EXACT INBREEDING COEFFICIENTS IN
POPULATIONS WITH OVERLAPPING GENERATIONS[1]

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ABSTRACT

A theory is given that allows inbreeding coefficients to be calculated exactly for populations with overlapping generations. Emphasis is placed on providing equations well suited for computer iteration. Both monoecious and dioecious populations are considered and family size is not restricted to being Poisson. One-locus and two-locus inbreeding coefficients are evaluated, although the reader may omit the two-locus sections. The exact treatment is shown to be preferable to approximate treatments in that it applies to both early and late generations for all population sizes. Inbreeding effective numbers found by the exact treatment are compared to various approximate numbers, and the approximate values are found to be generally very good.

BY studying inbreeding levels in populations with overlapping generations, we hope to quantify the effects of age structure in altering the genetic progress of populations. We know that, relative to populations of the same size with just one age class, inbreeding and hence homozygosity is delayed in populations with several age classes. We also know that the continued presence of individuals, generally females, over several years in breeding programs can delay the spread of favorable genes. In another direction, we recognize that human populations do not have discrete generations and that this should be reflected in models of these populations. Our study 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,b). Effective numbers offer a very convenient one-parameter description of the mating structure of a population. As such they are often used

as a basis for comparison of different populations. In populations other than idealized ones, however, effective 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 programs interest is likely to be centered on early generations. For this reason we concur with JOHNSON (1977) in concentrating on inbreeding levels in early generations, rather than in limiting values of rates of change of inbreeding. We differ from JOHNSON, however, in restricting attention to exact inbreeding levels.

We also broaden the scope of some previous inquiries by considering both monoecious and dioecious populations, and not restricting attention to Poisson family size. In this we follow HILL (1972b). The study of different gametic sampling plans points out another restriction in 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.

In other matters, such as the assumptions of constant overall population size and stable age distribution, we follow conventional models. We allow age-specific birth and death rates.

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 (1969). 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, we have recently shown (WEIR and COCKERHAM 1977) how the two-locus inbreeding coefficient is used in the prediction of means and variances of quantitative traits. Work similar to that presented here allows the evaluation of other two-locus parameters that can be used to predict linkage disequilibrium (COCKERHAM and WEIR 1977).

We recognize that the two-locus analysis may be of more limited interest than the usual one-locus study of inbreeding. Accordingly, the paper has been structured so that the two-locus sections may be omitted by the reader.

MONOECIOUS DIPLOIDS

Mating scheme

In all years t the population consists of $\mathcal{N}$ individuals belonging to various age classes. There are $\mathcal{N}_i$ individuals in the ith class, and n classes, so that

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

Age is measured in years. Each year $\mathcal{N}_1$ newborn are added to the population and all $\mathcal{N}_n$ n-year-olds die, while a random sample of $\mathcal{N}_i - \mathcal{N}_{i+1}$ 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.

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

Within age classes, we allow arbitrary distributions 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 $\mathcal{N}_i$ gametic numbers from the ith age class are then multinomially distributed. We will return to an analysis of the different distributions in the DISCUSSION, but note here that we have already (CHOY and WEIR 1977) discussed such schemes as "minimum" and "maximum" inbreeding for recurrent selection schemes. At present, we will assume that the gametic numbers have the same distribution for every member of an age class, and we work with gametic sampling probabilities (WEIR and COCKERHAM 1969) $P^2(i)$ 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 that age class. In this "equal-chance" case,

$$P^2(i) = 1/\mathcal{N}_i.$$

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

One-locus case

We wish to determine 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

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

The gametic set measure $\psi_{1_{ij}}(t)$ 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 it is helpful to define the average coancestry $\theta_{1_{I_i J_j}}(t)$ 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,

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

$$\psi_{1_{ij}}(t{+}1) = \theta_{1_{I_iJ_j}}(t{+}1), \quad 1 \leq i < j \leq n, \tag{3}$$

and there are the obvious symmetries

$$\psi_{1_{ij}}(t) = \psi_{1_{ji}}(t), \quad \theta_{1_{I_iJ_j}}(t) = \theta_{1_{J_jI_i}}(t) \ .$$

Now an individual of age i in year $t + 1$ was of age 1 in year $t - i + 2$, so that gametes from such individuals descended from parents in year $t - i + 1$. Identity-by-descent relations in equations (2) and (3) are preserved if we write them as

$$\psi_{1_{ii}}(t{+}1) = P^2(i)\, \theta_{1_{I_1I_1}}(t{-}i{+}2) + P^{11}(i)\, \theta_{1_{I_1I_1'}}(t{-}i{+}2), \quad 1 \leq i \leq n \tag{4}$$

$$\psi_{1_{ij}}(t{+}1) = \theta_{1_{I_1J_{j-i+1}}}(t{-}i{+}2), \quad 1 \leq i < j \leq n \ . \tag{5}$$

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. We have then

$$\theta_{1_{I_1I_1}}(t{-}i{+}2) = \left[1 + \sum_{i=1}^{n} \sum_{j=1}^{n} p_i p_j\, \psi_{1_{ij}}(t{-}i{+}1) \right]/2 \tag{6}$$

$$\theta_{1_{I_1I_1'}}(t{-}i{+}2) = \sum_{i=1}^{n} \sum_{j=1}^{n} p_i p_j\, \psi_{1_{ij}}(t{-}i{+}1) \tag{7}$$

$$\theta_{1_{I_1J_{j-i+1}}}(t{-}i{+}2) = \sum_{k=1}^{n} p_k\, \psi_{1_{k,j-i}}(t{-}i{+}1), \quad 1 \leq i < j \leq n \ . \tag{8}$$

