\qquad N \geq 5$$

$$= 0 \ . \qquad\qquad N < 5$$

In the maximum inbreeding case the common parent for two out of
the selected intercross individuals must be the selfed individual
which contributes (N-1) gametes. Two out of these (N-1) gametes
must unite with gametes from the two selfed individuals which con-
tribute two gametes, which means that the two selected intercross
individuals with a common parent can be chosen from (N-3) such indivi-
duals. The third individual for which P_{21111} is specified is then
determined and

$$P_{21111} = \binom{N-3}{2}/\binom{N}{3} \qquad\qquad N \geq 5$$

$$= 0 \ . \qquad\qquad N < 5$$

The notation for the sampling probabilities in Table 3.2 has
been extended in two places to prevent ambiguities. $P_{22211(i)}$ and
$P_{22211(ii)}$ are used according to whether or not each of the three indivi-
duals giving two gametes mates with the other two. Similarly $P_{221111(i)}$
and $P_{221111(ii)}$ distinguish the cases of whether or not the two
individuals giving two gametes mate.

In Table 3.2 also, and for the remainder of this Chapter, attention
will be restricted to the case of $N \geq 4$. When sampling probabilities
involve gametes from r parents, it is assumed that $N \geq r$, or
that the probability is zero if $r > N$.

3.4.3   Intercross Phase Expansions for Two-Locus Case

·   The intercross phase expansions amalgamate two steps. After
expanding through the selfing phase of cycle n, a set of measures
$\underline{v}_{(2,n-1)}$ was obtained involving gametes from members of the intercross
generation of the previous cycle. These gametes must first be
related to gametes received by that intercross generation and then
to gametes from the preceding self generation (i.e., to $\underline{u}_{(1,n-1)}$).
The first step takes account of recombination and the second step
of gametic sampling.

The simplest expansion is for the digametic measure θ_{00CC}.
Double non-identity can be maintained only if the four genes on the
two gametes from C descend from four distinct genes on two gametes
received by C. This occurs with probability $(1+\lambda^2)/4$ and these last
two gametes necessarily descend from distinct individuals D,D' so that

$$\theta_{00CC} = \frac{1+\lambda^2}{4} \theta_{00DD'} \quad .$$

$$(3.4.19)$$

The two gametes for which the other digametic measure $\theta_{00CC'}$
is defined trace back to two, three or four gametes received by C
and C', and then back to two, three or four distinct individuals D,
D', D" and D'" . When both gametes from C, C' are recombinant and
trace back to four gametes from the parents of C and C', the sampling
probabilities in Table 3.2 may be used directly. If either or both
of the gametes from C, C' are parental though, various sums of those
probabilities must be used. New notation is needed for these marginal
probabilities and $_{m}Q_{t_1 t_2 \ldots t_s}$ is used for a subset of q of the
2m gametes received by m members of generation 2 (offspring) of a cycle
from generation 1 of that cycle (parents). The q gametes are from
s of the parents in such a way that the ith parent contributed t_i
gametes. This requires that the t_i sum to q and that $q \geq m$. In those
cases considered here, there are never more than four genes, hence
never more than four gametes, and so $q \leq 4$. All of the marginal
probabilities required are shown in Table 3.3.

Table 3.3   Marginal Gametic Sampling Probabilities

Gametic Subset Numbers of			Marginal Probabilities
Offspring	Gametes	Parents	
2	2	1	$_2Q_2 = \frac{1}{4} P_{211}$
		2	$_2Q_{11} = \frac{3}{4} P_{211} + P_{1111}$
	3	2	$_2Q_{21} = \frac{1}{2} P_{211}$
		3	$_2Q_{111} = \frac{1}{2} P_{211} + P_{1111}$
	4	3	$_2Q_{211} = P_{211}$
		4	$_2Q_{1111} = P_{1111}$
3	3	1	$_3Q_3 = \frac{1}{8} P_{3111}$
		2	$_3Q_{21} = \frac{1}{2} P_{2211} + \frac{1}{4} P_{21111} + \frac{3}{4} P_{222}$ $+ \frac{3}{8} P_{3111}$
		3	$_3Q_{111} = P_{111111} + \frac{3}{4} P_{21111} + \frac{1}{2} P_{2211}$ $+ \frac{1}{4} P_{222} + \frac{1}{2} P_{3111}$
	4	2	$_3Q_{31} = \frac{1}{4} P_{3111}$
		2	$_3Q_{22} = \frac{1}{4} P_{222} + \frac{1}{12} P_{2211}$
		3	$_3Q_{211} = \frac{1}{2} P_{3111} + \frac{3}{4} P_{222} + \frac{2}{3} P_{2211}$ $+ \frac{5}{12} P_{21111}$
		4	$_3Q_{1111} = \frac{1}{4} P_{3111} + \frac{1}{4} P_{2211} + \frac{7}{12} P_{21111}$ $+ P_{111111}$

Table 3.3 (continued)

Gametic Subset Numbers of			Marginal Probabilities
Offspring	Gametes	Parents	
4	4	1	$_4Q_4 = \frac{1}{16} P_{41111}$

$_4Q_4 = \frac{1}{16} P_{41111}$

$_4Q_{22} = \frac{1}{8} P_{3221} + \frac{1}{8} P_{2222} + \frac{1}{16} P_{32111}$

$+ \frac{1}{16} P_{22211(ii)} + \frac{1}{16} P_{221111(ii)}$

$_4Q_{31} = \frac{1}{4} P_{41111} + \frac{1}{8} P_{3221} + \frac{1}{8} P_{32111}$

$+ \frac{1}{8} P_{311111}$

$_4Q_{211} = \frac{3}{8} P_{41111} + \frac{5}{8} P_{3221} + \frac{3}{4} P_{2222}$

$+ \frac{1}{2} P_{32111} + \frac{3}{4} P_{22211(i)}$

$+ \frac{5}{8} P_{22211(ii)} + \frac{3}{8} P_{311111}$

$+ \frac{3}{8} P_{221111(ii)} + \frac{1}{2} P_{221111(i)}$

$+ \frac{1}{4} P_{2111111}$

$_4Q_{1111} = \frac{5}{16} P_{41111} + \frac{1}{8} P_{3221} + \frac{1}{8} P_{2222}$

$+ \frac{5}{16} P_{32111} + \frac{1}{4} P_{22211(i)}$

$+ \frac{5}{16} P_{22211(ii)} + \frac{1}{2} P_{311111}$

$+ \frac{9}{16} P_{221111(ii)} + \frac{1}{2} P_{221111(i)}$

$+ \frac{3}{4} P_{2111111} + P_{11111111}$

The expansion for $\theta_{00CC'}$ is then

$$
\begin{aligned}
\theta_{00CC'} = \left(\frac{1+\lambda}{2}\right)^2 &\left(_2Q_2\,\theta_{00DD} + {}_2Q_{11}\,\theta_{00DD'}\right) \\
+ \frac{1-\lambda^2}{2} &\left(_2Q_{21}\,\gamma_{00D;\overline{DD'}} + {}_2Q_{111}\,\gamma_{00D;D'D''}\right) \\
+ \left(\frac{1-\lambda}{2}\right)^2 &\Big[_2Q_{211}\,(\delta_{00DD;D'D''} + \delta_{00DD';DD''})/2 \\
&+ {}_2Q_{1111}\,\delta_{00DD';D''D'''}\Big] \; .
\end{aligned}
$$

(3.4.20)

Use has been made here of some equalities among quadrigametic measures

$$
\delta_{00VW;YZ} = \delta_{00VZ;YW} = \delta_{00WV;ZY} \quad .
$$

Equation (3.4.20) also provides the expansions for $\gamma_{00C;C'C'}$ and $\delta_{00CC;C'C'}$. For the trigametic measure the three recombination coefficients are $(1+\lambda)/4, 1/2$ and $(1-\lambda)/4$ while for the quadrigametic measure they are $1/4$, $1/2$ and $1/4$.

In expanding $\gamma_{00C;\overline{CC'}}$ genes must be traced back to three gametes to preserve double non-identity

$$
\begin{aligned}
\gamma_{00C;\overline{CC'}} = \frac{1}{2}\Big[&{}_2Q_{21}(\gamma_{00D;\overline{DD'}} + \gamma_{00D;D'D'})/2 \\
&+ {}_2Q_{111}\,\gamma_{00D;D'D''}\Big] \quad .
\end{aligned}
$$

(3.4.21)

For the final trigametic measure genes are traced back to three or four gametes

$$
\begin{aligned}
\gamma_{00C;C'C''} = \frac{1+\lambda}{2}\Big[&{}_3Q_3\,\gamma_{00D;DD} + {}_3Q_{21}(2\gamma_{00D;\overline{DD'}} + \gamma_{00D;D'D'})/3 \\
&+ {}_3Q_{111}\,\gamma_{00D;D'D''}\Big] \\
+ \frac{1-\lambda}{2}\Big[&{}_3Q_{31}\,\delta_{00DD;\overline{DD'}} + {}_3Q_{22}(\delta_{00DD;D'D'} + \delta_{00DD';DD'})/2 \\
&+ (\tfrac{1}{2}P_{222} + \tfrac{1}{4}P_{3111} + \tfrac{5}{12}P_{2211} + \tfrac{1}{4}P_{21111})\delta_{00DD;D'D''} \\
&+ (\tfrac{1}{4}P_{222} + \tfrac{1}{4}P_{3111} + \tfrac{1}{4}P_{2211} + \tfrac{1}{6}P_{21111})\delta_{00DD';DD''} \\
&+ {}_3Q_{1111}\,\delta_{00DD';D''D'''}\Big] \; .
\end{aligned}
$$

(3.4.22)

If the recombination coefficients are changed from $(1+\lambda)/2$, $(1-\lambda)/2$ in (3.4.22) to $1/2$, $1/2$ then (3.4.22) provides the expansion for $\delta_{00CC;C'C''}$. The expansions for the remaining three quadrigametic measures are now listed.

$$\delta_{00CC';CC'} = \frac{1}{4} \left({}_2Q_{211}\, \delta_{00DD;D'D''} + {}_2Q_{1111}\, \delta_{00DD';D''D'''} \right) . \quad (3.4.23)$$

$$\delta_{00CC';CC''} = \frac{1}{2} \left[{}_3Q_{31}\, \delta_{00DD;DD'} + {}_3Q_{22}\, \delta_{00DD;D'D'} \right.$$

$$+ \left(\frac{1}{2} P_{222} + \frac{1}{2} P_{3111} + \frac{1}{2} P_{2211} + \frac{1}{3} P_{21111} \right) \delta_{00DD;D'D''}$$

$$+ \left(\frac{1}{4} P_{222} + \frac{1}{6} P_{2211} + \frac{1}{12} P_{21111} \right) \delta_{00DD';DD''}$$

$$\left. + {}_3Q_{1111}\, \delta_{00DD';D''D'''} \right] . \quad (3.4.24)$$

$$\delta_{00CC';C''C'''} = {}_4Q_4\, \delta_{00DD;DD} + {}_4Q_{31}\, \delta_{00DD;\overline{DD'}}$$

$$+ {}_4Q_{22}\, (2\delta_{00D;D'D'} + \delta_{00DD';DD'})/3$$

$$\quad (3.4.25)$$

$$+ {}_4Q_{211}\, (2\delta_{00DD;D'D''} + \delta_{00DD';DD''})/3$$

$$+ {}_4Q_{1111}\, \delta_{00DD';D''D'''} .$$

All of the intercross expansions may now be collected together as

$$\underline{v}_{(2,n-1)} = \Omega\, \underline{u}_{(1,n-1)} \quad (3.4.26)$$

where the 10×12 matrix Ω has elements defined by equations (3.4.19) to (3.4.25). A set of transition equations between successive self generations or between successive intercross generations is now very easily obtained as

$$\underline{u}_{(1,n)} = \Psi\, \Omega\, \underline{u}_{(1,n-1)} \quad (3.4.27)$$

$$\underline{v}_{(2,n)} = \Omega\, \Psi\, \underline{v}_{(2,n-1)} \quad (3.4.28)$$

3.5   Discussion

· Numerical results obtained by using the transition equations
(3.4.27), (3.4.28) are shown in Tables 3.4, 3.5 and 3.6. As men-
tioned above, the initial generation is assumed to be non-inbred
and unrelated so that for these initial individuals, prior to any
selfing,

$$\underline{v}'_{(0,1)} = [\frac{1+\lambda^2}{4}, 1, 1, 1/2, 1, 1, 1/4, 1, 1/4, 1]$$

and $\underline{u}_{(1,1)}$ follows from equation (3.4.18).

As shown in these tables, linkage has a complicated effect on
inbreeding at two loci. For complete linkage, $\lambda = 1$, the equations
(3.4.27), (3.4.28) do reduce correctly to the appropriate one-locus
results. When $\lambda = 0$, and the loci segregate independently, CAIN
and HINKELMANN (1970) claimed that the inbreeding coefficient $F_{11}(\lambda=0)$
was the square of the one-locus coefficient $F_1 = F_{11}(\lambda=1)$. This is
not the case here, or whenever there is a choice of mates, and for
general λ an identity disequilibrium $\eta_{11}(\lambda)$, mentioned on Page 2
was defined earlier by WEIR and COCKERHAM (1969b) as

$$\eta_{11}(\lambda) = F_{11}(\lambda) - (F_1)^2 \ .$$

Values for the identity disequilibrium are also shown in Tables 3.4,
3.5, and 3.6. The quantity is positive in early generations, reaches
a maximum, and decreases to zero with complete inbreeding. For completely
specified pedigrees, however, such as afforded by the cases of $N = 2$
or $N = 3$, there is no identity disequilibrium.

In general, increased population size is seen to delay the accrual of
inbreeding, and to allow selection to be practised for a longer period.
As N increases, the minimum and maximum inbreeding schemes become more
extreme. As noted above, the maximum inbreeding scheme actually permits
inbreeding to increase with N. The increasing divergence in inbreeding
levels between the minimum inbreeding scheme and unrestricted random
selection shows that the latter scheme falls further behind in exploiting
fully the advantages of the intercross phase in this respect.

As CAIN and HINKELMANN (1970, 1972) point out, the plant breeder
is likely to be more concerned with homozygosity than with measures of
inbreeding. An individual is homozygous when its homologous genes are
identical by descent or when they are identical in state. The former
is the effect of inbreeding and the probability of this occuring is
measured by the inbreeding coefficient. The latter depends on the
chance of the union of genes having the same allelic form. Therefore
the inbreeding coefficients, F_1, F_{11} always provide lower bounds on
the homozygosity at one and two loci respectively. When initial gametes
are taken randomly from an infinitely large random mating population
and individuals are reproduced by a process without selection, a
knowledge of the population gene frequencies, p_i for allele a_i, allows
the expression of population genotypic frequencies in generation t as

$$P^{a_i}_{a_i}(t) = p_i^2 + p_i(1-p_i)\ F_1(t) \ ,$$

$$P^{a_i}_{a_j}(t) = [1-F_1(t)]p_i p_j \ , \ i \neq j$$

and the total amount of homozygosity as

$$1 - H(t) = 1 - [1-F_1(t)]\ H(0)$$

where $H(t)$ is the amount of heterozygosity in generation t. Similar
expressions in the two-locus case can be found in COCKERHAM and WEIR
(1973). When initial individuals are taken from a heterozygous source,
as in recurrent selection programmes, homozygosity can only be caused by
identity by descent and identity in state of genes from different
initial individuals. The homozygosity indicated by the inbreeding
measures is then likely to be close to total homozygosity. A complete
discussion of this problem requires the knowledge of the initial
genotypic frequencies and would need to take into account the effects
of the selection programme on gene frequencies.