Equations (2) to (8) may now be combined to give the desired transition equations for gametic set measures:

$$\psi_{1_{ii}}(t{+}1) = \left[1 - \frac{1}{2}P^2(i) \right] \sum_{j=1}^{n} \sum_{k=1}^{n} p_j p_k\, \psi_{1_{jk}}(t{-}i{+}1) + \frac{1}{2}P^2(i), \ 1 \leq i \leq n \tag{9}$$

$$\psi_{1_{ij}}(t{+}1) = \sum_{k=1}^{n} p_k\, \psi_{1_{k,j-i}}(t{-}i{+}1), \quad 1 \leq i < j \leq n \ . \tag{10}$$

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 we always obtain sets of measures that rest only on values in the previous generation. We

can rearrange equations (9) and (10); however, to obtain equations which do span just consecutive pairs of years:

$$\psi_{1_{11}}(t+1) = \left[1 - \frac{1}{2}P^2(1)\right] \sum_{i=1}^{n} \sum_{j=1}^{n} p_i p_j \psi_{1_{ij}}(t) + \frac{1}{2}P^2(1) \qquad (11)$$

$$\psi_{1_{1j}}(t+1) = \sum_{i=1}^{n} p_i \psi_{1_{i,j-1}}(t), \quad 1 < j \le n \qquad (12)$$

$$\psi_{1_{ii}}(t+1) = \frac{1 - \frac{1}{2}P^2(i)}{1 - \frac{1}{2}P^2(i-1)} \psi_{1_{i-1,i-1}}(t) + \frac{P^2(i) - P^2(i-1)}{2[1 - \frac{1}{2}P^2(i-1)]}, \quad 1 < i \le n \qquad (13)$$

$$\psi_{1_{ij}}(t+1) = \psi_{1_{i-1,j-1}}(t), \quad 1 < i < j \le n . \qquad (14)$$

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).

Equations (11) through (14) are in a form that is highly suitable for computer programming. Exact treatment of inbreeding in situations as complex as those considered in this paper of necessity requires a numerical approach. Our hope is that readers with specific cases of overlapping-generation populations will find equations (11) through (14) of help in their numerical studies.

If there were only one age class per generation, $n = 1$, equations (11) through (14) provide

$$\psi_{1_{11}}(t+1) = \left[1 - \frac{1}{2}P^2(1)\right] \psi_{1_{11}}(t) + \frac{1}{2}P^2(1)$$

or

$$F_1(t) = \psi_{1_{11}}(t-1) = 1 - \left[1 - \frac{1}{2}P^2(1)\right]^t, \text{ if } F_1(0) = 0$$

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 our measures are

$$\psi_{1_{ii}}(0) = \frac{1}{2}P^2(i), \qquad 1 \le i \le n$$

$$\psi_{1_{ij}}(0) = 0, \qquad 1 \le i < j \le n ,$$

$$F_1(0) = 0$$

and then equations (1) and (11) through (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 (9) and (10), or (11) through (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, we set

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

This is the annual inbreeding effective number. Note that we would obtain the same rate of inbreeding and effective number if we took

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

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; JOHNSON 1977) have given analytical expressions that 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.

One-locus numerical results

We illustrate the evaluation of one-locus inbreeding coefficients in monoecious populations by considering a population with four age classes ($n = 4$), each with four individuals ($\mathscr{N}_i = 4$, $i = 1,2,3,4$). Equal-chance gamete formation is assumed. We set each of the mating probabilities p_i equal to $\frac{1}{4}$, and each of the probabilities $P^2(i)$ of drawing two gametes from the same member of an age class also equal to $\frac{1}{4}$.

Equations (11) through (14) become

$$\psi_{1_{11}}(t+1) = \frac{7}{128} \sum_{i=1}^{4} \sum_{j=1}^{4} \psi_{1_{ij}}(t) + \frac{1}{8}$$

$$\psi_{1_{1j}}(t+1) = \frac{1}{4} \sum_{i=1}^{4} \psi_{1_{i,j-1}}(t) , \qquad\qquad j = 2,3,4$$

$$\psi_{1_{ii}}(t+1) = \psi_{1_{i-1,i-1}}(t) , \qquad\qquad i = 2,3,4$$

$$\psi_{1_{ij}}(t+1) = \psi_{1_{i-1,j-1}}(t) , \qquad\qquad 2 \leq i < j \leq 4$$

so that there are ten distinct-valued measures to evaluate each year. These equations utilize the equalities $\psi_{1_{ij}} = \psi_{1_{ji}}$, but it may be more convenient for computing purposes to work with all 16 possible measures $\psi_{1_{ij}}$ ($i,j = 1,2,3,4$) as a two-dimensional array. The inbreeding coefficient in any year is the average of all gametic set measures in the previous year

$$F_1(t+1) = \frac{1}{16} \sum_{i=1}^{4} \sum_{j=1}^{4} \psi_{1_{ij}}(t) .$$

In Table 1 we display the one-locus inbreeding coefficients for this population and compare them with values obtained by the method of JOHNSON (1977). This approximate method, designed for early generations, assumes that $(2\mathscr{N}_i - 1)/2\mathscr{N}_i \approx 1$. In effect, JOHNSON's method linearizes the inbreeding coefficient, so that his effective number N_y is such that

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

The inbreeding rate r shown for the approximate F_1 values is therefore the limiting value of the differences between F_1 values in successive years.