Table 3.4   Progress of the Two-Locus Inbreeding Coefficient
             (F_{11}) in Intercross Generation and the Corresponding
             Value of Identity Disequilibrium (η_{11}) under Random
             Selection Scheme for Varying Population Sizes (N) and
             Varying Linkage Parameters (λ). Individuals in the
             Source Population are Non-Inbred and Unrelated.

| | | Recurrent Cycle Number | | | | | | | | | | | |
N	λ		1	2	3	4	5	6	7	8	9	10	20	100
2	1.00	F_{11}	.000	.375	.563	.703	.797	.861	.905	.935	.956	.970	.999	1.000
		η_{11}	.000	.234	.246	.209	.162	.119	.086	.061	.042	.029	.001	.000
	0.75	F_{11}	.000	.232	.394	.549	.671	.764	.833	.882	.918	.943	.999	1.000
		η_{11}	.000	.092	.078	.055	.036	.022	.013	.008	.004	.003	.000	.000
	0.25	F_{11}	.000	.145	.320	.497	.636	.743	.820	.875	.914	.941	.999	1.000
		η_{11}	.000	.005	.003	.002	.001	.001	.000	.000	.000	.000	.000	.000
	0.00	F_{11}	.000	.141	.316	.494	.635	.742	.820	.875	.914	.941	.999	1.000
		η_{11}	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
3	1.00	F_{11}	.000	.188	.328	.445	.542	.622	.688	.742	.787	.824	.974	1.000
		η_{11}	.000	.152	.221	.247	.248	.235	.215	.191	.168	.145	.025	.000
	0.75	F_{11}	.000	.112	.194	.278	.362	.442	.517	.585	.646	.700	.950	1.000
		η_{11}	.000	.077	.086	.080	.068	.055	.044	.034	.027	.020	.001	.000
	0.25	F_{11}	.000	.048	.116	.205	.299	.390	.476	.553	.621	.680	.949	1.000
		η_{11}	.000	.013	.009	.007	.005	.003	.003	.002	.001	.001	.000	.000
	0.00	F_{11}	.000	.035	.108	.198	.294	.387	.473	.551	.620	.679	.949	1.000
		η_{11}	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000

Table 3.4 (continued)

							Recurrent Cycle Number							
N	λ		1	2	3	4	5	6	7	8	9	10	20	100
4	1.00	F_{11}	.000	.150	.270	.374	.462	.539	.604	.660	.708	.750	.946	1.000
		η_{11}	.000	.128	.197	.234	.249	.249	.239	.224	.207	.188	.051	.000
	0.75	F_{11}	.000	.090	.156	.222	.289	.355	.420	.481	.539	.592	.897	1.000
		η_{11}	.000	.067	.083	.083	.075	.065	.055	.046	.038	.031	.002	.000
	0.25	F_{11}	.000	.038	.086	.151	.223	.297	.370	.440	.505	.565	.895	1.000
		η_{11}	.000	.016	.014	.011	.009	.007	.006	.004	.003	.003	.000	.000
	0.00	F_{11}	.000	.028	.077	.143	.216	.292	.366	.437	.503	.563	.894	1.000
		η_{11}	.000	.006	.004	.003	.003	.002	.002	.001	.001	.001	.000	.000
10	1.00	F_{11}	.000	.068	.130	.188	.242	.293	.340	.384	.425	.463	.730	.999
		η_{11}	.000	.064	.113	.153	.184	.207	.224	.237	.244	.249	.197	.001
	0.75	F_{11}	.000	.041	.070	.096	.122	.148	.175	.203	.232	.262	.551	.998
		η_{11}	.000	.036	.053	.061	.063	.062	.060	.056	.052	.047	.018	.000
	0.25	F_{11}	.000	.017	.031	.049	.071	.097	.126	.156	.189	.222	.536	.998
		η_{11}	.000	.013	.014	.014	.013	.012	.010	.009	.008	.007	.002	.000
	0.00	F_{11}	.000	.013	.025	.043	.066	.092	.121	.152	.185	.218	.535	.998
		η_{11}	.000	.008	.009	.008	.007	.006	.006	.005	.005	.004	.001	.000

Table 3.4 (continued)

N	λ		Recurrent Cycle Number											
			1	2	3	4	5	6	7	8	9	10	20	100
25	1.00	F_{11}	.000	.029	.057	.084	.110	.135	.160	.184	.207	.230	.424	.943
		η_{11}	.000	.028	.053	.077	.098	.117	.134	.150	.164	.177	.244	.054
	0.75	F_{11}	.000	.017	.029	.039	.047	.055	.063	.071	.079	.088	.203	.890
		η_{11}	.000	.016	.026	.032	.035	.037	.037	.037	.036	.035	.023	.000
	0.25	F_{11}	.000	.007	.001	.015	.020	.026	.033	.041	.050	.059	.183	.890
		η_{11}	.000	.007	.008	.008	.008	.008	.008	.007	.007	.007	.004	.000
	0.00	F_{11}	.000	.005	.009	.012	.017	.023	.030	.038	.047	.057	.182	.890
		η_{11}	.000	.005	.005	.005	.005	.005	.005	.004	.004	.004	.002	.000
100	1.00	F_{11}	.000	.007	.015	.022	.029	.037	.044	.051	.058	.065	.132	.521
		η_{11}	.000	.007	.015	.022	.029	.035	.042	.048	.054	.061	.114	.250
	0.75	F_{11}	.000	.004	.008	.010	.011	.013	.014	.015	.016	.017	.029	.275
		η_{11}	.000	.004	.007	.009	.011	.011	.012	.012	.012	.012	.011	.004
	0.25	F_{11}	.000	.002	.003	.003	.004	.004	.005	.005	.006	.007	.020	.272
		η_{11}	.000	.002	.002	.003	.003	.003	.003	.003	.003	.003	.002	.001
	0.00	F_{11}	.000	.001	.002	.002	.003	.003	.004	.004	.005	.006	.019	.272
		η_{11}	.000	.001	.002	.002	.002	.002	.002	.002	.002	.002	.001	.000

Table 3.5   Progress of the Two-Locus Inbreeding Coefficient (F_{11}) in Intercross Generation and the Corresponding Value of Identity Disequilibrium (η_{11}) under Minimum Inbreeding Selection Scheme for Varying Population Sizes (N) and Varying Linkage Parameters (λ). Individuals in the Source Population are Non-Inbred and Unrelated.

| | | Recurrent Cycle Number | | | | | | | | | | | |
N	λ		1	2	3	4	5	6	7	8	9	10	20	100
4	1.00	F_{11}	.000	.125	.229	.321	.402	.474	.536	.592	.641	.683	.912	1.000
		η_{11}	.000	.109	.177	.218	.240	.249	.249	.242	.230	.216	.081	.000
	0.75	F_{11}	.000	.075	.128	.180	.234	.289	.344	.398	.451	.501	.835	1.000
		η_{11}	.000	.059	.076	.077	.072	.065	.056	.048	.041	.034	.005	.000
	0.25	F_{11}	.000	.032	.067	.115	.171	.232	.294	.355	.414	.470	.831	1.000
		η_{11}	.000	.016	.014	.012	.009	.007	.006	.005	.004	.003	.000	.000
	0.00	F_{11}	.000	.023	.059	.108	.166	.227	.290	.352	.412	.468	.830	1.000
		η_{11}	.000	.008	.006	.005	.004	.003	.002	.002	.001	.001	.000	.000
10	1.00	F_{11}	.000	.042	.081	.119	.155	.190	.223	.255	.286	.315	.550	.984
		η_{11}	.000	.040	.075	.105	.131	.154	.173	.190	.204	.216	.248	.016
	0.75	F_{11}	.000	.025	.042	.056	.069	.082	.095	.109	.124	.139	.323	.969
		η_{11}	.000	.023	.036	.042	.045	.046	.045	.044	.042	.040	.021	.000
	0.25	F_{11}	.000	.011	.017	.024	.034	.045	.058	.073	.088	.106	.305	.969
		η_{11}	.000	.009	.010	.010	.010	.009	.008	.008	.007	.006	.003	.000
	0.00	F_{11}	.000	.008	.013	.020	.030	.041	.055	.069	.086	.103	.304	.969
		η_{11}	.000	.006	.007	.006	.006	.005	.005	.005	.004	.004	.002	.000

Table 3.5 (continued)

N	λ		1	2	3	4	5	6	7	8	9	10	20	100
							Recurrent Cycle Number							
25	1.00	F_{11}	.000	.016	.031	.046	.061	.075	.090	.104	.118	.132	.258	.788
		η_{11}	.000	.015	.030	.044	.057	.070	.082	.093	.104	.114	.191	.167
	0.75	F_{11}	.000	.009	.016	.021	.024	.028	.031	.034	.037	.040	.084	.623
		η_{11}	.000	.009	.015	.018	.021	.022	.023	.023	.023	.022	.018	.002
	0.25	F_{11}	.000	.004	.006	.007	.009	.011	.013	.015	.018	.022	.069	.621
		η_{11}	.000	.004	.005	.005	.005	.005	.005	.005	.004	.004	.003	.000
	0.00	F_{11}	.000	.003	.004	.005	.007	.009	.011	.014	.017	.020	.068	.621
		η_{11}	.000	.003	.003	.003	.003	.003	.003	.003	.003	.003	.002	.000
100	1.00	F_{11}	.000	.004	.008	.011	.015	.019	.023	.026	.030	.034	.070	.313
		η_{11}	.000	.004	.008	.011	.015	.018	.022	.026	.029	.032	.065	.215
	0.75	F_{11}	.000	.002	.004	.005	.006	.006	.007	.007	.007	.008	.011	.101
		η_{11}	.000	.002	.004	.005	.006	.006	.006	.006	.007	.007	.006	.004
	0.25	F_{11}	.000	.001	.001	.002	.002	.002	.002	.002	.002	.003	.006	.099
		η_{11}	.000	.001	.001	.001	.001	.001	.001	.001	.001	.001	.001	.001
	0.00	F_{11}	.000	.001	.001	.001	.001	.001	.001	.002	.002	.002	.006	.098
		η_{11}	.000	.001	.001	.001	.001	.001	.001	.001	.001	.001	.001	.000

Table 3.6   Progress of the Two-Locus Inbreeding Coefficient (F_{11}) in Intercross Generation and the Corresponding Value of Identity Disequilibrium (η_{11}) under Maximum Inbreeding Selection Scheme for Varying Population Sizes (N) and Varying Linkage Parameters (λ). Individuals in the Source Population are Non-Inbred and Unrelated.

							Recurrent Cycle Number						
N	λ		1	2	3	4	5	6	7	8	9	10	20	100
4	1.00	F_{11}	.000	.156	.280	.386	.476	.554	.619	.675	.723	.764	.952	1.000
		η_{11}	.000	.132	.202	.237	.249	.247	.236	.219	.200	.180	.046	.000
	0.75	F_{11}	.000	.093	.163	.233	.302	.371	.438	.501	.559	.613	.909	1.000
		η_{11}	.000	.069	.085	.084	.075	.065	.054	.045	.036	.029	.003	.000
	0.25	F_{11}	.000	.040	.092	.160	.236	.313	.389	.460	.526	.586	.907	1.000
		η_{11}	.000	.015	.013	.011	.009	.007	.005	.004	.003	.003	.000	.000
	0.00	F_{11}	.000	.029	.082	.152	.229	.308	.385	.457	.524	.584	.906	1.000
		η_{11}	.000	.005	.004	.003	.002	.002	.001	.001	.001	.001	.000	.000
10	1.00	F_{11}	.000	.158	.283	.390	.481	.558	.624	.680	.728	.769	.954	1.000
		η_{11}	.000	.133	.203	.238	.250	.247	.235	.218	.198	.178	.044	.000
	0.75	F_{11}	.000	.095	.169	.242	.314	.384	.451	.513	.571	.624	.913	1.000
		η_{11}	.000	.069	.089	.090	.083	.072	.061	.051	.041	.033	.003	.000
	0.25	F_{11}	.000	.040	.096	.166	.243	.321	.397	.469	.535	.594	.910	1.000
		η_{11}	.000	.015	.015	.014	.012	.010	.008	.006	.005	.004	.000	.000
	0.00	F_{11}	.000	.030	.085	.156	.234	.314	.392	.464	.531	.592	.910	1.000
		η_{11}	.000	.005	.004	.004	.003	.002	.002	.002	.001	.001	.000	.000

Table 3.6   (continued)

N	λ		1	2	3	4	5	6	7	8	9	10	20	100
							Recurrent Cycle Number							
25	1.00	F_{11}	.000	.174	.307	.420	.514	.593	.659	.715	.761	.800	.966	1.000
		η_{11}	.000	.144	.213	.244	.250	.241	.225	.204	.182	.160	.033	.000
	0.75	F_{11}	.000	.104	.186	.267	.346	.422	.492	.557	.616	.669	.935	1.000
		η_{11}	.000	.074	.092	.091	.082	.070	.058	.047	.037	.029	.002	.000
	0.25	F_{11}	.000	.044	.109	.189	.275	.360	.441	.516	.583	.643	.933	1.000
		η_{11}	.000	.014	.014	.013	.010	.008	.007	.005	.004	.003	.000	.000
	0.00	F_{11}	.000	.033	.097	.178	.266	.353	.436	.511	.580	.640	.933	1.000
		η_{11}	.000	.002	.002	.002	.002	.001	.001	.001	.001	.001	.000	.000
100	1.00	F_{11}	.000	.184	.323	.439	.535	.614	.680	.735	.780	.818	.972	1.000
		η_{11}	.000	.150	.219	.246	.249	.237	.218	.195	.171	.149	.027	.000
	0.75	F_{11}	.000	.110	.197	.283	.366	.445	.516	.584	.643	.696	.947	1.000
		η_{11}	.000	.076	.093	.091	.080	.067	.055	.044	.034	.027	.002	.000
	0.25	F_{11}	.000	.047	.117	.204	.295	.385	.469	.545	.612	.671	.945	1.000
		η_{11}	.000	.013	.013	.011	.009	.007	.006	.004	.003	.003	.001	.000
	0.00	F_{11}	.000	.035	.105	.193	.286	.378	.463	.541	.609	.669	.945	1.000
		η_{11}	.000	.001	.001	.001	.001	.000	.000	.000	.000	.000	.000	.000

4   ONE- AND TWO-LOCUS INBREEDING IN POPULATIONS
     WITH OVERLAPPING GENERATIONS

4.1   Introduction

In this Chapter, a study of the inbreeding levels in populations
with overlapping generations is presented with a view to quantifying
the effects of age structure in altering the genetic progress of
populations. Relative to populations of the same size with just one
age class, it is known that inbreeding and hence homozygosity is delayed
in populations with several age classes. It is also known that the
continued presence of individuals, generally females, over several
years in breeding programmes can delay the spread of favourable genes.
In another direction, human populations do not have discrete generations,
and this should be reflected in models of these populations. This
Chapter offers some novel features and presents some new results for
models of populations with overlapping generations.

Most previous work has concentrated on the evaluation of inbreeding
and variance effective numbers. Previous authors include MORAN (1962),
KIMURA and CROW (1963a), NEI (1970), NEI and IMAIZUMI (1966), GIESEL
(1969), TURNER and YOUNG (1969), FELSENSTEIN (1971), CROW and KIMURA
(1972) and HILL (1972a, 1972b). Effective numbers offer a very con-
venient one-parameter description of the mating structure of a popula-
tion. As such they are often used as a basis for comparison of different
populations. In populations other than idealized ones, however, effec-
tive numbers are defined as limiting values (over time) of rates of
increase of inbreeding or drift variance. Most populations do not
maintain the same characteristics for such long time periods, and in
breeding programmes interest is likely to be centered on early genera-
tions. For this reason the following study concentrates also on
inbreeding levels in early generations, as did that of JOHNSON (1977),
rather than solely on the limiting values of rates of change of
inbreeding. This study differs from that of JOHNSON, however, in
restricting attention to exact inbreeding levels.

This work follows HILL (1972a,b) in broadening the scope of some
previous enquiries by considering both monoecious and dioecious
populations, and not restricting attention to Poisson family size.

The study of different gametic sampling plans points out another restriction in the exclusive concentration on effective numbers. It has been shown (KIMURA and CROW 1963b, COCKERHAM 1970) that populations that avoid early inbreeding may have high final rates of inbreeding. The ranking of populations on the basis of such final rates may be opposite to a ranking on the basis of early inbreeding.

Other matters such as the assumptions of constant overall population size, stable age distribution and age-specific birth and death rates follow from conventional models.

The one entirely new feature of this work on overlapping generations is the treatment of inbreeding at two loci. The treatment is based on the general methodology of WEIR and COCKERHAM (1969b). In the absence of linkage disequilibrium and selection, the two-locus inbreeding coefficient evaluated here allows two-locus genotypic frequencies to be studied. Under the same conditions, as might hold in control populations, it has recently been shown (WEIR and COCKERHAM 1977) how the two-locus inbreeding coefficient is used in the prediction of means and variances of quantitative traits. Similar work to that presented here allows the evaluation of other two-locus parameters which can be used to predict linkage disequilibrium (COCKERHAM and WEIR 1977).

4.2   Monoecious Diploids

4.2.1   Mating Scheme

In all years t the population consists of N individuals belonging to various age classes. There are N_i individuals in the ith class, and n classes, so that

$$\sum_{i=1}^{n} N_i = N \ .$$

Age is measured in years. Each year N_1 newborn are added to the population, all N_n n-year-olds die, while a random sample of $N_i - N_{i+1}$ of the i-year-olds die.

The mating scheme is random union of gametes and is specified by two sets of parameters. Sampling between age classes is accommodated by parameters p_i, where p_i is the probability that a random gamete received by the newborn individuals in any year came from the ith age class in the previous year.

$$\sum_{i=1}^{n} p_i = 1 .$$

For within age classes sampling, arbitrary distributions are allowed for the numbers of gametes from individual members of the class. The usual approach is to assume that these numbers, or family sizes, are independently Poisson distributed subject to the numbers adding to the total gametic output from that class. The set of N_i gametic numbers from the ith age class are then multinomially distributed. An analysis of the different distributions will be given in Sections 4.4 and 4.5. At present it is assumed that the gametic numbers have the same distribution for every member of an age class, so that there is a need for the use of gametic sampling probabilities (WEIR and COCKERHAM 1969b) $P^2(i)$ and $P^{11}(i)$. These are the probabilities that two gametes from age class i are from one or two individuals respectively within that age class, and

$$P^2(i) + P^{11}(i) = 1 .$$

It is common (e.g. JOHNSON 1977) to restrict attention to the case where any output gamete from an age class is equally likely to have come from any individual within the age class. In this "equal-chance" case,

$$P^2(i) = 1/N_i .$$

There is a need in two-locus models for trigametic and quadrigametic sampling probabilities in addition to these digametic probabilities.

4.2.2 One-Locus Case

The quantity to be determined is the average inbreeding coefficient $F_1(t)$ of members of age class 1 in year t. This is the average of the

probabilities of identity by descent of pairs of genes drawn from individuals in the previous year, and each member of a pair has probability p_i of coming from an i-year-old, so that

$$F_1(t+1) = \sum_{i=1}^{n} \sum_{j=1}^{n} p_i p_j \psi_{1ij}(t) \qquad (4.2.1)$$

The gametic set measure $\psi_{1ij}(t)$ is the probability of identity by descent of a gene from age class i and a gene from age class j in year t, and it will be necessary to establish transition equations for these gametic set measures.

When two gametes are from the same age class, there is a chance that they are both from one individual in that class, and genes on the gametes may be copies of the same gene in that individual. Identity by descent is then assured, and to keep track of such cases the average coancestry $\theta_{1 I_i J_j}(t)$ has been defined in Section 2.2 as the probability of identity by descent of a gene from a random member I_i of age class i and a gene from a random member J_j of age class j, both in year t. The measure is averaged over all I_i and J_j.

If primes denote distinct individuals in the same age class then,

$$\psi_{1ii}(t+1) = P^2(i)\, \theta_{1 I_i I_i}(t+1) + P^{11}(i)\, \theta_{1 I_i I_i'}(t+1),$$

$$1 \leq i \leq n \qquad (4.2.2)$$

$$\psi_{1ij}(t+1) = \theta_{1 I_i J_j}(t+1), \qquad 1 \leq i < j \leq n \qquad (4.2.3)$$

and there are the obvious symmetries

$$\psi_{1ij}(t) = \psi_{1ji}(t), \qquad \theta_{1 I_i J_j}(t) = \theta_{1 J_j I_i}(t) \quad.$$

Now an individual of age i in year t+1 was of age 1 in year t-i+2, so gametes from such individuals descended from parents in year t-i+1. Identity-by-descent relations in equations (4.2.2) and (4.2.3) are preserved if they are written as

$$\psi_{1ii}(t+1) = P^2(i)\ \theta_{1I_1I_1}(t-i+2) + P^{11}(i)\ \theta_{1I_1I_1'}(t-i+2),$$

$$1 \le i \le n \qquad (4.2.4)$$

$$\psi_{1ij}(t+1) = \theta_{1I_1J_{j-i+1}}(t-i+2), \qquad 1 \le i < j \le n\ . \qquad (4.2.5)$$

Genes from individuals in age class 1 may have descended from any of the age classes in the previous year, and two genes from the same individual are equally likely to be copies of the same gene or of different genes received by that individual, hence

$$\theta_{1I_1I_1}(t-i+2) = \frac{1}{2} + \frac{1}{2} \sum_{i=1}^{n} \sum_{j=1}^{n} P_i P_j\ \psi_{1ij}(t-i+1)\ , \qquad (4.2.6)$$

$$\theta_{1I_1I_1'}(t-i+2) = \sum_{i=1}^{n} \sum_{j=1}^{n} P_i P_j\ \psi_{1ij}(t-i+1)\ , \qquad (4.2.7)$$

$$\theta_{1I_1J_{j-i+1}}(t-i+2) = \sum_{k=1}^{n} P_k\ \psi_{1k,j-i}(t-i+1),$$

$$1 \le i < j \le n\ . \qquad (4.2.8)$$

Equations (4.2.2) to (4.2.8) may now be combined to give the desired transition equations for the gametic set measures :

$$\psi_{1ii}(t+1) = [1-\frac{1}{2}P^2(i)] \sum_{j=1}^{n} \sum_{k=1}^{n} P_j P_k\ \psi_{1jk}(t-i+1) + \frac{1}{2}P^2(i),$$

$$1 \le i \le n \qquad (4.2.9)$$

$$\psi_{1ij}(t+1) = \sum_{k=1}^{n} P_k\ \psi_{1k,j-i}(t-i+1),\ \ 1 \le i < j \le n\ . \qquad (4.2.10)$$

These equations allow the determination of gametic set measures, and hence inbreeding coefficients, in all years but are not in a particularly convenient form for computing as they require the storing of measures for the previous n years. This is in contrast to the situation with discrete generations, where sets of measures always rest only on values in the previous generation. However, equations (4.2.9) and (4.2.10) can be re-arranged to obtain equations which do span just consecutive pairs of years :

$$\psi_{111}(t+1) = [1 - \frac{1}{2} P^2(1)] \sum_{i=1}^{n} \sum_{j=1}^{n} P_i P_j \psi_{ij}(t) + \frac{1}{2} P^2(1), \quad (4.2.11)$$

$$\psi_{11j}(t+1) = \sum_{i=1}^{n} P_i \psi_{1i,j-1}(t) , \quad 1 < j \leq n \quad\quad (4.2.12)$$

$$\psi_{1ii}(t+1) = \frac{1 - \frac{1}{2}P^2(i)}{1 - \frac{1}{2}P^2(i-1)} \psi_{1i-1,i-1}(t) + \frac{P^2(i) - P^2(i-1)}{2[1 - \frac{1}{2}P^2(i-1)]} ,$$

$$1 < i \leq n \quad\quad (4.2.13)$$

$$\psi_{1ij}(t+1) = \psi_{1i-1,j-1}(t), \quad\quad 1 < i < j \leq n . \quad\quad (4.2.14)$$

In the case of equal chance gamete formation, this set reduces to that given by FELSENSTEIN (1971) and is an exact alternative to the set given by JOHNSON(1977).

If there was only one age class per generation, n=1, equations (4.2.11) to (4.2.14) provide

$$\psi_{111}(t+1) = [1 - \frac{1}{2} P^2(1)] \psi_{111}(t) + \frac{1}{2} P^2(1)$$

or

$$F_1(t) = \psi_{111}(t-1) = 1 - [1 - \frac{1}{2} P^2(1)]^t, \text{ if } F_1(0) = 0$$

which is the usual result for discrete generations.

If all initial individuals (year 0) are not inbred and are unrelated, then the initial values of the measures are

$$\psi_{1ii}(0) = \frac{1}{2} P^2(i) , \quad 1 \leq i \leq n$$

$$\psi_{1ij}(0) = 0 , \quad\quad 1 \leq i < j \leq n$$

$$F_1(0) = 0$$

and then equations (4.2.1) and (4.2.11) to (4.2.14) provide

$$F_1(1) = \frac{1}{2} \sum_{i=1}^{n} p_i^2 P^2(i) ,$$

$$F_1(2) = \frac{1}{2} \{p_1^2 [1 - \frac{1}{2} P^2(1)] + 1\} \sum_{i=1}^{n} p_i^2 P^2(i) + p_1 \sum_{i=2}^{n} p_i p_{i-1} P^2(i-1).$$

Later values will generally require numerical iteration of equations (4.2.9) and (4.2.10), or (4.2.11) to (4.2.14), but this is also a feature of approximate treatments such as those of JOHNSON (1977).

It is common to compare populations on the basis of effective numbers. The inbreeding effective number is related to the asymptotic rate of increase r of $F_1(t)$. This rate is the limiting value, as time increases, of

$$r(t) = \frac{F_1(t) - F_1(t-1)}{F_1(\infty) - F_1(t-1)}$$

where $F_1(\infty) = 1$. Since $r = 1/2N$ for an ideal monoecious population of size N, the annual inbreeding effective number can be set as

$$N_y = \frac{1}{2r} .$$

Note that the same rate of inbreeding and effective number would be obtained if

$$r(t) = \frac{F_0(t) - F_0(t-1)}{F_0(\infty) - F_0(t-1)}$$

is used. This ratio uses the complement of the inbreeding coefficient, $F_0 = 1 - F_1$, and $F_0(\infty) = 0$.

The generation length L for the population is defined as the average age of the parents of newborn individuals

$$L = \sum_{i=1}^{n} i \, p_i$$

and the generation inbreeding effective number N_g is N_y/L.

Several authors (e.g. FELSENSTEIN 1971, HILL 1972a, 1972b, and JOHNSON 1977) have given analytical expressions which approximate N_y or N_g. Exact values in specific cases can be obtained by iteration of the transition equations above, but in any real situation interest is more likely to center on early generations when the concept of effective numbers is of less relevance.

4.2.3 Two-Locus Case

For inbreeding at two loci the identity status of two pairs of genes needs to be considered. For two genes a, a' and b, b' at the A and B loci respectively, the general identity measure $\underline{X}(ab,a'b')$ has been defined on Page 7. When ab, a'b' are uniting gametes, the measure is written as $\underline{F}$ and the one-locus inbreeding coefficients, assumed to be the same at each locus, are $F_1 = F_{11} + F_{10} = F_{11} + F_{01}$. If ab, a'b' are gametes taken from age classes i and j in year t, the measure $\underline{X}(ab, a'b')$ is written as $\underline{\psi}_{ij}(t)$, so that

$$\underline{F}(t+1) = \sum_{i=1}^{n} \sum_{j=1}^{n} P_i P_j \underline{\psi}_{ij}(t) . \qquad (4.2.15)$$

This vector equation is analogous to (4.2.1), and adding the first and third rows of (4.2.15) in fact gives (4.2.1). Two other gametic set measures $\underline{\nu}_{i;jk}$, $\underline{\zeta}_{ij;k\ell}$ are needed (see Section 2.4).

Just as in the one-locus case, whenever more than one gamete is drawn from a single age class, there is a chance that two or more gametes may originate from one individual in that age class, and an accompanying chance of identity by descent for genes at each locus on those gametes.

Hence two-locus average individual measures are needed (see Section 2.4). For instance, let i denote age class i (i = 1,2,...,n) and I_i denote a random member of age class i (I_i = 1,2,...,N_i); the digametic measure $\underline{\theta}_{I_i J_j}$ is then defined as

$$\underline{\theta}_{I_i J_j} : ab, a'b' \text{ on two gametes from individuals } I_i, J_j, \text{ respectively.}$$

Measures are averaged over all such random members. Determination of the inbreeding measure requires an evaluation of gametic set measures, and hence of average individual measures. A general procedure has been established (WEIR and COCKERHAM 1969b) and details are given here for the digametic measures. As before, primes denote distinct individuals within age classes, and subscripts i,j,k,ℓ,s range over the integers 1 to n.

Gametic sampling probabilities are needed to express gametic set measures as average individual measures. The analogues of equations (4.2.2), (4.2.3) are

$$\underline{\psi}_{ii}(t+1) = P^2(i) \, \underline{\theta}_{I_i I_i}(t+1) + P^{11}(i) \, \underline{\theta}_{I_i I_i'}(t+1),$$

$$1 \leq i \leq n \qquad\qquad (4.2.16)$$

$$\underline{\psi}_{ij}(t+1) = \underline{\theta}_{I_i J_j}(t+1), \qquad 1 \leq i < j \leq n \qquad\qquad (4.2.17)$$

Expression of average individual measures as gametic set measures involves the mating scheme via the probabilities p_i as in the one-locus case, but also involves recombination between the loci.

For simplicity attention will be restricted to the fourth, double non-identity, component of all measures. The one-locus inbreeding coefficient then allows other components of the inbreeding measure to be recovered, as for example $F_{11} = F_{00} + 2F_1 - 1$.

To preserve double non-identity, genes on two gametes from a single individual must have descended from genes on the two gametes received by that individual, but there is no restriction for genes on gametes from different individuals. Gametes received by age class 1 may be from any

of the age classes in the previous year:

$$\theta_{00_{I_iI_i}}(t+1) = \frac{1+\lambda^2}{4} \underset{j}{\Sigma}\ \underset{k}{\Sigma}\ P_jP_k\ \psi_{00jk}(t-i+1),\ 1 \le i \le n \qquad (4.2.18)$$

$$\theta_{00_{I_iI_i'}}(t+1) = (\frac{1+\lambda}{2})^2\ \underset{j}{\Sigma}\ \underset{k}{\Sigma}\ P_jP_k\ \psi_{00jk}(t-i+1)$$

$$+ \frac{1-\lambda^2}{2}\ \underset{j}{\Sigma}\ \underset{k}{\Sigma}\ \underset{\ell}{\Sigma}\ P_jP_kP_\ell\ \nu_{00j;k\ell}(t-i+1)$$

$$+ (\frac{1-\lambda}{2})^2\ \underset{j}{\Sigma}\ \underset{k}{\Sigma}\ \underset{\ell}{\Sigma}\ \underset{s}{\Sigma}\ P_jP_kP_\ell P_s\ \zeta_{00jk;\ell s}(t-i+1),$$

$$1 \le i \le n \qquad (4.2.19)$$

$$\theta_{00_{I_iJ_j}}(t+1) = \frac{1+\lambda}{2}\ \underset{k}{\Sigma}\ P_k\ \psi_{00k,j-i}(t-i+1)$$

$$+ \frac{1-\lambda}{2}\ \underset{k}{\Sigma}\ \underset{\ell}{\Sigma}\ P_kP_\ell\ \nu_{00j-i;k\ell}(t-i+1),$$

$$1 \le i < j \le n\ . \qquad (4.2.20)$$

The transition equations for the digametic set measures now follow from combining equations (4.2.16) to (4.2.20):

$$\psi_{00ii}(t+1) = [(\frac{1+\lambda}{2})^2 - \frac{\lambda}{2}\ P^2(i)]\ \underset{j}{\Sigma}\ \underset{k}{\Sigma}\ P_jP_k\ \psi_{00jk}(t-i+1)$$

$$+ P^{11}(i)\ \frac{1-\lambda^2}{2}\ \underset{j}{\Sigma}\ \underset{k}{\Sigma}\ \underset{\ell}{\Sigma}\ P_jP_kP_\ell\ \nu_{00j;k\ell}(t-i+1)$$

$$+ P^{11}(i)\ (\frac{1-\lambda}{2})^2\ \underset{j}{\Sigma}\ \underset{k}{\Sigma}\ \underset{\ell}{\Sigma}\ \underset{s}{\Sigma}\ P_jP_kP_\ell P_s\ \zeta_{00jk;\ell s}(t-i+1)\ ,$$

$$1 \le i \le n \qquad (4.2.21)$$

$$\psi_{00ij}(t+1) = \frac{1+\lambda}{2}\ \underset{k}{\Sigma}\ P_k\ \psi_{00k,j-i}(t-i+1)$$

$$+ \frac{1-\lambda}{2}\ \underset{k}{\Sigma}\ \underset{\ell}{\Sigma}\ P_kP_\ell\ \nu_{00j-i;k\ell}(t-i+1)\ ,$$

$$1 \le i < j \le n\ . \qquad (4.2.22)$$

Just as in the one-locus situation, numerical work will require the storing of measures for n years when equations (4.2.21) and (4.2.22) are used. Unlike the one-locus case however, these equations cannot be re-arranged to arrive at a set of equations which span only pairs of consecutive years unless the sampling probabilities $P^2(i)$ are the same for every age class. This can be the case when every age class is the same size. Equal $P^2(i)$ values for $i=1,\ldots,n$ lead to

$$\psi_{00_{ij}}(t+1) = \psi_{00_{i-1,j-1}}(t) , \qquad 1 < i,j \leq n \qquad (4.2.23)$$

and the cases for $i=1$ follow directly from (4.2.21) and (4.2.22).

Further sampling probabilities are needed for the evaluation of trigametic and quadrigametic measures. These probabilities all refer to the origins of gametes taken from age class i:

$P^3(i)$ — three gametes from one individual

$P^{21}(i)$ — two gametes from one individual and one from a different individual

$P^{111}(i)$ — one gamete from each of three different individuals

$P^4(i)$ — four gametes from one individual

$P^{31}(i)$ — three gametes from one individual and one from a different individual

$P^{22}(i)$ — two gametes from one individual and two from a different individual

$P^{211}(i)$ — two gametes from one individual and one from each of two different individuals

$P^{1111}(i)$ — one gamete from each of four different individuals.