TABLE 1

Inbreeding coefficients for monoecious populations:
Four individuals in each of four age classes, one-locus case

t (Year)	$F_1(t)$ (Exact)	$F_1(t)$ (Approx.)
0	0.0000	0.0000
1	0.0313	0.0313
2	0.0447	0.0449
3	0.0607	0.0614
4	0.0794	0.0810
5	0.1010	0.1041
10	0.1872	0.2025
15	0.2665	0.3025
20	0.3380	0.4025
50	0.6423	1.0025
100	0.8718	2.0025
r	0.0203	0.0200

Two-locus case

For inbreeding at two loci, we need to consider the identity status of two pairs of genes. If a,a' and b,b' are two genes at the A and B loci, respectively, the general identity measure $\underline{X}(ab,a'b')$ has four components according to the identity relations at each locus.

Component	Identical genes
X_{11}	$a \equiv a'$, $b \equiv b'$
X_{10}	$a \equiv a'$
X_{01}	$b \equiv b'$
X_{00}	none

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

$$\underline{F}(t+1) = \sum_{i=1}^{n} \sum_{j=1}^{n} p_i p_j \underline{\psi}_{ij}(t) \ . \tag{15}$$

This vector equation is analogous to (1), and adding the first and third rows of (15) in fact gives (1). Two other gametic set measures are needed:

$\underline{\nu}_{i;jk}$: ab,a',b' on three gametes from age classes i,j,k, respectively;

$\underline{\zeta}_{ij;kl}$: a,b,a',b' on four gametes from age classes i,j,k,l, respectively.

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 we need two-locus average individual measures (WEIR and COCKERHAM 1969), and here we define the digametic measure. We let i denote age class i $(i = 1,2,\ldots,n)$ and I_i denote a random member of age class i $(I_i = 1,2,\ldots,N_i)$. Measures are averaged over all such random members.

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

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 1969), and we give details 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 analogs of equations (2), (3) are

$$\underline{\psi}_{ii}(t+1) = P^2(i)\,\underline{\theta}_{I_iI_i}(t+1) + P^{11}(i)\,\underline{\theta}_{I_iI_i'}(t+1)\,, \quad 1 \le i \le n \qquad (16)$$

$$\underline{\psi}_{ij}(t+1) = \underline{\theta}_{I_iJ_j}(t+1)\,, \quad 1 \le i < j \le n\,. \qquad (17)$$

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. We allow the loci to be linked to an arbitrary extent λ, where λ is one minus twice the recombination coefficient $(0 \le \lambda \le 1)$.

For simplicity we restrict attention to the fourth, double nonidentity, 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 nonidentity, genes in two gametes from a single individual must have descended from genes in the two gametes received by that individual, but there is no restriction for genes in gametes from different individuals. Gametes received by age class 1 may be from any of the age classes in the previous years:

$$\theta_{00_{I_iI_i}}(t+1) = \frac{1+\lambda^2}{4} \sum_j \sum_k p_j p_k\, \psi_{00_{jk}}(t-i+1),\quad 1 \le i \le n \qquad (18)$$

$$\theta_{00_{I_iI_i'}}(t+1) = \left(\frac{1+\lambda}{2}\right)^2 \sum_j \sum_k p_j p_k\, \psi_{00_{jk}}(t-i+1)$$

$$+ \frac{1-\lambda^2}{2} \sum_j \sum_k \sum_l p_j p_k p_l\, v_{00_{j;kl}}(t-i+1)$$

$$+ \left(\frac{1-\lambda}{2}\right)^2 \sum_j \sum_k \sum_l \sum_s p_j p_k p_l p_s\, \zeta_{00_{jk;ls}}(t-i+1),\quad 1 \le i \le n \quad (19)$$

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

$$+ \frac{1-\lambda}{2} \sum_k \sum_l p_k p_l\, v_{00_{j-i;kl}}(t-i+1),\quad 1 \le i < j \le n\,. \qquad (20)$$

The transition equations for the digametic set measures now follow from combining equations (16) to (20):

$$\psi_{00_{ii}}(t+1) = \left[\left(\frac{1+\lambda}{2}\right)^2 - \frac{\lambda}{2}\,P^2(i)\right] \sum_j \sum_k p_j p_k\, \psi_{00_{jk}}(t-i+1)$$

$$+ P^{11}(i)\,\frac{1-\lambda^2}{2} \sum_j \sum_k \sum_l p_j p_k p_l\, v_{00_{j;kl}}(t-i+1)$$

$$+ P^{11}(i)\left(\frac{1-\lambda}{2}\right)^2 \sum_j \sum_k \sum_l \sum_s p_j p_k p_l p_s\, \zeta_{00_{jk;ls}}(t-i+1),$$

$$1 \le i \le n \qquad (21)$$

$$\psi_{00_{ij}}(t+1) = \frac{1+\lambda}{2} \sum_k p_k\, \psi_{00_{k,j-i}}(t-i+1) + \frac{1-\lambda}{2} \sum_k \sum_l p_k p_l\, v_{00_{j-i;kl}}(t-i+1),$$

$$1 \le i < j \le n\,. \qquad (22)$$

Just as in the one-locus situation, numerical work will require the storing of measures for n years when equations (21) and (22) are used. Unlike the one-locus case, however, we cannot rearrange things to arrive at a set of equations that 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

$$\psi_{00_{ij}}(t+1) = \psi_{00_{i-1,j-1}}(t), \quad 1 < i,j \leq n , \tag{23}$$

and the cases for $i = 1$ follow directly from (21) and (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 (1969), trigametic and quadrigametic set measures are first expressed as average individual measures, which in turn are expanded back to gametic set measures. We now list the resulting set of transition equations for gametic set measures in the special case of equal age-class sampling probabilities