Following the general procedure of WEIR and COCKERHAM (1969b), trigametic and quadrigametic set measures are first expressed as average individual measures, which in turn are expanded back to gametic set measures. Listed below is the resulting set of transition equations for gametic set measures in the special case of equal age-class sampling probabilities

$$P^2(i) = P^2(1) \quad \text{for} \quad 1 \leq i \leq n .$$

$$\nu_{001;11}(t+1) = [\tfrac{1}{4} P^3(1) + \tfrac{1+\lambda}{12} P^{21}(1)] \sum_i \sum_j P_i P_j \psi_{00ij}(t)$$

$$+[\tfrac{1}{2} P^{21}(1) + \tfrac{1+\lambda}{2} P^{111}(1)] \sum_i \sum_j \sum_k P_i P_j P_k \nu_{00i;jk}(t)$$

$$+\tfrac{1-\lambda}{2} [\tfrac{1}{6} P^{21}(1) + P^{111}(1)] \sum_i \sum_j \sum_k \sum_\ell P_i P_j P_k P_\ell \zeta_{00ij;k\ell}(t) \; ,$$

$$(4.2.24)$$

$$\nu_{001;1j}(t+1) = [\tfrac{1}{2} P^2(1) + \tfrac{1+\lambda}{2} P^{11}(1)] \sum_i \sum_k P_i P_k \nu_{00i;k,j-1}(t)$$

$$+ \tfrac{1-\lambda}{2} P^{11}(1) \sum_i \sum_k \sum_\ell P_i P_k P_\ell \zeta_{00ik;\ell,j-1}(t) \; ,$$

$$1 < j \le n \qquad (4.2.25)$$

$$\nu_{00j;11}(t+1) = \tfrac{1}{2} P^2(1) \sum_i P_i \psi_{00i,j-1}(t)$$

$$(4.2.26)$$

$$+[1 - \tfrac{1}{2} P^2(1)] \sum_i \sum_k P_i P_k \nu_{00j-1;ik}(t) \; , \quad 1 < j \le n$$

$$\nu_{001;jk}(t+1) = \tfrac{1+\lambda}{2} \sum_i P_i \nu_{00i;j-1,k-1}(t) + \tfrac{1-\lambda}{2} \sum_i \sum_\ell P_i P_\ell \zeta_{00i\ell;j-1,k-1}(t) \; ,$$

$$1 < j,k \le n \qquad (4.2.27)$$

$$\nu_{00j;1k}(t+1) = \sum_i P_i \nu_{00j-1;i,k-1}(t) \; , \quad 1 < j,k \le n \qquad (4.2.28)$$

$$\nu_{00i;jk}(t+1) = \nu_{00i-1;j-1,k-1}(t) \; , \qquad 1 < i,j,k \le n \qquad (4.2.29)$$

$$\zeta_{0011;11}(t+1) = \tfrac{1}{4} [P^4(1) + \tfrac{2}{3} P^{22}(1)] \sum_i \sum_j P_i P_j \psi_{00ij}(t)$$

$$+\{[\tfrac{1}{2} P^{31}(1) + \tfrac{1}{3} P^{22}(1) + \tfrac{1}{3} P^{211}(1)] \times$$

$$\sum_i \sum_j \sum_k P_i P_j P_k \nu_{00i;jk}(t)\}$$

$$+\{[\tfrac{1}{4} P^{22}(1) + \tfrac{1}{2} P^{211}(1) + P^{1111}(1)] \times$$

$$\sum_i \sum_j \sum_k \sum_\ell P_i P_j P_k P_\ell \zeta_{00ij;k\ell}(t)\} \; , \qquad (4.2.30)$$

$$\zeta_{00_{11;1j}}(t+1) = [\tfrac{1}{2} P^3(1) + \tfrac{1}{3} P^{21}(1)] \sum_i \sum_k P_i P_k \, \nu_{00_{i;k,j-1}}(t)$$

$$+ [\tfrac{1}{2} P^{21}(1) + P^{111}(1)] \sum_i \sum_k \sum_\ell P_i P_k P_\ell \, \zeta_{00_{ik;\ell,j-1}}(t) \, ,$$

$$1 < j \le n \qquad (4.2.31)$$

$$\zeta_{00_{11;jk}}(t+1) = \tfrac{1}{2} P^2(1) \sum_i P_i \, \nu_{00_{i;j-1,k-1}}(t)$$

$$+ [1 - \tfrac{1}{2} P^2(1)] \sum_i \sum_\ell P_i P_\ell \, \zeta_{00_{i\ell;j-1,k-1}}(t) \, ,$$

$$1 < j,k \le n \qquad (4.2.32)$$

$$\zeta_{00_{1j;1k}}(t+1) = [1 - \tfrac{1}{2} P^2(1)] \sum_i \sum_\ell P_i P_\ell \, \zeta_{00_{i,j-1;\ell,k-1}}(t) \, ,$$

$$1 < j,k \le n \qquad (4.2.33)$$

$$\zeta_{00_{1j;k\ell}}(t+1) = \sum_i P_i \, \zeta_{00_{i,j-1;k-1,\ell-1}}(t) \, , \quad 1 < j,k,\ell \le n \qquad (4.2.34)$$

$$\zeta_{00_{ij;k\ell}}(t+1) = \zeta_{00_{i-1,j-1;k-1,\ell-1}}(t) \, , \qquad 1 < i,j,k,\ell \le n \, . \quad (4.2.35)$$

Since equal inbreeding is assumed at each locus, the following equalities hold

$$\nu_{00_{i;jk}} = \nu_{00_{i;kj}} \, , \qquad\qquad 1 \le i,j,k \le n$$

$$\zeta_{00_{ij;k\ell}} = \zeta_{00_{i\ell;kj}} = \zeta_{00_{kj;i\ell}} = \zeta_{00_{k\ell;ij}} = \zeta_{00_{ji;\ell k}} = \zeta_{00_{\ell i;jk}}$$

$$= \zeta_{00_{jk;\ell i}} = \zeta_{00_{\ell k;ji}} \, , \qquad 1 \le i,j,k,\ell \le n$$

so that equations (4.2.21) to (4.2.35) are sufficient for all (not distinct) n^2 digametic, n^3 trigametic and n^4 quadrigametic measures. The numbers of distinct measures are $n(n+1)/2$ digametic, $n^2(n+1)/2$ trigametic and $n(n^3+18n^2-13n+18)/24$ quadrigametic.

In the discrete generation case, n = 1, only equations (4.2.24), (4.2.30), and (4.2.21) with i = 1 are needed. These reduce to the equations given previously (WEIR and COCKERHAM 1969b).

4.2.4 Numerical Results

The smallest population for which all possible types of two-locus measures are required is one with four age classes, each with four individuals. Table 4.1 displays the two-locus inbreeding coefficients in this case for equal chance gamete formation. Each of the mating probabilities p_i, and each of the probabilities $P^2(i)$ of drawing two gametes from the same member of an age class has been set equal to 1/4.

When $\lambda=1$, $F_{11}(t) = F_1(t)$. Alongside the column for this one-locus inbreeding coefficient is a column of values obtained by the method of JOHNSON (1977). This approximate method, designed for early generations, assumes that $(2N_i - 1)/2N_i \simeq 1$.

Table 4.1 also shows the identity disequilibrium coefficients $\eta_{11}(t) = F_{11}(t) - [F_1(t)]^2$ for $\lambda=0$. These small values represent the identity association between unlinked genes caused by the mating systems.

The limiting inbreeding rates, r, also given in Table 4.1 are defined in terms of the double non-identity measure:

$$r = \lim_{t \to \infty} \frac{F_{00}(t) - F_{00}(t-1)}{F_{00}(\infty) - F_{00}(t-1)}$$

with $F_{00}(\infty) = 0$. The homogeneous form of the transition equations shows that F_{00} can eventually be written as

$$F_{00}(t) \propto [s(\lambda)]^t$$

with $s(\lambda)$ the largest eigenvalue of the system of equations. The limiting inbreeding rate is evidently $1 - s(\lambda)$. These final rates at which double non-identity is decreasing give a better picture of the population than would rates defined in terms of $F_{11}(t)$. These latter rates would be functions of both $s(\lambda)$ and $s(1)$, which tends to obscure the effects of linkage. As mentioned above, both approaches give the same result for $\lambda = 1$, the one-locus case.

The inbreeding rate shown for the approximate F_1 values is the limiting value of the difference between F_1 values in successive years. This is because JOHNSON's method linearizes the inbreeding coefficient: JOHNSON's effective number N_y is such that

$$F_1(t) = \frac{t}{2N_y}$$

Table 4.1   Inbreeding Coefficients for Monoecious Populations.
            Four Individuals in Each of Four Age Classes

t	$F_{11}(t)$					$F_1(t)$	$\eta_{11}(t)$
(year)	$\lambda=0$	$\lambda=1/4$	$\lambda=1/2$	$\lambda=3/4$	$\lambda=1$	(approx.)	$\lambda=0$
0	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
1	0.0156	0.0166	0.0195	0.0244	0.0313	0.0313	0.0146
2	0.0193	0.0213	0.0259	0.0336	0.0447	0.0449	0.0173
3	0.0231	0.0263	0.0330	0.0441	0.0607	0.0614	0.0194
4	0.0272	0.0316	0.0406	0.0558	0.0794	0.0810	0.0209
5	0.0317	0.0373	0.0486	0.0684	0.1010	0.1041	0.0215
10	0.0547	0.0620	0.0783	0.1133	0.1872	0.2025	0.0197
15	0.0880	0.0949	0.1116	0.1537	0.2665	0.3025	0.0170
20	0.1286	0.1347	0.1501	0.1935	0.3380	0.4025	0.0144
50	0.4177	0.4200	0.4263	0.4496	0.6423	1.0025	0.0051
100	0.7608	0.7613	0.7624	0.7674	0.8718	2.0025	0.0009
r	0.0400	0.0399	0.0395	0.0380	0.0203	0.0200	

4.3   Dioecious Diploids

4.3.1   Mating Scheme

Consider a diploid population which consists of M males and F females, with m male and f female age classes. "Age class i" will refer to male age class i if $1 \leq i \leq m$ and to female age class i-m if $m+1 \leq i \leq m+f$. The sizes of age classes are written as M_i and F_i for males and females respectively, so that

$$\sum_{i=1}^{m} M_i = M \quad , \quad \sum_{i=m+1}^{m+f} F_i = F .$$

Each year M_1+F_{m+1} newborns enter the population, while death claims all M_m m-year-old males, all F_{m+f} f-year-old females, and a random sample of $M_i-M_{i+1} (1 \leq i \leq m-1)$ i-year-old males and $F_{m+i}-F_{m+i+1} (1 \leq i \leq f-1)$ i-year-old females.

Since newborn males and females may have different parental age distributions, sampling of gametes between age classes is accommodated by two sets of parameters p_{1j}, $p_{m+1,j}$ where $p_{ij} (i=1, m+1 ; 1 \leq j \leq m+f)$ is the probability that a random gamete received by a newborn individual in age class i in any year came from the jth age class in the previous year. Because half of the genes for an individual came from its mother and half from its father

$$\sum_{j=1}^{m} p_{ij} = \sum_{j=m+1}^{m+f} p_{ij} = \frac{1}{2} \quad , \quad i = 1, m+1 .$$

For sampling of gametes within age classes, a combined sampling plan (WEIR and COCKERHAM 1969b) is assumed. This means that any set of gametes from a given age class are a random sample from the total gametic output from that class. Two gametes have the same chance of coming from the same individual member of the age class whether they each go to male or female offspring for example. Failure to assume the combined sampling scheme would require the identification of gametic sampling probabilities and gametic set measures according to the age classes that receive the gametes as well as those that give them (see Sections 2.2 and 2.4). In this treatment the same type of sampling probabilities P(i) within age classes can be used as in the monoecious case.

4.3.2   One-Locus Case

The average inbreeding coefficient $F_{1_i}(t+1)$, $i = 1,m+1$, for members of age class i in year t+1 is defined as the probability of identity by descent of genes on pairs of gametes from year t received by group i. These pairs of gametes are chosen at random subject to the condition that one must be from a male and one must be from a female. Given that a random gamete received by age class i(i=1,m+1) is male, there is probability $2p_{ij}$, $1 \leq j \leq m$, that it is from male age class j. Given that such a gamete is female there is a probability $2p_{ik}$, $m + 1 \leq k \leq m + f$, that it is from female age class k, so that

$$F_{1_i}(t+1) = 4 \sum_{j=1}^{m} \sum_{k=m+1}^{m+f} p_{ij} p_{ik} \psi_{1jk}(t) , \quad i = 1,m+1 \qquad (4.3.1)$$

The calculation of $F_{1_i}(t)$ now rests on the establishment of a set of transition equations for the gametic set measures $\psi_{1ij}(t)$. As before these set measures refer to random gametes from age classes i and j. The simplest situations are those for which the measures refer to gametes from different age classes. A gene from an individual in age class 1 of either sex may have descended from any age class in the previous year, while identity relations for a gene from any other age class may as well be made about genes from the one-year-younger age class in the previous year :

$$\psi_{1 1,m+1}(t+1) = \sum_{i=1}^{m+f} \sum_{j=1}^{m+f} p_{1i} p_{m+1,j} \psi_{1ij}(t) \qquad (4.3.2)$$

$$\psi_{1ij}(t+1) = \sum_{k=1}^{m+f} p_{ik} \psi_{1k,j-1}(t), \quad i=1,m+1; \\ 2 \leq j \leq m+f ; \; j \neq m+1 \qquad (4.3.3)$$

$$\psi_{1ij}(t+1) = \psi_{1i-1,j-1}(t), \quad 2 \leq i,j \leq m+f; \; i,j \neq m+1; \; i \neq j. \qquad (4.3.4)$$

As in the monoecious case, equation (4.3.4) can be taken back until members of the first age class in either sex are involved. For example

$$\psi_{1ij}(t+1) = \sum_{k=1}^{m+f} p_{1k} \psi_{1k,j-i}(t-i+1) , \quad 1 \leq i < j \leq m$$

but it is more convenient to use (4.3.4).

Two gametes from the same age class require the introduction of average individual measures again. Corresponding to equations (4.2.2) and (4.2.4)

$$\psi_{1_{ii}}(t+1) = P^2(i)\,\theta_{1_{I_i,I_i}}(t+1) + P^{11}(i)\,\theta_{1_{I_i,I_i'}}(t+1),\ 1\le i\le m+f \quad (4.3.5)$$

$$= P^2(i)\,\theta_{1_{I_i^*,I_i^*}}(t-i+i^*+1) + P^{11}(i)\,\theta_{1_{I_i,I_i^*}'}(t-i+i^*+1),$$

$$1 \le i \le m+f$$

where
$$i^* = 1 \quad \text{if} \quad 1 \le i \le m$$
$$= m+1 \quad \text{if} \quad m+1 \le i \le m+f .$$

When two gametes are drawn from one individual in the first age class of either sex, there is probability one-half that they are copies of the same gene and so identical by descent, and there is probability one-half that they descend from two individuals of different sex in the previous year :

$$\theta_{1_{I_i,I_i}}(t+1) = \left[1 + 4 \sum_{j=1}^{m} \sum_{k=m+1}^{m+f} P_{i^*j} P_{i^*k}\,\psi_{1_{jk}}(t-i+i^*)\right]/2 ,$$

$$1 \le i \le m+f . \qquad (4.3.6)$$

There is no restriction though on parental age classes for genes from distinct individuals :

$$\theta_{1_{I_i,I_i'}}(t+1) = \sum_{j=1}^{m+f} \sum_{k=1}^{m+f} P_{i^*j} P_{i^*k}\,\psi_{1_{jk}}(t-i+i^*),\ 1 \le i \le m+f . \qquad (4.3.7)$$

Combining equations (4.3.5) to (4.3.7) gives the remaining gametic set measure transition equation

$$\psi_{1_{ii}}(t+1) = 2P^2(i) \sum_{j=1}^{m} \sum_{k=m+1}^{m+f} P_{i^*j} P_{i^*k}\,\psi_{1_{jk}}(t-i+i^*)$$

$$+ P^{11}(i) \sum_{j=1}^{m+f} \sum_{k=1}^{m+f} P_{i^*j} P_{i^*k}\,\psi_{1_{jk}}(t-i+i^*) + \frac{1}{2} P^2(i),$$

$$1 \le i \le m+f . \qquad (4.3.8)$$

As in the monoecious case, simplification results when sampling probabilities are the same for every age class. Then (4.3.8) is appropriate as it stands for i = 1, m + 1 but otherwise can be replaced by

$$\psi_{1ii}(t+1) = \psi_{1i-1,i-1}(t) \quad .$$

The set of equations (4.3.2) to (4.3.4) and (4.3.8) generalize those of JOHNSON (1977) and in the discrete-generation case of m = f = 1 reduce to

$$\psi_{111}(t+1) = \{P^{11}(1)[\psi_{111}(t) + \psi_{122}(t)] + 2\psi_{112}(t) + 2P^2(1)\}/4$$

$$\psi_{122}(t+1) = \{P^{11}(2)[\psi_{111}(t) + \psi_{122}(t)] + 2\psi_{112}(t) + 2P^2(2)\}/4$$

$$\psi_{112}(t+1) = [\psi_{111}(t) + \psi_{122}(t) + 2\psi_{112}(t)]/4$$

with the usual equation for $F_1(t) = \psi_{112}(t-1)$:

$$F_1(t+2) = [1 - \frac{P^2(1) + P^2(2)}{4}] F_1(t+1) + \frac{P^2(1) + P^2(2)}{8} [F_1(t) + 1].$$

When the initial individuals, in year 0, are not inbred and are unrelated, the initial values of the measures are

$$\psi_{1ii}(0) = \frac{1}{2} P^2(i) , \qquad 1 \le i \le m+f$$

$$\psi_{1ij}(0) = 0 , \qquad 1 \le i < j \le m+f$$

$$F_i(0) = 0 , \qquad i = 1, m+1 .$$

Equations (4.3.1) to (4.3.4), (4.3.8) then provide

$$F_{1i}(1) = 0 , \quad i = 1, m+1$$

$$F_{1i}(2) = 2[p_{i1}p_{i,m+1} \sum_{j=1}^{m+f} P_{1j}P_{m+1,j}P^2(j) + p_{i1} \sum_{j=m+2}^{m+f} P_{ij}P_{1,j-1}P^2(j-1)$$

$$+ p_{i,m+1} \sum_{j=2}^{m} P_{ij}P_{m+1,j-1}P^2(j-1)] \quad , \quad i = 1, m+1 \ .$$

Average inbreeding levels for the male and female in the same year can differ because of different parental age distributions for the two sexes. It is convenient to define an average inbreeding coefficient $\overline{F}_1(t)$ for the newborn in year t as a weighted average of the coefficients in each sex :

$$\overline{F}_1(t) = [M_1 F_{11}(t) + F_{m+1}F_{1m+1}(t)]/(M_1 + F_{m+1}).$$

An inbreeding effective number may be defined, as in the monoecious case, by reference to an idealized population without age structure. An ideal dioecious population of effective size N_e accrues inbreeding according to

$$F_1(t+2) = \frac{1}{2N_e} + \frac{N_e-1}{N_e} F_1(t+1) + \frac{1}{2N_e} F_1(t)$$

which, for large t and N_e, leads to

$$F_1(t) = 1 - \left(\frac{2N_e-1}{2N_e}\right)^t$$

as in the monoecious case. Years and generations are the same here.