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

$$v_{00_{1;11}}(t+1) = \left[\frac{1}{4}P^3(1) + \frac{1+\lambda}{12}P^{21}(1)\right] \sum_i \sum_j p_i p_j \psi_{00_{ij}}(t)$$

$$+ \left[\frac{1}{2}P^{21}(1) + \frac{1+\lambda}{2}P^{111}(1)\right] \sum_i \sum_j \sum_k p_i p_j p_k v_{00_{i;jk}}(t)$$

$$+ \frac{1-\lambda}{2}\left[\frac{1}{6}P^{21}(1) + P^{111}(1)\right] \sum_i \sum_j \sum_k \sum_l p_i p_j p_k p_l \zeta_{00_{ij;kl}}(t), \tag{24}$$

$$v_{00_{1;1j}}(t+1) = \left[\frac{1}{2}P^2(1) + \frac{1+\lambda}{2}P^{11}(1)\right] \sum_i \sum_k p_i p_k v_{00_{i;k,j-1}}(t)$$

$$+ \frac{1-\lambda}{2}P^{11}(1) \sum_i \sum_k \sum_l p_i p_k p_l \zeta_{00_{ik;l,j-1}}(t), \quad 1 < j \leq n , \tag{25}$$

$$v_{00_{j;11}}(t+1) = \frac{1}{2}P^2(1)\sum_i p_i \psi_{00_{i,j-1}}(t)$$

$$+ \left[1 - \frac{1}{2}P^2(1)\right]\sum_i\sum_k p_ip_k v_{00_{j-1,ik}}(t), \quad 1 < j \le n, \tag{26}$$

$$v_{00_{1;jk}}(t+1) = \frac{1+\lambda}{2}\sum_i p_i v_{00_{i;j-1,k-1}}(t) + \frac{1-\lambda}{2}\sum_i\sum_l p_ip_l \zeta_{00_{il;j-1,k-1}}(t),$$
$$1 < j,k \le n, \tag{27}$$

$$v_{00_{j;1k}}(t+1) = \sum_i p_i v_{00_{j-1;i,k-1}}(t), \quad 1 < j,k \le n, \tag{28}$$

$$v_{00_{i;jk}}(t+1) = v_{00_{i-1;j-1,k-1}}(t), \quad 1 < i,j,k \le n, \tag{29}$$

$$\zeta_{00_{11;11}}(t+1) = \frac{1}{4}\left[P^4(1) + \frac{2}{3}P^{22}(1)\right]\sum_i\sum_j p_ip_j \psi_{00_{ij}}(t)$$

$$+ \left[\frac{1}{2}P^{31}(1) + \frac{1}{3}P^{22}(1) + \frac{1}{3}P^{211}(1)\right]\sum_i\sum_j\sum_k p_ip_jp_k v_{00_{i;jk}}(t)$$

$$+ \left[\frac{1}{4}P^{22}(1) + \frac{1}{2}P^{211}(1) + P^{1111}(1)\right]\sum_i\sum_j\sum_k\sum_l p_ip_jp_kp_l \zeta_{00_{ij;kl}}(t), \tag{30}$$

$$\zeta_{00_{11;1j}}(t+1) = \left[\frac{1}{2}P^3(1) + \frac{1}{3}P^{21}(1)\right]\sum_i\sum_k p_ip_k v_{00_{i;k,j-1}}(t)$$

$$+ \left[\frac{1}{2}P^{21}(1) + P^{111}(1)\right]\sum_i\sum_k\sum_l p_ip_kp_l \zeta_{00_{ik;l,j-1}}(t),$$
$$1 < j \le n, \tag{31}$$

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

$$+ \left[1 - \frac{1}{2}P^2(1)\right]\sum_i\sum_l p_ip_l \zeta_{00_{il;j-1,k-1}}(t), \quad 1 < j,k \le n, \tag{32}$$

$$\zeta_{00_{1j;1k}}(t+1) = \left[1 - \frac{1}{2}P^2(1)\right]\sum_i\sum_l p_ip_l \zeta_{00_{i,j-1;l,k-1}}(t), \quad 1 < j,k \le n, \tag{33}$$

$$\zeta_{00_{1j;kl}}(t+1) = \sum_i p_i \zeta_{00_{i,j-1;k-1,l-1}}(t), \quad 1 < j,k,l \le n, \tag{34}$$

$$\zeta_{00_{ij;kl}}(t+1) = \zeta_{00_{i-1,j-1;k-1,l-1}}(t), \quad 1 < i,j,k,l \le n. \tag{35}$$

Since we assume equal inbreeding at each locus, the following equalities hold
$$v_{00_{i;jk}} = v_{00_{i;kj}}, \quad 1 \le i,j,k \le n,$$

$$\zeta_{00_{ij;kl}} = \zeta_{00_{il;kj}} = \zeta_{00_{kj;il}} = \zeta_{00_{kl;ij}}$$

$$= \zeta_{00_{ji;lk}} = \zeta_{00_{li;jk}} = \zeta_{00_{jk;li}} = \zeta_{00_{lk;ji}}, \quad 1 \le i,j,k,l \le n$$

so that equations (21) to (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 (24), (30), and (21) with $i=1$ are needed. These reduce to the equations given previously (WEIR and COCKERHAM 1969).

Two-locus numerical results

The smallest population for which all possible types of two-locus measures are required is the one of four age classes, each with four individuals. This is the example we considered to illustrate the one-locus case, and we retain the values of $p_i = \dfrac{1}{4}$, $P^2(i) = \dfrac{1}{4}$. The other probabilities needed have the values, for $i = 1,2,3,4$,

$$P^{11}(i) = \frac{3}{4}, \quad P^3(i) = \frac{1}{16}, \quad P^{21}(i) = \frac{9}{16}$$

$$P^{111}(i) = \frac{6}{16}, \quad P^4(i) = \frac{1}{64}, \quad P^{31}(i) = \frac{12}{64}$$

$$P^{22}(i) = \frac{9}{64}, \quad P^{211}(i) = \frac{36}{64}, \quad P^{1111}(i) = \frac{6}{64}.$$

In Table 2 we display two-locus inbreeding coefficients $F_{11}(t)$ for this population for a range of linkage values. For $\lambda = 1$, the values have already been displayed as $F_1(t)$ in Table 1. In Table 2 we also show 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 system.

TABLE 2

Inbreeding coefficients for monoecious populations:
Four individuals in each of four age classes; two-locus case

t (Year)	$F_{11}(t)$				$\eta_{11}(t)$
	$\lambda = 0$	$\lambda = 1/4$	$\lambda = 1/2$	$\lambda = 3/4$	$\lambda = 0$
0	0.0000	0.0000	0.0000	0.0000	0.0000
1	0.0156	0.0166	0.0195	0.0244	0.0146
2	0.0193	0.0213	0.0259	0.0336	0.0173
3	0.0231	0.0263	0.0330	0.0441	0.0194
4	0.0272	0.0316	0.0406	0.0558	0.0209
5	0.0317	0.0373	0.0486	0.0684	0.0215
10	0.0547	0.0620	0.0783	0.1133	0.0197
15	0.0880	0.0949	0.1116	0.1537	0.0170
20	0.1286	0.1347	0.1501	0.1935	0.0144
50	0.4177	0.4200	0.4263	0.4496	0.0051
100	0.7608	0.7613	0.7624	0.7674	0.0009
r	0.0400	0.0399	0.0395	0.0380	

The limiting inbreeding rates, r, also given in Table 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 with 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.

DIOECIOUS DIPLOIDS

Mating scheme

We now consider a diploid population which consists of $\mathcal{M}$ males and $\mathcal{F}$ females, with m male and f female age classes. We use "age class i" to 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 $\mathcal{M}_i$ and $\mathcal{F}_i$ for males and females respectively, so that

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

Each year $\mathcal{M}_1 + \mathcal{F}_{m+1}$ newborns enter the population, while death claims all $\mathcal{M}_m$ m-year-old males, all $\mathcal{F}_{m+f}$ f-year-old females, and a random sample of $\mathcal{M}_i - \mathcal{M}_{i+1}$ ($1 \leq i \leq m-1$) i-year-old males and $\mathcal{F}_{m+i} - \mathcal{F}_{m+i+1}$ ($1 \leq i \leq f-1$) 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

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

For sampling of gametes within age classes, we will assume a combined sampling plan (WEIR and COCKERHAM 1969). 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 us to identify gametic sampling probabilities and gametic set measures according to the age classes that receive the gametes as well as those that give them. In this treatment then we can use the same type of sampling probabilities $P(i)$ within age classes as we used in the monoecious case.

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

$$F_{1_i}(t+1) = 4 \sum_{j=1}^{m} \sum_{k=m+1}^{m+f} p_{ij}p_{ik}\, \psi_{1_{jk}}(t) \ , \quad i = 1, m + 1 \ . \tag{36}$$

The calculation of $F_{1_i}(t)$ now rests on the establishment of a set of transition equations for the gametic set measures $\psi_{1_{ij}}(t)$. 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:

$$\psi_{1_{1,m+1}}(t+1) = \sum_{i=1}^{m+f} \sum_{j=1}^{m+f} p_{1i}p_{m+1,j}\, \psi_{1_{ij}}(t) \tag{37}$$

$$\psi_{1_{ij}}(t+1) = \sum_{k=1}^{m+f} p_{ik}\, \psi_{1_{k,j-1}}(t), \ i = 1, m + 1; \ 2 \leq j \leq m + f; \ j \neq m + 1 \tag{38}$$

$$\psi_{1_{ij}}(t+1) = \psi_{1_{i-1,j-1}}(t), \quad 2 \leq i,j \leq m + f; \ i,j \neq m + 1; \ i \neq j \ . \tag{39}$$

As in the monoecious case, we can take equation (39) back until members of the first age class in either sex are involved. For example

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

but it is probably more convenient to use (39).