In the present case the per-year effective population size is then defined as

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

where r is the limiting value, as time increases, of

$$r(t) = \frac{\overline{F}_1(t) - \overline{F}_1(t-1)}{1 - \overline{F}_1(t-1)} \ .$$

For discrete generations this becomes

$$\frac{1}{N_e} = \frac{1}{4} \left[P^2(1) + P^2(2) \right] .$$

The generation length L is now defined to be the average age of parents when progeny are born, averaged over the four parent-progeny types (male-male, male-female, female-male and female-female).

$$L = \frac{1}{2} \left[\sum_{i=1}^{m} i(p_{1i} + p_{m+1,i}) + \sum_{j=m+1}^{m+f} (j-m)(p_{1j} + p_{m+1,j}) \right].$$

4.3.3 Two-Locus Case

Two-locus measures are defined as in the monoecious case, and the two-locus inbreeding function for newborn individuals in year t is

$$\underline{F}_i(t+1) = 4 \sum_{j=1}^{m} \sum_{k=m+1}^{m+f} P_{ij} P_{ik} \underline{\psi}_{jk}(t) , \quad i = 1, m+1 . \qquad (4.3.9)$$

For gametes from different age classes, (4.3.2) to (4.3.4) need to be modified to take account of recombination. Parental gametes from members of the first age class in either sex can come from parents of either sex and any age in the previous year, but recombinant gametes must carry one gene from a male parent and one from a female.

$$\psi_{00\,1,m+1}(t+1) = \left(\frac{1+\lambda}{2}\right)^2 \sum_{i=1}^{m+f} \sum_{j=1}^{m+f} P_{1i} P_{m+1,j} \, \psi_{00\,ij}(t)$$

$$+ \frac{1-\lambda^2}{4} \sum_{i=1}^{m+f} \sum_{j=1}^{m} \sum_{k=m+1}^{m+f} 4(P_{1i} P_{m+1,j} P_{m+1,k}$$

$$+ P_{1j} P_{1k} P_{m+1,i}) \, \nu_{00\,i;jk}(t)$$

$$+ \left(\frac{1-\lambda}{2}\right)^2 \sum_{i=1}^{m} \sum_{j=m+1}^{m+f} \sum_{k=1}^{m} \sum_{\ell=m+1}^{m+f} (16 p_{1i} P_{1j} P_{m+1,k} P_{m+1,\ell}) \times$$

$$\zeta_{00\,ij;\overline{k\ell}}(t)$$

$$(4.3.10)$$

$$\psi_{00ij}(t+1) = \frac{1+\lambda}{2} \sum_{k=1}^{m+f} P_{ik} \, \psi_{00k,j-1}(t)$$

$$+ \frac{1-\lambda}{2} \sum_{k=1}^{m} \sum_{l=m+1}^{m+f} 4 P_{ik} P_{il} \, v_{00j-1;kl}(t),$$

$$i = 1, m+1 \; ; \; 2 \leq j \leq m+f \; ;$$
$$j \neq m+1 \qquad\qquad (4.3.11)$$

$$\psi_{00ij}(t+1) = \psi_{00i-1,j-1}(t) \; , \; 1 < i < j \leq m+f \; ;$$
$$i,j \neq m+1 \; . \qquad\qquad (4.3.12)$$

Note that the above expansions have made use of the symmetries

$$\psi_{00ij}(t) = \psi_{00ji}(t)$$

$$v_{00i;jk}(t) = v_{00i;kj}(t)$$

$$\zeta_{00ij;kl}(t) = \zeta_{00il;kj}(t) = \zeta_{00kj;il}(t) = \zeta_{00kl;ij}(t) = \zeta_{00ji;lk}(t)$$

$$= \zeta_{00li;jk}(t) = \zeta_{00jk;li}(t) = \zeta_{00lk;ji}(t)$$

and the average

$$\zeta_{00ij;\overline{kl}}(t) = [\zeta_{00ij;kl}(t) + \zeta_{00ij;lk}(t)]/2 \; .$$

Just as with equation (4.3.4), equation (4.3.12) could be expanded back until members of the first age class in either sex were involved, but equation (4.3.12) is in the more convenient form for computing.

For gametes from the same age class, as previously

$$\psi_{00ii}(t+1) = P^2(i) \, \theta_{00I_iI_i}(t+1) + P^{11}(i) \, \theta_{00I_iI_i'}(t+1)$$

$$= P^2(i) \frac{1+\lambda^2}{4} \sum_{j=1}^{m} \sum_{k=m+1}^{m+f} 4 \, P_{i*j} P_{i*k} \, \psi_{00jk}(t-i+i*)$$

$$+ P^{11}(i) \left[\left(\frac{1+\lambda}{2}\right)^2 \sum_{j=1}^{m+f} \sum_{k=1}^{m+f} P_{i*j} P_{i*k} \, \psi_{00jk}(t-i+i*) \right.$$

$$+ \frac{1-\lambda^2}{2} \sum_{j=1}^{m+f} \sum_{k=1}^{m} \sum_{l=m+1}^{m+f} 4 P_{i*j} P_{i*k} P_{i*l} \, v_{00j;kl}(t-i+i*)$$

$$+ \ (\frac{1-\lambda}{2})^2 \ \sum_{j=1}^{m} \ \sum_{k=m+1}^{m+f} \ \sum_{\ell=1}^{m} \ \sum_{u=m+1}^{m+f} \ (16 p_{i*j} p_{i*k} p_{i*\ell} p_{i*u}) \ \times$$

$$\zeta_{00jk;\overline{\ell u}}(t-i+i*) \ ]$$

$$1 \leq i \leq m+f \ . \qquad (4.3.13)$$

For equal within-age-class sampling probabilities in the two sexes,

$$P^2(i) = P^2(1) \qquad \text{if} \quad 1 \leq i \leq m$$

$$= P^2(m+1) \quad \text{if} \quad m+1 \leq i \leq m+f$$

equation (4.3.13) can be replaced by

$$\psi_{00ii}(t+1) = \psi_{00i-1,i-1}(t) \qquad \text{when} \quad 2 \leq i \leq m+f \ , \ i \neq m+1 \ .$$

In the discrete generation case, m = f = 1, (4.3.10) and (4.3.13) reduce to the results given by WEIR and COCKERHAM (1969b). The methods established by those authors also allow the trigametic and quadrigametic expansions to be found. The complete set of transition equations for gametic set measures is listed below, for the special case of equal within-age-class sampling probabilities.

$$\nu_{00i;ii}(t+1) = P^3(i)\, \gamma_{00_{I_i};I_iI_i}(t+1) + \frac{1}{3}P^{21}(i)\,[\gamma_{00_{I_i};I_i'I_i'}(t+1)$$

$$+ 2\,\gamma_{00_{I_i};\overline{I_iI_i'}}(t+1)] + P^{111}(i)\,\gamma_{00_{I_i};I_i'I_i''}(t+1)$$

$$= \frac{1}{4}P^3(i) \sum_{j=1}^{m} \sum_{k=m+1}^{m+f} 4\, P_{ij}P_{ik}\, \psi_{00jk}(t)$$

$$+ \frac{1}{3}P^{21}(i)\,\{\, \frac{1+\lambda}{4} \sum_{j=1}^{m+f} \sum_{k=1}^{m+f} P_{ij}P_{ik}\psi_{00jk}(t)$$

$$+ \frac{1}{2} \sum_{j=1}^{m+f} \sum_{k=1}^{m} \sum_{\ell=m+1}^{m+f} 4P_{ij}P_{ik}P_{i\ell}\, \nu_{00j;k\ell}(t)$$

$$+ \frac{1}{4}\frac{\lambda}{} \sum_{j=1}^{m} \sum_{k=m+1}^{m+f} \sum_{\ell=1}^{m} \sum_{u=m+1}^{m+f} 16P_{ij}P_{ik}P_{i\ell}P_{iu}\, \zeta_{00jk;\overline{\ell u}}(t)$$

$$+ \sum_{j=1}^{m} \sum_{k=m+1}^{m+f} \sum_{\ell=1}^{m+f} 4P_{ij}P_{ik}P_{i\ell}\,[\frac{1}{2}\nu_{00j;k\ell}(t)+\frac{1}{2}\nu_{00k;j\ell}(t)]\,\}$$

$$+ P^{111}(i)\,[\, \frac{1+\lambda}{2} \sum_{j=1}^{m+f} \sum_{k=1}^{m+f} \sum_{\ell=1}^{m+f} P_{ij}P_{ik}P_{i\ell}\, \nu_{00j;k\ell}(t)$$

$$+ \frac{1-\lambda}{2} \sum_{j=1}^{m} \sum_{k=m+1}^{m+f} \sum_{\ell=1}^{m+f} \sum_{u=1}^{m+f} 4P_{ij}P_{ik}P_{i\ell}P_{iu}\, \zeta_{00jk;\ell u}(t)]$$

$$i = 1,\, m+1\, . \quad (4.3.14)$$

$$\nu_{00i;jj}(t+1) = P^2(j)\, \gamma_{00_{I_i};J_jJ_j}(t+1) + P^{11}(j)\, \gamma_{00_{I_i};J_jJ_j'}(t+1)$$

$$= P^2(j)\,\{\, \frac{1+\lambda}{4} \sum_{k=1}^{m+f} \sum_{\ell=1}^{m+f} P_{ik}P_{j\ell}\, \psi_{00k\ell}(t)$$

$$+ \sum_{k=1}^{m+f} \sum_{\ell=1}^{m} \sum_{u=m+1}^{m+f} [(\frac{1+\lambda}{4})4P_{ik}P_{j\ell}P_{ju}+(\frac{1-\lambda}{4})4P_{i\ell}P_{iu}P_{jk}]\, \nu_{00k;\ell u}(t)$$

$$+ \frac{1-\lambda}{4} \sum_{k=1}^{m} \sum_{\ell=m+1}^{m+f} \sum_{u=1}^{m} \sum_{r=m+1}^{m+f} 16P_{ik}P_{i\ell}P_{ju}P_{jr}\, \zeta_{00k\ell;\overline{ur}}(t)\,\}$$

$$+ P^{11}(j)\,[\, \frac{1+\lambda}{2} \sum_{k=1}^{m+f} \sum_{\ell=1}^{m+f} \sum_{u=1}^{m+f} P_{ik}P_{j\ell}P_{ju}\, \nu_{00k;\ell u}(t)$$

$$+ \frac{1-\lambda}{2} \sum_{k=1}^{m} \sum_{\ell=m+1}^{m+f} \sum_{u=1}^{m+f} \sum_{r=1}^{m+f} 4P_{ik}P_{i\ell}P_{ju}P_{jr}\, \zeta_{00k\ell;ur}(t)]$$

$$i,j = 1,\, m+1\, ;\ i \neq j\, . \quad (4.3.15)$$

$$\nu_{00_{i;ij}}(t+1) = P^2(i)\, \gamma_{00_{I_i;I_iJ_j}}(t+1) + P^{11}(i)\, \gamma_{00_{I_i;I_i'J_j}}(t+1)$$

$$= \frac{1}{2}P^2(i) \sum_{k=1}^{m} \sum_{\ell=m+1}^{m+f} \sum_{u=1}^{m+f} {}^4P_{ik}P_{i\ell}P_{ju} \left[\frac{1}{2}\nu_{00_{k;\ell u}}(t) + \frac{1}{2}\nu_{00_{\ell;ku}}(t)\right]$$

$$+ P^{11}(i) \left[\frac{1+\lambda}{2} \sum_{k=1}^{m+f} \sum_{\ell=1}^{m+f} \sum_{u=1}^{m+f} P_{ik}P_{i\ell}P_{ju}\, \nu_{00_{k;\ell u}}(t) \right.$$

$$\left. + \frac{1-\lambda}{2} \sum_{k=1}^{m} \sum_{\ell=m+1}^{m+f} \sum_{u=1}^{m+f} \sum_{r=1}^{m+f} {}^4P_{ik}P_{i\ell}P_{iu}P_{jr}\, \zeta_{00_{k\ell;ur}}(t) \right]$$

$$i,j = 1,m+1 \;;\; i \neq j \;. \quad (4.3.16)$$

$$\nu_{00_{i;ij}}(t+1) = P^2(i)\, \gamma_{00_{I_i;I_iJ_j}}(t+1) + P^{11}(i)\, \gamma_{00_{I_i;I_i'J_j}}(t+1)$$

$$= \frac{1}{2}P^2(i) \sum_{k=1}^{m} \sum_{\ell=m+1}^{m+f} {}^4P_{ik}P_{i\ell} \left[\frac{1}{2}\nu_{00_{k;\ell,j-1}}(t) + \frac{1}{2}\nu_{00_{\ell;k,j-1}}(t)\right]$$

$$+ P^{11}(i) \left[\frac{1+\lambda}{2} \sum_{k=1}^{m+f} \sum_{\ell=1}^{m+f} P_{ik}P_{i\ell}\, \nu_{00_{k;\ell,j-1}}(t) \right.$$

$$\left. + \frac{1-\lambda}{2} \sum_{k=1}^{m} \sum_{\ell=m+1}^{m+f} \sum_{u=1}^{m+f} {}^4P_{ik}P_{i\ell}P_{iu}\, \zeta_{00_{\overline{k\ell};u,j-1}}(t) \right]$$

$$i = 1,m+1 \;;\; 1 < j \leq m+f \;;\; j \neq m+1 \;. \quad (4.3.17)$$

$$\nu_{00_{j;ii}}(t+1) = P^2(i)\, \gamma_{00_{J_j;I_iI_i}}(t+1) + P^{11}(i)\, \gamma_{00_{J_j;I_iI_i'}}(t+1)$$

$$= P^2(i) \left[\frac{1}{2} \sum_{k=1}^{m+f} P_{ik}\, \psi_{00_{k,j-1}}(t) \right.$$

$$\left. + \frac{1}{2} \sum_{k=1}^{m} \sum_{\ell=m+1}^{m+f} {}^4P_{ik}P_{i\ell}\, \nu_{00_{j-1;k\ell}}(t) \right]$$

$$+ P^{11}(i) \sum_{k=1}^{m+f} \sum_{\ell=1}^{m+f} P_{ik}P_{i\ell}\, \nu_{00_{j-1;k\ell}}(t)$$

$$i = 1,m+1 \;;\; 1 < j \leq m+f \;;\; j \neq m+1 \;. \quad (4.3.18)$$

$$\nu_{00_{i;jk}}(t+1) = \frac{1+\lambda}{2} \sum_{\ell=1}^{m+f} \sum_{u=1}^{m+f} P_{i\ell} P_{ju} \nu_{00_{\ell;u,k-1}}(t)$$

$$+ \frac{1-\lambda}{2} \sum_{\ell=1}^{m} \sum_{u=m+1}^{m+f} \sum_{r=1}^{m+f} {}^4P_{i\ell}P_{iu}P_{jr} \zeta_{00\overline{\ell u};r,k-1}(t)$$

$$i,j = 1,m+1 \ ; \ i \neq j \ ;$$
$$1 < k \leq m+f \ ; \ k \neq m+1 \ . \quad (4.3.19)$$

$$\nu_{00_{k;ij}}(t+1) = \sum_{\ell=1}^{m+f} \sum_{u=1}^{m+f} P_{i\ell}P_{ju} \nu_{00_{k-1;\ell u}}(t)$$

$$i,j = 1,m+1 \ ; \ i \neq j \ ;$$
$$1 < k \leq m+f \ ; \ k \neq m+1 \ . \quad (4.3.20)$$

$$\nu_{00_{i;jk}}(t+1) = \frac{1+\lambda}{2} \sum_{\ell=1}^{m+f} P_{i\ell} \nu_{00_{\ell;j-1,k-1}}(t)$$

$$+ \frac{1-\lambda}{2} \sum_{\ell=1}^{m} \sum_{u=m+1}^{m+f} {}^4P_{i\ell}P_{iu} \zeta_{00\overline{\ell u};j-1,k-1}(t)$$

$$i = 1,m+1 \ ; \ 1 < j,k \leq m+f \ ; \ j,k \neq m+1 \ . \quad (4.3.21)$$

$$\nu_{00_{j;ik}}(t+1) = \sum_{\ell=1}^{m+f} P_{i\ell} \nu_{00_{j-1;\ell,k-1}}(t)$$

$$i = 1,m+1 \ ; \ 1 < j,k \leq m+f \ ; \ j,k \neq m+1 \ . \quad (4.3.22)$$

$$\nu_{00_{i;jk}}(t+1) = \nu_{00_{i-1;j-1,k-1}}(t)$$

$$1 < i,j,k \leq m+f \ ; \ i,j,k \neq m+1 \quad (4.3.23)$$

$$\zeta_{00_{ii;ii}}(t+1) = P^4(i) \ \delta_{00_{I_i I_i;I_i I_i}}(t+1) + P^{31}(i) \ \delta_{00_{I_i I_i;I_i I_i'}}(t+1)$$

$$+ \frac{1}{3} P^{22}(i) \ [\ \delta_{00_{I_i I_i';I_i I_i'}}(t+1) + 2 \ \delta_{00_{I_i' I_i';I_i I_i}}(t+1) \ ]$$

$$+ \frac{1}{3} P^{211}(i) \ [\ \delta_{00_{I_i I_i';I_i I_i''}}(t+1) + 2 \ \delta_{00_{I_i I_i;I_i' I_i''}}(t+1) \ ]$$

$$+ P^{1111}(i) \ \delta_{00_{I_i I_i';I_i'' I_i'''}}(t+1)$$

$$= \frac{1}{4} P^4(i) \sum_{j=1}^{m} \sum_{k=m+1}^{m+f} {}^4P_{ij}P_{ik} \psi_{00_{jk}}(t)$$