Two gametes from the same age class require the introduction of average indi-

vidual measures again. Corresponding to equations (2) and (4), we have

$$\psi_{1_{ii}}(t+1) = P^2(i)\,\theta_{1_{I_iI_i}}(t+1) + P^{11}(i)\,\theta_{1_{I_iI_i'}}(t+1), \quad 1 \le i \le m+f \quad (40)$$

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

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

where, from now on, we use

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

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:

$$\theta_{1_{I_iI_i}}(t+1) = [1 + 4 \sum_{j=1}^{m} \sum_{k=m+1}^{m+f} p_{i*j} p_{i*k}\, \psi_{1_{jk}}(t-i+i^*)]/2, \quad 1 \le i \le m+f \ . \quad (41)$$

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

$$\theta_{1_{I_iI_i'}}(t+1) = \sum_{j=1}^{m+f} \sum_{k=1}^{m+f} p_{i*j} p_{i*k}\, \psi_{1_{jk}}(t-i+i^*), \quad 1 \le i \le m+f. \quad (42)$$

Combining equations (40) to (42) gives the remaining gametic set measure transition equation

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

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

$$1 \le i \le m+f \ . \quad (43)$$

As in the monoecious case, simplification results when sampling probabilities are the same for every age class. Then (43) is appropriate as it stands for $i = 1, m+1$ but otherwise can be replaced by

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

The set of equations (37) to (39) and (43) generalize those of JOHNSON (1977) and in the discrete-generation case of $m = f = 1$ reduce to

$$\psi_{1_{11}}(t+1) = \{P^{11}(1)\,[\psi_{1_{11}}(t) + \psi_{1_{22}}(t)] + 2\psi_{1_{12}}(t) + 2P^2(1)\}/4$$

$$\psi_{1_{22}}(t+1) = \{P^{11}(2)\,[\psi_{1_{11}}(t) + \psi_{1_{22}}(t)] + 2\psi_{1_{12}}(t) + 2P^2(2)\}/4$$

$$\psi_{1_{12}}(t+1) = [\psi_{1_{11}}(t) + \psi_{1_{22}}(t) + 2\psi_{1_{12}}(t)]/4$$

with the usual equation for $F_1(t) = \psi_{1_{12}}(t-1)$:

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

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

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

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

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

Equations (36) to (39), (43) then provide

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

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

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

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 $\bar{F}_1(t)$ for newborn in year t as a weighted average of the coefficients in each sex:

$$\bar{F}_1(t) = [\mathcal{M}_1 F_{1_1}(t) + \mathcal{I}_{m+1}F_{1_{m+1}}(t)]/(\mathcal{M}_1 + \mathcal{I}_{m+1}) .$$

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 then we define the per-year effective population size as

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

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

$$r(t) = \frac{F_1(t) - F_1(t-1)}{1 - \bar{F}_1(t-1)} .$$

For discrete generations this becomes

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

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).

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

One-locus numerical results

To illustrate the progress of inbreeding for dioecious populations with age structure, we 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 $\mathcal{M}_i = \mathcal{I}_i = 4$, $2 \leq i \leq 5$. We assume a multinomial distribution for progeny numbers, both between and within age classes $(p_{i1} = \frac{1}{2}, \, p_{ij} = \frac{1}{8}$, for $i = 1,2$ and $2 \leq j \leq 5$ while $P^2(i) = \frac{1}{4}$ for $1 \leq i \leq 5)$. All individuals in the initial $(t = 0)$ population are assumed to be not inbred and unrelated.

The transition equations (37) to (39) and (43) then provide

$$\psi_{1_{ii}}(t+1) = \frac{3}{16} \psi_{1_{11}}(t) + \frac{1}{8} \sum_{j=2}^{5} \psi_{1_{1j}}(t) + \frac{3}{256} \sum_{j=2}^{5} \sum_{k=2}^{5} \psi_{1_{jk}}(t) + \frac{1}{8} , \quad i = 1,2$$

$$\psi_{1_{12}}(t+1) = \frac{1}{4} \psi_{1_{11}}(t) + \frac{1}{8} \sum_{j=2}^{5} \psi_{1_{1j}}(t) + \frac{1}{64} \sum_{j=2}^{5} \sum_{k=2}^{5} \psi_{1_{jk}}(t)$$

$$\psi_{1_{ij}}(t+1) = \frac{1}{2} \psi_{1_{1,j-1}}(t) + \frac{1}{8} \sum_{k=2}^{5} \psi_{1_{k,j-1}}(t) , \quad i = 1,2; j = 3,4,5$$

$$\psi_{1_{ij}}(t+1) = \psi_{1_{i-1,j-1}}(t) , \quad 3 \leq i,j \leq 5 .$$

In each year there are 15 distinct-valued measures, or a total of 25 measures, four of which contribute to the inbreeding coefficient in male or female offspring

$$F_{1_i}(t+1) = \frac{1}{4} \sum_{j=2}^{5} \psi_{1_{1j}}(t) , \quad i = 1,2 .$$

In Table 3 we show the one-locus inbreeding coefficient and the approximate values obtained by the method of JOHNSON (1977).

Two-locus case

Two-locus measures can be defined as in the monoecious case and the two-locus inbreeding coefficient found for newborn individuals in any year. Complete details are given by CHOY (1978) and are available from the authors.

<div align="center">DISCUSSION</div>

We have given a general and exact treatment of the determination of inbreeding coefficients at one or two loci in populations with overlapping generations.

TABLE 3

Inbreeding coefficients for dioecious populations:
Four individuals in each of one male and four female age classes; one-locus case

t (Year)	$F_1(t)$ (Exact)	$F_1(t)$ (Approx.)
0	0.0000	0.0000
1	0.0000	0.0000
2	0.0215	0.0215
3	0.0386	0.0396
4	0.0557	0.0582
5	0.0749	0.0795
10	0.1614	0.1817
15	0.2398	0.2837
20	0.3108	0.3858
50	0.6174	0.9980
100	0.8566	2.0184
r	0.0194	0.0204

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 we need digametic, trigametic and quadrigametic measures.

Linear transition equations between gametic set measures are established, and this suggests that standard matrix techniques could be employed to discuss the behavior 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 that there is no real loss.

We suggest 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 behavior of such populations is required, then effective numbers may be sufficient and in some cases we may use approximate values of such numbers. We now turn to a consideration of exact and approximate effective numbers.

Inbreeding effective numbers for Poisson family sizes

We have already 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. We can use our exact results here to check on such approximations. In particular we wish to investigate 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

$$N_g = (4\mathcal{N}_1 - 2) \, L/(\sigma_n^2 + 2) \tag{44}$$

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 $(1 \leq j \leq \mathcal{N}_1, \ 1 \leq i \leq n)$. 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

$$g_j \sim B\left(2\mathcal{N}_1, \frac{1}{\mathcal{N}_1}\right) \ , \quad \sigma_n^2 = 2\left(1 - \frac{1}{\mathcal{N}_1}\right)$$

so that

$$N_g = \mathcal{N}_1 L, \quad N_y = \mathcal{N}_1 L^2 \ .$$

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

$$N_g = (n+1) \, \mathcal{N}_1/2, \quad N_y = (n+1)^2 \, \mathcal{N}_1/4 \ . \tag{45}$$

Now equation (45) is for the case we have referred to as equal chance gamete formation. In our numerical example we set $n = \mathcal{N}_1 = 4$, so that (45) gives $N_y = 25$ while the exact result, from Table 1, is $N = 24.62$. There is a very good agreement between exact and approximate effective numbers for Poisson family sizes. These approximate results also follow from the work of FELSENSTEIN (1971).

Inbreeding effective numbers for constant family sizes

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

$$\mathcal{N}_g = (2\mathcal{N}_1 - 1) \, L \ . \tag{46}$$

For exact inbreeding levels and effective sizes, however, it is not sufficient to consider only lifetime family sizes. We saw that the gametic set measure transition equations required knowledge of within-age-class sampling probabilities, which means that we need to know annual family sizes.

Some numerical cases for small monoecious populations were considered by CHOY (1978). In the examples, lifetime family sizes were set equal to two for every newborn individual in every year but annual contributions were varied. Mating schemes, admittedly extreme, can be constructed to give effective numbers quite different from the approximate result (46). Overall however, provided random gametic union is preserved, result (46) is quite good and can be used with confidence provided it is remembered that effective numbers may not reflect actual inbreeding levels in early generations.

Inbreeding effective numbers for dioecious populations

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

$$N_y = \frac{4L^2 \mathcal{M}_1 \mathcal{F}_1}{\mathcal{M}_1 + \mathcal{F}_1} \ . \tag{47}$$

In our numerical example, $\mathcal{M}_1 = \mathcal{F}_1 = 4$ and $L = 1.75$ to give the approximate value $N_y = 24.50$ while, from Table 2, we find the exact value $N_y = 25.77$. Agreement is still good for Poisson lifetime family sizes.

For fixed equal family sizes, HILL doubles the value in (47) and again 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 were illustrated for some small populations by CHOY (1978).

There is another possibility for dioecious populations. Family sizes may be Poisson in one sex but constant in the other. In a beef cattle selection scheme at North Carolina State University, the best son of each sire is selected so that males contribute exactly one gamete to male offspring per lifetime. Other gametic contributions need not be fixed, however, and we could envision situations where there were Poisson lifetime family sizes for female offspring from males and females. Annual family sizes for the cattle scheme though would generally be zero or one for females.

We pursue the North Carolina scheme to illustrate how constant family sizes can be handled. Because matings in this scheme were also made in such a way as to ensure minimum inbreeding, we will suppose for illustration that all individuals give exactly **two gametes** per lifetime.

For the control herd we further simplify matters by supposing that there are three age classes of males and four age classes of females every year. All these classes contain three individuals. The three oldest males mate each year and are replaced in the following year by one son each. Each of these breeding males

also leaves one daughter in the following year. The offspring for the three females born in year t are as follows:

Female Number	Son in Year	Daughter in Year
		Offspring
1	$t+2$	$t+3$
2	$t+3$	$t+4$
3	$t+4$	$t+2$

In other words, males are mated three years after birth, and females mated at two, three and four years after birth.

As we now need to keep a strict accounting of annual gametic contributions, the sampling probabilities $P(i)$ and gametic set measures are not appropriate and we use another type of individual measure. For the one-locus case it is sufficient to define the digametic measure

$$\phi(i,j;k,l)_t = \phi(k,l;i,j)_t$$

as the probability of identity by descent of a gene from the jth member of age class i and 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. We retain $F_1(t)$ for the inbreeding coefficient in year t.

Every breeding male (age class 3) in year t gives one gamete to the male offspring and one gamete to the female offspring. In female age class i ($5 \leq i \leq 7$) female $i - 4$ gives a gamete to the male offspring and female $i^\dagger$ ($= [3i^2 - 37i + 116]/2$) gives a gamete to the female offspring. Male and female gametes combine at random. The inbreeding coefficients for newborn males and females are written as $F_{1_1}(t)$ and $F_{1_4}(t)$, respectively.