$$+ \frac{1}{2} P^{31}(i) \sum_{j=1}^{m} \sum_{k=m+1}^{m+f} \sum_{\ell=1}^{m+f} 4 P_{ij} P_{ik} P_{i\ell} \left[\frac{1}{2} \nu_{00j;k\ell}(t) + \frac{1}{2} \nu_{00k;j\ell}(t) \right]$$

$$+ \frac{1}{3} P^{22}(i) \left\{ \frac{1}{4} \cdot \sum_{j=1}^{m} \sum_{k=m+1}^{m+f} \sum_{\ell=1}^{m} \sum_{u=m+1}^{m+f} 16 P_{ij} P_{ik} P_{i\ell} P_{iu} \times \right.$$

$$\left[\zeta_{00j\ell;ku}(t) + 2 \zeta_{00jk;\overline{\ell u}}(t) \right]$$

$$+ 2 \left[\frac{1}{4} \sum_{j=1}^{m+f} \sum_{k=1}^{m+f} P_{ij} P_{ik} \psi_{00jk}(t) \right.$$

$$\left. \left. + \frac{1}{2} \sum_{j=1}^{m+f} \sum_{k=1}^{m} \sum_{\ell=m+1}^{m+f} 4 P_{ij} P_{ik} P_{i\ell} \nu_{00j;k\ell}(t) \right] \right\}$$

$$+ \frac{1}{3} P^{211}(i) \left\{ \frac{1}{2} \sum_{j=1}^{m} \sum_{k=m+1}^{m+f} \sum_{\ell=1}^{m+f} \sum_{u=1}^{m+f} 4 P_{ij} P_{ik} P_{i\ell} P_{iu} \times \right.$$

$$\left[\zeta_{00j\ell;ku}(t) + 2 \zeta_{00jk;\ell u}(t) \right]$$

$$\left. + \sum_{j=1}^{m+f} \sum_{k=1}^{m+f} \sum_{\ell=1}^{m+f} P_{ij} P_{ik} P_{i\ell} \nu_{00j;k\ell}(t) \right\}$$

$$+ P^{1111}(i) \sum_{j=1}^{m+f} \sum_{k=1}^{m+f} \sum_{\ell=1}^{m+f} \sum_{u=1}^{m+f} P_{ij} P_{ik} P_{i\ell} P_{iu} \zeta_{00jk;\ell u}(t)$$

$$i = 1, m+1 \ . \qquad (4.3.24)$$

$$\zeta_{00ii;ij}(t+1) = P^3(i) \delta_{00 I_i I_i ; I_i J_j}(t+1)$$

$$+ \frac{1}{3} P^{21}(i) \left[\delta_{00 I_i I_i' ; I_i J_j}(t+1) + 2 \delta_{00 I_i I_i ; I_i' J_j}(t+1) \right]$$

$$+ P^{111}(i) \delta_{00 I_i I_i' ; I_i'' J_j}(t+1)$$

$$= \frac{1}{2} P^3(i) \sum_{k=1}^{m} \sum_{\ell=m+1}^{m+f} \sum_{u=1}^{m+f} 4 P_{ik} P_{i\ell} P_{ju} \left[\frac{1}{2} \nu_{00k;\ell u}(t) + \frac{1}{2} \nu_{00\ell;ku}(t) \right]$$

$$+ \frac{1}{3} P^{21}(i) \left\{ \frac{1}{2} \sum_{k=1}^{m} \sum_{\ell=m+1}^{m+f} \sum_{u=1}^{m+f} \sum_{r=1}^{m+f} 4 P_{ik} P_{i\ell} P_{iu} P_{jr} \times \right.$$

$$\left[\zeta_{00ku;\ell r}(t) + 2 \zeta_{00k\ell;ur}(t) \right]$$

$$\left. + \sum_{k=1}^{m+f} \sum_{\ell=1}^{m+f} \sum_{u=1}^{m+f} P_{ik} P_{i\ell} P_{ju} \nu_{00k;\ell u}(t) \right\}$$

$$+ P^{111}(i) \sum_{k=1}^{m+f} \sum_{\ell=1}^{m+f} \sum_{u=1}^{m+f} \sum_{r=1}^{m+f} P_{ik}P_{i\ell}P_{iu}P_{jr} \zeta_{00_{k\ell;ur}}(t)$$

$$i;j = 1,m+1 \; ; \; i \neq j \; . \quad (4.3.25)$$

$$\zeta_{00_{ii;jj}}(t+1) = P^2(i)P^2(j) \, \delta_{00_{I_iI_i;J_jJ_j}}(t+1)$$

$$+ P^2(i)P^{11}(j) \, \delta_{00_{I_iI_i;J_jJ_j'}}(t+1)$$

$$+ P^{11}(i)P^2(j) \, \delta_{00_{I_iI_i';J_jJ_j}}(t+1)$$

$$+ P^{11}(i)P^{11}(j) \, \delta_{00_{I_iI_i';J_jJ_j'}}(t+1)$$

$$= P^2(i)P^2(j) \{ \frac{1}{4} \sum_{k=1}^{m+f} \sum_{\ell=1}^{m+f} P_{ik}P_{j\ell} \, \psi_{00_{k\ell}}(t)$$

$$+ \frac{1}{4} \sum_{k=1}^{m+f} \sum_{\ell=1}^{m} \sum_{u=m+1}^{m+f} [4P_{ik}P_{j\ell}P_{ju}+4P_{jk}P_{i\ell}P_{iu}] \, \nu_{00_{k;\ell u}}(t)$$

$$+ \frac{1}{4} \sum_{k=1}^{m} \sum_{\ell=m+1}^{m+f} \sum_{u=1}^{m} \sum_{r=m+1}^{m+f} 16P_{ik}P_{i\ell}P_{ju}P_{jr} \, \zeta_{00_{k\ell;\overline{ur}}}(t) \}$$

$$+ \frac{1}{2} \sum_{k=1}^{m+f} \sum_{\ell=1}^{m+f} \sum_{u=1}^{m+f} [P^2(i)P^{11}(j)P_{ik}P_{j\ell}P_{ju}$$

$$+P^{11}(i)P^2(j)P_{jk}P_{i\ell}P_{iu}] \, \nu_{00_{k;\ell u}}(t)$$

$$+ \frac{1}{2} \sum_{k=1}^{m} \sum_{\ell=m+1}^{m+f} \sum_{u=1}^{m+f} \sum_{r=1}^{m+f} [4P^2(i)P^{11}(j) \, P_{ik}P_{i\ell}P_{ju}P_{jr}$$

$$+4P^{11}(i)P^2(j)P_{jk}P_{j\ell}P_{iu}P_{ir}] \, \zeta_{00_{k\ell;ur}}(t)$$

$$+ P^{11}(i)P^{11}(j) \sum_{k=1}^{m+f} \sum_{\ell=1}^{m+f} \sum_{u=1}^{m+f} \sum_{r=1}^{m+f} P_{ik}P_{i\ell}P_{ju}P_{jr} \, \zeta_{00_{k\ell;ur}}(t)$$

$$i,j = 1,m+1 \; ; \; i \neq j \; . \quad (4.3.26)$$

$$\zeta_{00_{ij;ij}}(t+1) = P^2(i)P^2(j) \, \delta_{00_{I_iJ_j;I_iJ_j}}(t+1)$$

$$+ P^2(i)P^{11}(j) \, \delta_{00_{I_iJ_j;I_iJ_j'}}(t+1)$$

$$+ P^{11}(i)P^2(j) \, \delta_{00_{I_iJ_j;I_i'J_j}}(t+1)$$

$$+ P^{11}(i)P^{11}(j) \, \delta_{00_{I_i J_j; I_i' J_j'}}(t+1)$$

$$= \frac{1}{4} P^2(i)P^2(j) \sum_{k=1}^{m} \sum_{\ell=m+1}^{m+f} \sum_{u=1}^{m} \sum_{r=m+1}^{m+f} 16 P_{ik}P_{i\ell}P_{ju}P_{jr} \, \zeta_{00_{ku; \ell r}}(t)$$

$$+ \frac{1}{2} \sum_{k=1}^{m} \sum_{\ell=m+1}^{m+f} \sum_{u=1}^{m+f} \sum_{r=1}^{m+f} [4P^2(i)P^{11}(j)P_{ik}P_{i\ell}P_{ju}P_{jr}$$

$$+4P^{11}(i)P^2(j)P_{jk}P_{j\ell}P_{iu}P_{ir}]\zeta_{00_{ku; \ell r}}(t)$$

$$+ P^{11}(i)P^{11}(j) \sum_{k=1}^{m+f} \sum_{\ell=1}^{m+f} \sum_{u=1}^{m+f} \sum_{r=1}^{m+f} P_{ik}P_{i\ell}P_{ju}P_{jr} \, \zeta_{00_{ku; \ell r}}(t)$$

$$i,j = 1,m+1 \; ; \; i \neq j \; . \quad (4.3.27)$$

$$\zeta_{00_{ii; ij}}(t+1) = P^3(i) \, \delta_{00_{I_i I_i; I_i J_j}}(t+1)$$

$$+ \frac{1}{3} P^{21}(i) \, [\, \delta_{00_{I_i I_i'; I_i J_j}}(t+1) + 2\delta_{00_{I_i I_i; I_i' J_j}}(t+1) \,]$$

$$+ P^{111}(i) \, \delta_{00_{I_i I_i'; I_i'' J_j}}(t+1)$$

$$= \frac{1}{2} P^3(i) \sum_{k=1}^{m} \sum_{\ell=m+1}^{m+f} 4 P_{ik}P_{i\ell} \, [\frac{1}{2}\nu_{00_{k; \ell, j-1}}(t)+\frac{1}{2}\nu_{00_{\ell; k, j-1}}(t)]$$

$$+ \frac{1}{3} P^{21}(i)\{ \frac{1}{2} \sum_{k=1}^{m} \sum_{\ell=m+1}^{m+f} \sum_{u=1}^{m+f} 4 P_{ik}P_{i\ell}P_{iu}$$

$$[\zeta_{00_{ku; \ell, j-1}}(t)+2\zeta_{00_{\overline{k\ell}; u, j-1}}(t)]$$

$$+ \sum_{k=1}^{m+f} \sum_{\ell=1}^{m+f} P_{ik}P_{i\ell} \, \nu_{00_{k; \ell, j-1}}(t) \, \}$$

$$+ P^{111}(i) \sum_{k=1}^{m+f} \sum_{\ell=1}^{m+f} \sum_{u=1}^{m+f} P_{ik}P_{i\ell}P_{iu} \, \zeta_{00_{k\ell; u, j-1}}(t)$$

$$i=1,m+1 \; ; \; 1 < j \le m+f \; ; \; j \neq m+1 \; . \quad (4.3.28)$$

$$\zeta_{00_{ii; jk}}(t+1) = P^2(i) \, \delta_{00_{I_i I_i; J_j K_k}}(t+1) + P^{11}(i) \, \delta_{00_{I_i I_i'; J_j K_k}}(t+1)$$

$$= P^2(i) \left[\frac{1}{2} \sum_{\ell=i}^{m+f} \sum_{u=1}^{m+f} P_{i\ell} P_{ju} \, \nu_{00\ell;u,k-1}(t) \right.$$

$$+ \frac{1}{2} \sum_{\ell=1}^{m} \sum_{u=m+1}^{m+f} \sum_{r=1}^{m+f} 4 \, P_{i\ell} P_{iu} P_{jr} \, \zeta_{00\overline{\ell u};r,k-1}(t) \right]$$

$$+ P^{11}(i) \sum_{\ell=i}^{m+f} \sum_{u=1}^{m+f} \sum_{r=1}^{m+f} P_{i\ell} P_{iu} P_{jr} \, \zeta_{00\ell u;r,k-1}(t)$$

$$i,j = 1,m+1 \; ; \; i \neq j \; ;$$

$$1 < k \leq m+f \; ; \; k \neq m+1 \; . \quad (4.3.29)$$

$$\zeta_{00ij;ik}(t+1) = P^2(i) \, \delta_{00I_iJ_j;I_iK_k}(t+1) + P^{11}(i) \, \delta_{00I_iJ_j;I_i'K_k}(t+1)$$

$$= \frac{1}{2} P^2(i) \sum_{\ell=1}^{m} \sum_{u=m+1}^{m+f} \sum_{r=1}^{m+f} 4 \, P_{i\ell} P_{iu} P_{jr} \, \zeta_{00\ell r;u,k-1}(t)$$

$$+ P^{11}(i) \sum_{\ell=1}^{m+f} \sum_{u=1}^{m+f} \sum_{r=1}^{m+f} P_{i\ell} P_{iu} P_{jr} \, \zeta_{00\ell r;u,k-1}(t)$$

$$i,j = 1,m+1 \; ; \; i \neq j \; ;$$

$$1 < k \leq m+f \; ; \; k \neq m+1 \; . \quad (4.3.30)$$

$$\zeta_{00ii;jk}(t+1) = P^2(i) \, \delta_{00I_iI_i;J_jK_k}(t+1) + P^{11}(i) \, \delta_{00I_iI_i';J_jK_k}(t+1)$$

$$= P^2(i) \left[\frac{1}{2} \sum_{\ell=1}^{m+f} P_{i\ell} \, \nu_{00\ell;j-1,k-1}(t) \right.$$

$$+ \frac{1}{2} \sum_{\ell=i}^{m} \sum_{u=m+1}^{m+f} 4 \, P_{i\ell} P_{iu} \, \zeta_{00\overline{\ell u};j-1,k-1}(t) \right]$$

$$+ P^{11}(i) \sum_{\ell=1}^{m+f} \sum_{u=1}^{m+f} P_{i\ell} P_{iu} \, \zeta_{00\ell u;j-1,k-1}(t)$$

$$i = 1,m+1 \; ; \; 1 < j,k \leq m+f \; ;$$

$$j,k \neq m+1 \; . \quad (4.3.31)$$

$$\zeta_{00ij;ik}(t+1) = P^2(i) \, \delta_{00I_iJ_j;I_iK_k}(t+1) + P^{11}(i) \, \delta_{00I_iJ_j;I_i'K_k}(t+1)$$

$$= \frac{1}{2} P^2(i) \sum_{\ell=1}^{m} \sum_{u=m+1}^{m+f} 4 \, P_{i\ell} P_{iu} \, \zeta_{00\ell,j-1;u,k-1}(t)$$

$$+ P^{11}(i) \sum_{\ell=1}^{m+f} \sum_{u=1}^{m+f} P_{i\ell} P_{iu} \; \zeta_{00\ell,j-1,u,k-1}(t)$$

$$i = 1,m+1 \; ; \; 1 < j,k \le m+f \; ;$$

$$j,k \ne m+1 \; . \tag{4.3.32}$$

$$\zeta_{00ij;k\ell}(t+1) = \sum_{u=1}^{m+f} \sum_{r=1}^{m+f} P_{iu} P_{jr} \; \zeta_{00ur;k-1,\ell-1}(t)$$

$$i,j = 1,m+1 \; ; \; i \ne j \; ;$$

$$1 < k,\ell \le m+f \; ; \; k,\ell \ne m+1 \; . \tag{4.3.33}$$

$$\zeta_{00ik;j\ell}(t+1) = \sum_{u=1}^{m+f} \sum_{r=1}^{m+f} P_{iu} P_{jr} \; \zeta_{00u,k-1;r,\ell-1}(t)$$

$$i,j = 1,m+1 \; ; \; i \ne j \; ;$$

$$1 < k, \ell \le m+f \; ; \; k, \ell \ne m+1 \; . \tag{4.3.34}$$

$$\zeta_{00ij;k\ell}(t+1) = \sum_{u=1}^{m+f} P_{iu} \; \zeta_{00u,j-1;k-1,\ell-1}(t)$$

$$i = 1,m+1 \; ; \; 1 < j,k,\ell \le m+f \; ;$$

$$j,k,\ell \ne m+1 \; . \tag{4.3.35}$$

$$\zeta_{00ij;k\ell}(t+1) = \zeta_{00i-1,j-1;k-1,\ell-1}(t)$$

$$1 < i,j,k,\ell \le m+f \; ;$$

$$i,j,k,\ell \ne m+1 \; . \tag{4.3.36}$$

4.3.4   Numerical Results

. To illustrate the progress of inbreeding for dioecious populations
with age structure, consider the situation present in a control flock
of sheep at Massey University. In each year there are twenty individuals,
in five equal-sized age classes. There is one class of males and four
classes of females so that $m = 1$, $f = 4$, and $M_1 = F_i = 4$, $2 \le i \le 5$.
A multinomial distribution is assumed for the progeny numbers, both
between and within age classes, so that $p_{i1} = \frac{1}{2}$, $p_{ij} = \frac{1}{8}$, for $i = 1,2$
and $2 \le j \le 5$ while $P^2(i) = \frac{1}{4}$ for $1 \le i \le 5$. All the individuals in the
initial ($t = 0$) population are assumed to be not inbred and unrelated.
Some values of the two-locus inbreeding coefficients $F_{11}(t)$ for various link-
age parameter values, and of the identity disequilibrium coefficient $\eta_{11}(t)$
for free recombination ($\lambda = 0$), are displayed in Table 4.2. Limiting
rates of inbreeding (or decrease of F_{00}), r, are also shown. The
approximate values are those which follow from the method of JOHNSON
(1977), and the r value in that column is the limiting value of the
difference between successive values of the approximate F_1 values.