The required transition equations are as follows:

$$9F_{1_1}(t+1) = \sum_{i=1}^{3} \sum_{j=5}^{7} \phi(3,i;j,j-4)_t$$

$$9F_{1_4}(t+1) = \sum_{i=1}^{3} \sum_{j=5}^{7} \phi(3,i;j,j^\dagger)_t$$

$$2\phi(1,i;1,i)_{t+1} = 1 + F_{1_1}(t+1) \ , \quad 1 \leq i \leq 3$$

$$2\phi(4,i;4,i)_{t+1} = 1 + F_{1_4}(t+1) \ , \quad 1 \leq i \leq 3$$

$$36\phi(1,i;1,j)_{t+1} = 3 \sum_{k=1}^{2} \sum_{l=k+1}^{3} \phi(3,k;3,l)_t + 3 \sum_{k=5}^{6} \sum_{l=k+1}^{7} \phi(k,k-4;l,l-4)_t$$

$$+ 2 \sum_{k=1}^{3} \sum_{l=5}^{7} \phi(3,k;l,l-4)_t \ , \quad 1 \leq i < j \leq 3$$

$$36\phi(4,i;4,j)_{t+1} = 3 \sum_{k=1}^{2} \sum_{l=k+1}^{3} \phi(3,k;3,l)_t + 3 \sum_{k=5}^{6} \sum_{l=k+1}^{7} \phi(k,k^\dagger;l,l^\dagger)_t$$

$$+ 2 \sum_{k=1}^{3} \sum_{l=5}^{7} \phi(3,k;l,l^\dagger)_t \ , \quad 1 \leq i < j \leq 3$$

$$36\phi(1,i;4,j)_{t+1} = \sum_{k=1}^{3} \sum_{l=1}^{3} \phi(3,k;3,l)_t + \sum_{k=5}^{7} \sum_{l=5}^{7} \phi(k,k-4;l,l^\dagger)_t$$

$$+ \sum_{k=1}^{3} \sum_{l=5}^{7} [\phi(3,k;l,l^\dagger)_t + \phi(l,l-4;3,k)_t] , \quad 1 \le i,j \le 3$$

$$6\phi(1,i;j,k)_{t+1} = \sum_{l=1}^{3} \phi(3,l;j-1,k)_t + \sum_{l=5}^{7} \phi(l,l-4;j-1,k)_t , \quad \begin{array}{l} 1 \le i,k \le 3 \\ j \ne 1, j \ne 4 \end{array}$$

$$6\phi(i,j;4,k)_{t+1} = \sum_{l=1}^{3} \phi(i-1,j;3,l)_t + \sum_{l=5}^{7} \phi(i-1,j;l,l^\dagger) , \quad \begin{array}{l} 1 \le j,k \le 3 \\ i \ne 1, i \ne 4 \end{array}$$

$$\phi(i,j;k,l)_{t+1} = \phi(i-1,j;k-1,l)_t , \quad \begin{array}{l} 1 \le j,l \le 3 \\ i,k \ne 1, i,k \ne 4 \end{array} .$$

In Table 4 we display the inbreeding coefficient $F_1(t) = F_{1_1}(t) = F_{1_4}(t)$ for this system. The inbreeding rate $r = 0.0048$ shown there leads to an annual inbreeding effective population size of 103.97. The generation length is $L = 3$ years, so that HILL's approximate effective size is 108. Good agreement is again found, although as we have stresssed and as JOHNSON (1977) suggests, inbreeding coefficients based on $N_y = 108$ will be misleading in early generations. Such approximate values are also shown in Table 4.

As the examples considered by CHOY (1978) show, the onset of inbreeding may be delayed by various non-random mating schemes. This is at the expense of higher later inbreeding and effective population sizes which are markedly lower than the approximations. For this reason it is important to remember that HILL's result is derived and stated for random mating situations.

TABLE 4

One-locus inbreeding coefficients for dioecious population:
Three individuals in each of three male and four female age classes;
Two gametes per individual per lifetime

t (Year)	$F_1(t)$ (Exact)	$F_1(t)$ (Based on $N_y = 108$)
0	0.0000	0.0000
1	0.0000	0.0046
2	0.0000	0.0092
3	0.0000	0.0138
4	0.0231	0.0184
5	0.0231	0.0229
10	0.0461	0.0453
15	0.0679	0.0672
20	0.0903	0.0886
50	0.2128	0.2071
100	0.3814	0.3713
r	0.0048	0.0046

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

$$\sigma_{\hat{p}}^2 = \theta_l\, p(1-p) \ .$$

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 group coancestry and inbreeding coefficients are the same, as are the inbreeding and variance effective numbers. The annual change of gene frequency variance follows:

$$\sigma_{\hat{p}}^2(t) = \left[1 - \left(\frac{2N_y-1}{2N_y}\right)^t \right] p(1-p) \ .$$

We refer to COCKERHAM (1969, 1970) for cases such as maximum avoidance of inbreeding where the group coancestry and inbreeding coefficients are different.

CONCLUSION

The study of inbreeding in populations with overlapping generations has always stopped short of an exact treatment, probably because of the apparent complexity. We have shown in this paper that very general equations can be written that allow inbreeding coefficients to be determined. The equations are well suited to computer iteration, and we recommend that they be used in cases where inbreeding coefficients or variances of gene frequencies are required.

In large populations, or in very long-term situations, it appears that published approximate values of inbreeding or variance effective numbers may be used with fair confidence. For small populations and in early generations, however, we caution against their use and again recommend an exact treatment. Exact treatments should also be used when union of gametes is not random.

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