Table 4.2   Inbreeding Coefficients for Dioecious Population. Four
             Individuals in Each of One Male and Four Female Age Classes

| t (year) | $F_{11}(t)$ | | | | | $F_1(t)$ (approx.) | $\eta_{11}(t)$ |
	$\lambda=0$	$\lambda=1/4$	$\lambda=1/2$	$\lambda=3/4$	$\lambda=1$		$\lambda=0$
0	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
1	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
2	0.0043	0.0060	0.0090	0.0139	0.0215	0.0215	0.0038
3	0.0064	0.0092	0.0142	0.0233	0.0386	0.0396	0.0049
4	0.0085	0.0120	0.0188	0.0319	0.0557	0.0582	0.0054
5	0.0112	0.0152	0.0236	0.0408	0.0749	0.0795	0.0056
10	0.0313	0.0358	0.0470	0.0768	0.1614	0.1817	0.0053
15	0.0621	0.0662	0.0768	0.1103	0.2398	0.2837	0.0046
20	0.1006	0.1041	0.1136	0.1464	0.3108	0.3858	0.0040
50	0.3829	0.3843	0.3881	0.4038	0.6174	0.9980	0.0017
100	0.7340	0.7343	0.7350	0.7384	0.8566	2.0184	0.0003
r	0.0384	0.0383	0.0381	0.0373	0.0194	0.0204	

4.4   Discussion

A general and exact treatment has been given for the determination
of inbreeding coefficients at one or two loci in populations with over-
lapping generations. Two types of identity measures are required. One
type is defined for genes as they are located in sets of gametes and
the other type for genes identified by the individuals from which they
are drawn. In the one-locus case, only digametic measures are needed,
but in the two-locus case digametic, trigametic and quadrigametic
measures are required.

Linear transition equations between gametic set measures are
established, and this suggests that standard matrix techniques could
be employed to discuss the behaviour of these measures, which include
the inbreeding coefficients. In fact, the number of measures required
is too large for analytical work [$n(n+1)/2$ measures for the one-locus
monoecious situation and $(m+f)(m+f+1)/2$ for the one-locus dioecious
situation], but it is a simple matter to code the transition equations
for computer iteration. The formal elegance of approximate methods
such as those of JOHNSON(1977) is thereby lost. In practice however,
the calculation of inbreeding coefficients by approximate methods also
required numerical treatment, so there is no real loss.

It is therefore suggested that the exact transition equations be
iterated numerically if levels of inbreeding are required for populations
with overlapping generations. This is particularly important in early
generations, when values based on effective numbers are not appropriate.
If the long-term behaviour of such populations is required, then effective
numbers may be sufficient and in some cases approximate values of such
numbers may be used. It is therefore appropriate to turn to a consi-
deration of exact and approximate effective numbers.

4.4.1   Inbreeding Effective Numbers for Poisson Family Sizes :
Monoecious Case

It has already been demonstrated how the transition equations for
gametic set measures lead to numerical values of exact inbreeding
effective numbers. It would be desirable if analytical values for

such numbers could be used, even if they gave only approximate values. The exact results are used here to check on such approximations. In particular, consider the following general rule of HILL (1972b).

"The effective sizes of random mating populations of constant size and sex ratio with overlapping generations are equal to the effective sizes of populations with discrete generations which have the same numbers of individuals entering the population each generation and the same variance of lifetime family number."

This rule refers to generation effective numbers.

For monoecious random mating populations, HILL (1972b) gives

$$N_g = (4N_1 - 2) L/(\sigma_n^2 + 2) \tag{4.4.1}$$

when σ_n^2 is the variance of lifetime family size (total gametic output per individual). Suppose that the jth newborn in any year contributes g_{ij} gametes to newborn individuals i years later ($1 \le j \le N_1$, $1 \le i \le n$). The lifetime family size of the jth newborn in any year is then

$$g_j = \sum_{i=1}^{n} g_{ij}$$

For "Poisson" lifetime family sizes, the g_j's are multinomially distributed, and

$$g_j \sim B(2N_1, \frac{1}{N_1}) , \qquad \sigma_n^2 = 2(1 - \frac{1}{N_1})$$

so that

$$N_g = N_1 L , \qquad N_y = N_1 L^2 .$$

When gametes are drawn with equal probabilities from each age class in each year, $p_i = 1/n$, and $L = (n+1)/2$, therefore

$$N_g = (n+1) N_1/2 , \qquad N_y = (n+1)^2 N_1/4 . \tag{4.4.2}$$

Now equation (4.4.2) is for the case referred to as equal chance gamete formation. In the numerical example in Section 4.2.4, $n = N_1 = 4$, so that (4.4.2) gives $N_y = 25$ while the exact result, from Table 4.1, is $N_y = 24.62$. There is very good agreement between exact and approximate effective numbers for Poisson family sizes. These approximate results also follow from the work of FELSENSTEIN (1971).

4.4.2 Inbreeding Effective Numbers for Constant Family Sizes : Monoecious Case

Now consider the case where there is no variance among lifetime family sizes. The discrete result, HILL (1972b), provides

$$N_g = (2N_1 - 1)L .$$ (4.4.3)

For exact inbreeding levels and effective sizes however, it is not sufficient to consider only life-time family sizes. It was shown that gametic set measure transition equations required knowledge of within-age-class sampling probabilities, which means that a knowledge of the annual family sizes is needed.

To illustrate the situation with non-Poisson family sizes, consider three cases where the lifetime family size is exactly two for every new-born individual in any year. All cases have $n = 4$, $N_i = 4$ for $i = 1,2,3,4$. In the first case, each age class is also constrained to provide exactly two gametes in any year. This is achieved by numbering the newborn individuals in year t in such a way that individuals give gametes in the following years :

Individuals	Years
1	t+1,t+4
2	t+2,t+3
3	t+3,t+2
4	t+4,t+1 .

The eight gametes each year are combined at random.

In the second case, gametes are provided only by the youngest and oldest age classes in any year. In other words, each newborn gives one gamete at age 1 and one at age 4. Random gametic union is preserved.

Finally, a maximum avoidance scheme is used. Every newborn individual has a 1-year-old parent and a 4-year-old parent. Gametes are provided by youngest and oldest age classes only as in the second case, but there is no longer random union of gametes. Matings are specified.

The following annual effective numbers are found :

$$
\begin{array}{lll}
\text{two gametes per age class} & N_y & = 46.58 \\
\text{oldest and youngest age class} & N_y & = 45.98 \\
\text{maximum avoidance} & N_y & = 8.91
\end{array}
$$

Details of the appropriate transition equations are given in Section 4.5. With a generation length of 2.5, equation (4.4.3) gives

$$
\text{approximate result} \qquad N_y = 43.75 \; .
$$

Note that in situations where matings of gametes are specified, the inbreeding and variance effective numbers are not the same. Therefore it is not appropriate to compare the maximum avoidance exact inbreeding result to the approximate value which was derived for predicting variance of gene frequency changes. With the random union of gametes there is still some agreement between exact and approximate effective numbers, but this disguises the quite real differences in inbreeding levels in early generations. Table 4.3 displays the exact inbreeding coefficients, and they are compared to the approximate values

$$
F_1(t)(\text{approx.}) = 1 - \left(\frac{2N_y - 1}{2N_y}\right)^t \; .
$$

This Table also shows that exact inbreeding coefficients do not always rank in the same order as inbreeding effective numbers. It is not until generation five that the inbreeding for the maximum avoidance scheme exceeds that of the equal chance scheme for example. The reverse relationship in the first four generations goes against the relationship of

the inbreeding effective numbers.

Table 4.3   Exact and Approximate One-Locus Inbreeding Coefficients: Monoecious Population with Four Individuals in Each of Four Age Classes

| | | | Two gametes per parent | | | | | |
| | Equal Chance | | Two gametes per age class | | Oldest and Youngest | | Maximum Avoidance | |
Year	Exact	Approx.	Exact	Approx.	Exact	Approx.	Exact	Approx.
0	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
1	0.0313	0.0203	0.0000	0.0107	0.0000	0.0109	0.0000	0.0561
2	0.0447	0.0402	0.0089	0.0214	0.0000	0.0216	0.0000	0.1091
3	0.0607	0.0596	0.0115	0.0319	0.0000	0.0323	0.0000	0.1591
4	0.0794	0.0786	0.0295	0.0423	0.0089	0.0428	0.0625	0.2063
5	0.1010	0.0971	0.0399	0.0525	0.0287	0.0532	0.1875	0.2508
10	0.1872	0.1838	0.0892	0.1023	0.0762	0.1036	0.3760	0.4387
15	0.2665	0.2649	0.1371	0.1495	0.1228	0.1513	0.5242	0.5795
20	0.3380	0.3305	0.1824	0.1941	0.1691	0.1964	0.6433	0.6850
50	0.6423	0.6415	0.4085	0.4170	0.4015	0.4211	0.9370	0.9443
100	0.8718	0.8715	0.6552	0.6601	0.6536	0.6649	0.9965	0.9969
N_y	24.62		46.58		45.98		8.91	

4.4.3 Inbreeding Effective Numbers for Poisson Family Sizes : Dioecious Case

For dioecious populations with equal chance gamete formation, HILL (1972b) gives

$$N_y = \frac{4L^2 M_1 F_1}{M_1 + F_1} .$$ (4.4.4)

In the numerical example in Section 4.3.4., $M_1 = F_1 = 4$ and $L = 1.75$ to give the approximate value $N_y = 24.50$ while, from Table 4.2, the exact value is $N_y = 25.77$. Agreement is still good for Poisson life-time family sizes.

4.4.4 Inbreeding Effective Numbers for Constant Family Sizes : Dioecious Case

For fixed equal family sizes, HILL doubles the value in (4.4.4) and points out that the approximate effective number depends on the lifetime family size and not on annual family sizes. The exact effective numbers however do not follow this rule, and depart from it as in the monoecious case. The departures are illustrated by the previous case of one male and four female age classes, each with four individuals. Considered below are two cases where every individual has a lifetime contribution of one male gamete and one female gamete.

The first case is where each female age class is also restricted to providing one male and one female gamete in any year. This is accomplished by numbering the newborn females in year t in such a way that they give gametes in the following years :

Individual	Gamete to Males in Year	Gamete to Females in Year
1	t + 1	t + 4
2	t + 2	t + 3
3	t + 3	t + 2
4	t + 4	t + 1

In the second case, the first two females in age class two (youngest) and the last two in age class five (oldest) give male gametes, while the other females in these two classes give female gametes. In both these examples, random union of gametes is preserved and details of transition equations are given in Section 4.5. The exact and approximate effective numbers are :

two gametes per age class : N_y = 46.81

oldest and youngest age classes : N_y = 47.02

approximate effective size : N_y = 49.00

Table 4.4 shows the exact inbreeding coefficients together with the values based on inbreeding effective numbers.

Table 4.4 Exact and Approximate One-Locus Inbreeding Coefficients: Dioecious Populations with Four Individuals in One Male and Four Female Age Classes

			Two gametes per parent					
			Two gametes per age class			Oldest and Youngest		
	Equal Chance		Exact			Exact		
Year	Exact	Approx.	Males	Females	Approx.	Males	Females	Approx.
0	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
1	0.0000	0.0194	0.0000	0.0000	0.0107	0.0000	0.0000	0.0106
2	0.0215	0.0385	0.0078	0.0234	0.0212	0.0156	0.0156	0.0212
3	0.0386	0.0572	0.0159	0.0315	0.0317	0.0195	0.0195	0.0316
4	0.0557	0.0755	0.0260	0.0433	0.0420	0.0276	0.0334	0.0419
5	0.0749	0.0934	0.0375	0.0548	0.0523	0.0442	0.0501	0.0521
10	0.1614	0.1782	0.0875	0.1040	0.1018	0.0944	0.1000	0.1014
15	0.2398	0.2594	0.1352	0.1509	0.1488	0.1415	0.1468	0.1482
20	0.3108	0.3246	0.1804	0.1953	0.1933	0.1861	0.1912	0.1925
50	0.6174	0.6251	0.4061	0.4169	0.4155	0.4094	0.4131	0.4141
100	0.8566	0.8594	0.6529	0.6592	0.6583	0.6540	0.6561	0.6567
N_y	25.77			46.81			47.02	

4.4.5 Variance Effective Numbers

If genetic drift is of more interest than inbreeding, the variance effective numbers should be used. The simplest way of obtaining these numbers, and the variance in gene frequencies due to drift, is by use of group coancestry coefficients (COCKERHAM 1969). If θ_ℓ is the group coancestry coefficient of a population, then COCKERHAM showed that the variance of the sample gene frequency $\hat{p}$ when the population frequency is p (so that $\hat{p}$ has an expected value of p) is

$$\sigma^2_{\hat{p}} = \theta_\ell \; p(1-p) \quad .$$

Furthermore, if gametes unite at random every pair of gametes received by the group carries genes with the same probabilities of identity by descent. The inbreeding and variance effective numbers are the same. The annual change of gene frequency variance follows :

$$\sigma^2_{\hat{p}}(t) = [1 - (\frac{2N_y - 1}{2N_y})^t] \; p(1-p) \quad .$$

Cases such as maximum avoidance of inbreeding with non-random union of gametes were discussed by COCKERHAM (1969, 1970).

4.5 Appendix : Two Gametes Per Parent

When individuals provide exactly two gametes per lifetime, a strict accounding must be kept of annual gametic contributions. The sampling probabilities P(i) and gametic set measures are not appropriate, and a new type of individual measure is used. For the one-locus case it is sufficient to define the digametic measure

$$\varphi(i,j;k,\ell)_t = \varphi(k,\ell;i,j)_t$$

as the probability of identity of a gene from the jth member of age class i and the ℓth member of age class k in year t. The notation is deliberately different from that used previously to emphasize that φ is different from the digametic measures θ and ψ. $F_1(t)$ still refers to the inbreeding coefficient in year t. The necessary transition equations for the cases illustrated in Tables 4.3 and 4.4 are presented here.

There is an obvious extension to more general cases.

In each case studied, the following initial conditions apply :

$$\varphi(i,j;k,\ell) = 0 \qquad i \neq k \text{ or } j \neq \ell$$
$$= 1/2 \qquad i = k, \quad j = \ell \quad .$$

Monoecious: Two gametes per age class

There are four age classes of size four. In any year one gamete is provided by individuals i and 5 - i in each age class i. Gametes unite at random.

$$28F_1(t+1) = \sum_{i=1}^{4} \varphi(i,i;i,5-i)_t + \sum_{i=1}^{3} \sum_{j=i+1}^{4} [\varphi(i,i;j,j)_t$$

$$+ \varphi(i,i;j,5-j)_t + \varphi(i,5-i;j,j)_t + \varphi(i,5-i;j,5-j)_t]$$

$$2\varphi(1,i;1,i)_{t+1} = 1 + F_1(t+1) , \qquad 1 \leq i \leq 4$$

$$\varphi(1,i;1,j)_{t+1} = F_1(t+1) , \qquad 1 \leq i < j \leq 4$$

$$8\varphi(1,i;j,k)_{t+1} = \sum_{\ell=1}^{4} [\varphi(\ell,\ell;j-1,k)_t + \varphi(\ell,5-\ell;j-1,k)_t] ,$$
$$1 \leq i,k \leq 4, \quad 2 \leq j \leq 4$$

$$\varphi(i,j;k,\ell)_{t+1} = \varphi(i-1,j;k-1,\ell)_t , \quad 2 \leq i,k \leq 4, \quad 1 \leq j,\ell \leq 4 .$$

Monoecious: Oldest and Youngest Age Classes

There are four age classes of size four. In any year one gamete is provided by each individual in age classes one and four. Gametes unite at random.

$$28F_1(t+1) = \sum_{i=1}^{3} \sum_{j=i+1}^{4} [\varphi(1,i;1,j)_t + \varphi(4,i;4,j)_t]$$

$$+ \sum_{i=1}^{4} \sum_{j=1}^{4} \varphi(1,i;4,j)_t$$

$$2\varphi(1,i;1,i)_{t+1} = 1 + F_1(t+1) \, , \qquad 1 \leq i \leq 4$$

$$\varphi(1,i;1,j)_{t+1} = F_1(t+1) \, , \qquad 1 \leq i < j \leq 4$$

$$8\varphi(1,i;j,k)_{t+1} = \sum_{\ell=1}^{4} \left[\varphi(1,\ell;j-1,k)_t + \varphi(4,\ell;j-1,k)_t \right] \, ,$$
$$1 \leq i,k \leq 4 \, , \quad 2 \leq j \leq 4$$

$$\varphi(i,j;k,\ell)_{t+1} = \varphi(i-1,j;k-1,\ell)_t \, , \quad 2 \leq i,k \leq 4 \, , \quad 1 \leq j,\ell \leq 4 \, .$$

Monoecious: Maximum Avoidance

There are four age classes of size four. In any year, newborn
individual i has as parents individual i in each of age classes 1 and
4. All gametic pairings are specified.

$$4F_1(t+1) = \sum_{i=1}^{4} \varphi(1,i;4,i) \, ,$$

$$2\varphi(1,i;1,i)_{t+1} = 1 + F_1(t+1) \, , \qquad 1 \leq i \leq 4$$

$$4\varphi(1,i;1,j)_{t+1} = \varphi(1,i;1,j)_t + \varphi(1,i;4,j)_t + \varphi(4,i;1,j)_t$$
$$+ \varphi(4,i;4,j)_t \, , \quad 1 \leq i < j \leq 4$$

$$2\varphi(1,i;j,k)_{t+1} = \varphi(1,i;j-1,k)_t + \varphi(4,i;j-1,k)_t \, ,$$
$$1 \leq i,k \leq 4 \, , \quad 2 \leq j \leq 4$$

$$\varphi(i,j;k,\ell)_{t+1} = \varphi(i-1,j;k-1,\ell)_t \, , \quad 2 \leq i,k \leq 4 \, , \quad 1 \leq j,\ell \leq 4 \, .$$

Dioecious: Two Gametes Per Age Class

There is one male age class and four female age classes, all with
four members. In any year, every male (age class 1) gives one male and
one female gamete. In female age class i ($2 \leq i \leq 5$), female i-1 gives
a male gamete and female 6-i gives a female gamete. Gametes from males
and females combine at random. $F_{1_1}(t)$ and $F_{1_2}(t)$ still refer to the
inbreeding coefficients for newborn males and females respectively.

$$16 F_{1_1}(t+1) = \sum_{i=1}^{4} \sum_{j=2}^{5} \varphi(1,i;j,j-1)_t$$

$$16 F_{1_2}(t+1) = \sum_{i=1}^{4} \sum_{j=2}^{5} \varphi(1,i;j,6-j)_t$$

$$2\varphi(1,i;1,i)_{t+1} = 1 + F_{1_1}(t+1) , \qquad\qquad 1 \le i \le 4$$

$$2\varphi(2,i;2,i)_{t+1} = 1 + F_{1_2}(t+1) , \qquad\qquad 1 \le i \le 4$$

$$4\varphi(1,i;1,j)_{t+1} = \frac{1}{6} \sum_{k=1}^{3} \sum_{\ell=k+1}^{4} [\varphi(1,k;1,\ell)_t + \varphi(k+1,k;\ell+1,\ell)_t]$$

$$+ \frac{1}{16} \sum_{k=1}^{4} \sum_{\ell=2}^{5} [\varphi(1,k;\ell,\ell-1)_t + \varphi(\ell,\ell-1;1,k)_t] ,$$

$$1 \le i < j \le 4$$

$$4\varphi(2,i;2,j)_{t+1} = \frac{1}{6} \sum_{k=1}^{3} \sum_{\ell=k+1}^{4} [\varphi(1,k;1,\ell)_t + \varphi(k+1,5-k;\ell+1,5-\ell)_t]$$

$$+ \frac{1}{16} \sum_{k=1}^{4} \sum_{\ell=2}^{5} [\varphi(1,k;\ell,6-\ell)_t + \varphi(\ell,6-\ell;1,k)_t] .$$

$$1 \le i < j \le 4$$

$$64\varphi(1,i;2,j)_{t+1} = \sum_{k=1}^{4} \sum_{\ell=2}^{5} [\varphi(1,k;1,\ell-1)_t + \varphi(1,k;\ell,6-\ell)_t$$

$$+ \varphi(k+1,k;1,\ell-1)_t + \varphi(k+1,k,\ell,6-\ell)_t] ,$$

$$1 \le i,j \le 4$$

$$8\varphi(1,i;j,k)_{t+1} = \sum_{\ell=1}^{4} [\varphi(1,\ell;j-1,k)_t + \varphi(\ell+1,\ell;j-1,k)_t]$$

$$1 \le i,k \le 4 , \qquad 3 \le j \le 5$$

$$8\varphi(2,i;j,k)_{t+1} = \sum_{\ell=2}^{5} [\varphi(1,\ell-1;j-1,k)_t + \varphi(\ell,6-\ell;j-1,k)_t] ,$$

$$1 \le i,k \le 4 , \qquad 3 \le j \le 5$$

$$\varphi(i,j;k,\ell)_{t+1} = \varphi(i-1,j;k-1,\ell)_t , \quad 3 \le i,k \le 5 , \quad 1 \le j,\ell \le 4 .$$

Dioecious: Oldest and Youngest Age Classes

· There is one male age class and four female age classes, all with four members. In any year, every male (age class 1) gives one male and one female gamete. In female age class 2, female 1 and 2 give a male gamete and females 3 and 4 give a female gamete. In female age class 5, females 1 and 2 give a female gamete and females 3 and 4 give a male gamete. Gametes from males and females combine at random.

$$16F_{1_1}(t+1) = \sum_{i=1}^{4} \sum_{j=1}^{2} [\varphi(1,i;2,j)_t + \varphi(1,i;5,j+2)_t]$$

$$16F_{1_2}(t+1) = \sum_{i=1}^{4} \sum_{j=1}^{2} [\varphi(1,i;2,j+2)_t + \varphi(1,i;5,j)_t]$$

$$2\varphi(1,i;1,i)_{t+1} = 1 + F_{1_1}(t+1)$$

$$2\varphi(2,i;2,i)_{t+1} = 1 + F_{1_2}(t+1)$$

$$4\varphi(1,i;1,j)_{t+1} = \frac{1}{6} \sum_{k=1}^{3} \sum_{\ell=k+1}^{4} \varphi(1,k;1,\ell)_t$$

$$+ \frac{1}{6} [\varphi(2,1;2,2)_t + \varphi(2,1;5,3)_t + \varphi(2,1;5,4)_t$$

$$+ \varphi(2,2;5,3)_t + \varphi(2,2;5,4) + \varphi(5,3;5,4)_t]$$

$$+ \frac{1}{16} \sum_{k=1}^{4} \sum_{\ell=1}^{2} [\varphi(1,k;2.\ell)_t + \varphi(1,k;5,\ell+2)_t$$

$$+ \varphi(2,\ell;1,k) + \varphi(5,\ell+2;1,k)_t] , \quad 1 \le i < j \le 4$$

$$4\varphi(2,i;2,j)_{t+1} = \frac{1}{6} \sum_{k=1}^{3} \sum_{\ell=k+1}^{4} \varphi(1,k;1,\ell)_t$$

$$+ \frac{1}{6} [\varphi(2,3;2,4)_t + \varphi(2,3;5,1)_t + \varphi(2,3,5,2)_t$$

$$+ \varphi(2,4;5,1)_t + \varphi(2,4;5,2)_t + \varphi(5,1;5,2)_t]$$

$$+ \frac{1}{16} \sum_{k=1}^{4} \sum_{\ell=1}^{2} [\varphi(1,k;2,\ell+2)_t + \varphi(1,k;5,\ell)_t$$

$$+ \varphi(2,\ell+2;1,k)_t + \varphi(5,\ell;1,k)_t] , \quad 1 \le i < j \le 4 .$$

$$64\varphi(1,i;2,j)_{t+1} = \sum_{k=1}^{4}\sum_{\ell=1}^{4} \varphi(1,k;1,\ell)_t$$

$$+ \sum_{k=1}^{2}\sum_{\ell=1}^{2} [\varphi(2,k;2,\ell+2)_t + \varphi(2,k;5,\ell)_t$$

$$+ \varphi(5,k+2;5,\ell)_t + \varphi(2,k+2;5,\ell+2)_t]$$

$$+ \sum_{k=1}^{4}\sum_{\ell=1}^{2} [\varphi(1,k;2,\ell)_t + \varphi(1,k;5,\ell+2)_t$$

$$+ \varphi(1,k;2,\ell+2)_t + \varphi(1,k;5,\ell)_t] , \quad 1 \le i,j \le 4$$

$$8\varphi(1,i;j,k)_{t+1} = \sum_{\ell=1}^{4} \varphi(1,\ell;j-1,k)_t$$

$$+ \sum_{\ell=1}^{2} [\varphi(2,\ell;j-1,k)_t + \varphi(5,\ell+2;j-1,k)_t] ,$$

$$1 \le i,k \le 4 , \quad 3 \le j \le 5$$

$$8\varphi(2,i;j.k)_{t+1} = \sum_{\ell=1}^{4} \varphi(1,\ell;j-1,k)_t$$

$$+ \sum_{\ell=1}^{2} [\varphi(2,\ell+2;j-1,k)_t + \varphi(5,\ell;j-1,k)_t] ,$$

$$1 \le i,k \le 4, \quad 3 \le j \le 5$$

$$\varphi(i,j;k,\ell)_{t+1} = \varphi(i-1,j;k-1,\ell) , \quad 1 \le j,\ell \le 4 , \quad 3 \le i,k \le 5 .$$

5   GENERAL DISCUSSION

.   In a population of finite size, individuals are related to each
other by ancestry. Compared to infinite random mating populations,
this raises the chance of an individual carrying genes identical by
descent and thereby increases the frequency of homozygotes in the
population. This process, known as the inbreeding effect of a finite
population, is conventionally and conveniently described in terms of
the inbreeding coefficients. In breeding programmes, usually with a
finite number of breeding individuals, the inbreeding effect can to
some extent be manipulated by various selection schemes. This thesis
has dealt with this problem and has sought to develop a general method
by which the magnitude of the joint effect of finite population size,
the selection and mating schemes in altering the genetic content of a
population can be assessed.

Recently there has been a demand for the maintenance of control
populations to provide standard material for the evaluation of the
efficiencies of selection experiments. The merit of a control
population is therefore judged by the ability of the selection
scheme to minimize gene frequency drift as well as inbreeding.
It is known that schemes which give high levels of inbreeding may
not be applicable if the control population is to be used for traits
showing much inbreeding depression. Traditionally, the comparison
between the inbreeding effects of alternative designs for controls has
been made in terms of inbreeding effective numbers. These numbers,
defined as the reciprocal of the limiting rate of increase of
inbreeding, are useful for approximating asymptotic inbreeding
levels. Some populations do not maintain the same characteristics
for a long time period and the effective numbers then may not reflect
the true inbreeding levels in early generations. As shown in some
examples, populations that avoid initial inbreeding by mating the
least related individuals may have a high final rate of inbreeding.

In this regard, it is more appropriate to compare populations
on the basis of their exact inbreeding levels. This is particularly
important in practical situations. Most breeding programmes are
maintained for only a small number of generations and therefore only

early inbreeding levels are of interest, and these may not be accurately predicted by the effective numbers.

Following MALECOT (1948) and WEIR and COCKERHAM (1969a, 1969b), the determination of the one- and two-locus inbreeding coefficients makes use of inbreeding measures, which are probability statements concerning the identity status of genes on gametes. For one-locus systems, the two genes of interest are necessarily carried on two distinct gametes and the information on their identity relations is provided by the two digametic measures, the inbreeding and the coancestry functions. Genes for two loci may be carried on two, three or four gametes. The analysis of two-locus systems thus depends on digametic, trigametic and quadrigametic measures.

With the recurring nature of the regular mating systems, the determination of the exact inbreeding coefficients relies on the establishment of a set of transition equations relating the necessary measures (including the inbreeding coefficient) in any two successive generations. The number of equations may be large for numerical iteration, but with the universal availability of computers, this is no great disadvantage.

Apart from their concern about inbreeding levels, breeders are also concerned about the amount of random gene frequency drift arising from the sampling of a finite number of genes in each generation. It is known that a selection scheme that minimizes one of these processes may not minimize the other. Many authors have been seeking measures of this gene frequency drift, usually in terms of variance effective numbers. COCKERHAM (1969) showed that, in any generation, the total variance in gene frequencies due to drift can be found from a knowledge of the inbreeding and coancestry coefficients. There is then no real advantage for the traditional use of variance effective numbers, which are related to the limiting rate of increase in variance of gene frequency. For a population maintained with constant size and random union of gametes, the asymptotic rates of change of inbreeding and drift are the same, and so are the inbreeding and variance effective numbers. Some inbreeding values obtained here under these conditions can therefore be used to check on various approximate values obtained from the consideration of variance changes.

The inbreeding coefficients have been found to contain a great
deal of information about the characteristics of a population. They
are used in conjunction with other descent measures as well as the
initial linkage disequilibrium and gene frequencies to provide
expressions for two-locus genotypic frequencies. With no initial
linkage disequilibrium only the one- and two-locus inbreeding
coefficients are sufficient (COCKERHAM and WEIR 1973). Hence the
inbreeding coefficients provide lower bounds as well as exact measures
of homozygosity. Furthermore, in the absence of initial linkage
disequilibrium, the inbreeding coefficients provide expressions for
the means and variances of quantitative traits (WEIR and COCKERHAM
1977) and hence they quantify the effects of linkage and inbreeding
on inbreeding depression and on the genetic variance among individuals.

The one-locus inbreeding coefficients have been used in recent
research to correlate changes in isozyme frequencies with quantitative
traits. Allelic frequencies for some marker genes may be affected by
selection on other genes. A measure of such an effect may be provided
by the departure of the isozyme frequency data from those expected on
the basis of random drift under the particular mating system. Using
the variance effective number as a measure of drift, SCHAFFER et al
(1977) were able to construct statistical tests to decide whether the
observed isozyme frequency variation is consistent with that which
would have been predicted by the null hypothesis of drift acting alone,
and to decide if there exists any linear trend in isozyme frequency
over generations due to selection. This method was later employed
by STUBER et al (1978) to analyse the data obtained from their selection
experiments for increased grain yield in maize. Making use of the
effective numbers for the selection schemes, these authors suggested
that the eight different loci under study were influenced by selection.
They then obtained correlations between the isozyme frequencies of
these loci with accumulated selection gain in grain yield. The
effective numbers used in these studies were based on inbreeding
coefficient transition equations of the type presented in this thesis.

One-locus theory is appropriate for the study of the progress of
a gene when the gene is observed in isolation and it exists in random
combination with other genes. It is very often desirable to study

the progress of two genes together as might be the situations when two genes control some characters of interest.

As the one-locus inbreeding coefficients have been found useful in the analysis of isozyme frequency data at a single locus, it seems natural that the corresponding two-locus quantities should be useful in the study of two-locus data.

However, the analysis of two-locus data is often made complicated by the fact that two genes do not always act independently. It is of common interest to study the effect of the interaction between two loci on genotypic frequencies as well as the extent to which the interaction is the result of linkage or the constraints of finite population size or the system of mating. A classical measure of this interaction is provided by the linkage disequilibrium. If alleles A and B at two different loci occur in the population with frequencies p_A and p_B respectively while the chromosomes carrying them together have frequency p_{AB}, the linkage disequilibrium Δ_{AB} is defined as

$$\Delta_{AB} = p_{AB} - p_A p_B \quad .$$

It has been shown that linkage disequilibrium values in late generations are determined entirely by the initial disequilibrium and the parental descent measure, written as F^1 (COCKERHAM and WEIR 1973). A possible extension of the work in this thesis is therefore to evaluate the parental descent measures and hence the linkage disequilbrium values for the particular populations studied.

To characterize an effect of linkage on the identity of two pairs of linked genes, an identity disequilibrium was used. Unlike the linkage disequilibrium this quantity depends only on linkage and mating system and not on the frequencies of particular alleles. This quantity has been discussed by WEIR and COCKERHAM (1969a). It increases with the amount of linkage; its value is always small and is zero in a non-inbred initial population, increases to a maximum, then decreases to zero when complete double identity is obtained.

The effect of linkage is seen to increase the frequency of double homozygotes over that expected for genes which combine freely. However, linkage effects do not increase linearly with the amount of linkage. Numerical results show that it is only for high values of λ that linkage produces significant effects, and even then the effects are not as great as those of population size.

The thesis is primarily concerned with the analysis of genetic properties in control populations. Attention has therefore been restricted to those selection schemes which attempt to maintain genetic constancy in populations.

Two selection schemes, the recurrent selection and overlapping generations selection schemes, which have found great use in plant and animal breeding, were chosen for the purpose of illustrating the technique of obtaining exact inbreeding levels for any regular mating system. For these two schemes, no correct methods have previously been given for the calculation of the exact one- and two-locus inbreeding coefficients or the inbreeding effective numbers.

For the determination of the inbreeding coefficients in systems of matings among individuals, the general procedure is first to express the inbreeding coefficient of a random member in generation t+1 as the coancestry of its parents. This coancestry measure in generation t+1 is then expanded back into measures of the previous generation. The types of additional measures introduced on the right hand side of this equation are noted, and transition equations established relating their values in generation t+1 to measures in generation t. This process is continued until no new types of measures are introduced in the expansions and was illustrated for the case of recurrent selection in Chapter 3. Transition equations were established for measures concerning gametes drawn from individuals. These measures are termed the individual measures.

For systems of matings among groups of individuals, transition equations are established for gametic set measures as gametes are drawn from groups of individuals. The quantity to be determined is

the group inbreeding coefficient which is the average of the inbreeding
coefficients for all members in the group of interest. To identify
the individuals from which the gametes are drawn, average individual
measures need to be used in addition to the gametic set measures. The
usual procedure is to express the gametic set measures as linear
combinations of average individual measures, and then to express
these average individual measures back to gametic set measures of the
previous generation. Such a procedure was demonstrated for the
overlapping generations selection scheme in Chapter 4.

The thesis has given a general and exact treatment of the
determination of inbreeding coefficients at one and two loci in
populations with regular systems of mating. Its generalization in
n-locus systems requires the use of x-gametic measures, x=2,3,...,2n,
subject to $x \leq 2N$ for a population of size N. Once again, transition
equations could be established and exact inbreeding coefficients
could be found by numerical iteration of these equations. It is
doubtful if the considerable effort involved in such extensions
is worthwhile however. This thesis has demonstrated the great
complexity of even two-locus analysis. Real progress towards a
multi-locus theory of inbreeding is likely to depend on an adequate
set of approximate measures. A start in this direction has been made
by CHEVALET et al (1977). The exact two-locus results presented in
this thesis will allow some evaluation of the adequacy of any approximate
measures.

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