

On the maximum avoidance of inbreeding*

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1. INTRODUCTION

In his classical 1921 paper Sewall Wright determined the decrease in heterozygosity in successive generations with various mating systems. Some systems, such as regular mating of double first cousins in a population of 4, quadruple second cousins in a population of 8, octuple third cousins in a population of 16, etc., have the property that the matings are between individuals that are least related. Wright designated such systems as having maximum avoidance of inbreeding.

It might be thought that such systems would lead to the minimum decrease of heterozygosity, but this is not generally true. Although the 'maximum avoidance' systems have the slowest initial rate of decrease of heterozygosity, there are other systems which have more remaining heterozygosity in later generations. The purpose of this article is to discuss some mating systems for which this is true.

Inbreeding has two related, but distinct effects. One is the decrease in average heterozygosity; the other is random drift in gene frequencies. A system that minimizes one of these processes is not necessarily minimum for the other. We shall consider first some systems that have very slow ultimate rates of decrease in heterozygosity, and compare these with those having maximum avoidance of inbreeding. Later, in section 6, we shall consider systems that minimize gene frequency drift.

Other things being comparable, either kind of inbreeding effect will be less when the number of progeny per parent is constant. We shall consider only mating systems in which this is true; we assume that the number of progeny per parent (or per pair) is exactly two each generation so that the population size remains constant.

Figures 1, 2, and 3 illustrate the three principal systems of mating to be compared for a population of size 8. Figure 1 shows maximum avoidance of inbreeding (quadruple second cousins), Figs. 2 and 3 show, respectively, the systems that we shall call circular mating and circular pair mating.

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2. CIRCULAR MATING

In the simplest system to be considered, n males and n females are arranged alternately so that each individual is mated with its neighbour. The last individual is mated with the first, so that the system is most easily visualized as circular. Under this system, each individual after the second generation is the product of a half-sib mating. Figure 2 illustrates continued circular mating for the case, $n = 4$.

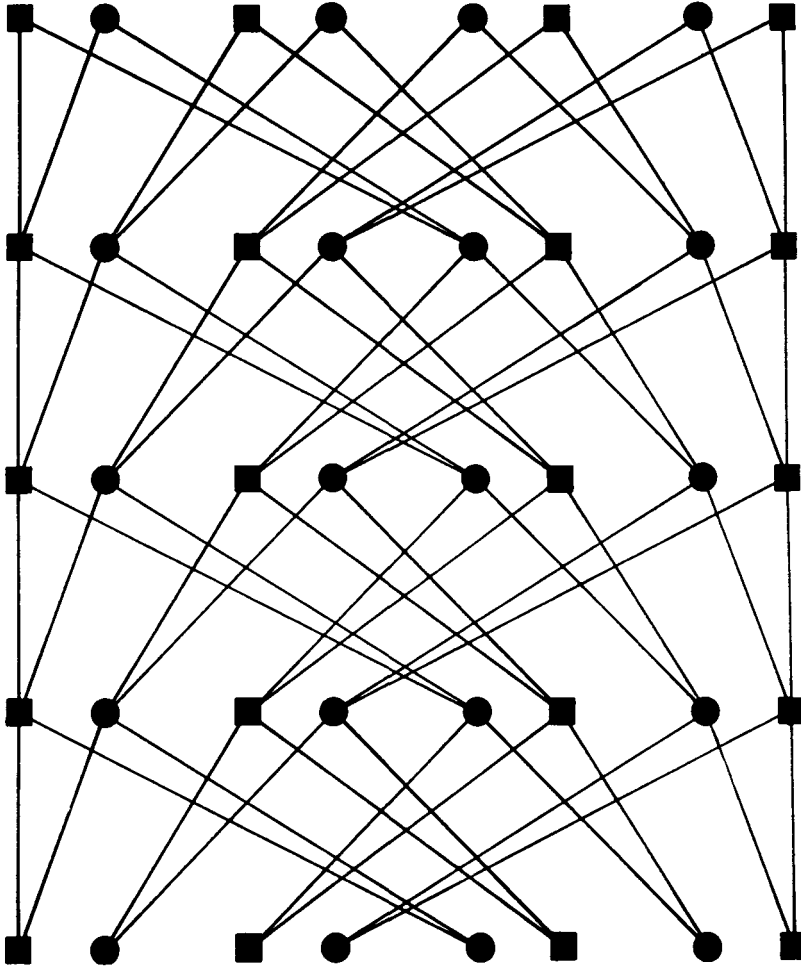


Fig. 1. Maximum avoidance of inbreeding in a population of constant size 8. This and the other pedigrees are to be read down; the oldest generation is at the top.

Let the total number of individuals in a generation be $N = 2n$. We designate by I_t the probability that two homologous loci in an individual in generation t ($t = 0, 1, 2, \dots$) share the same allele; that is, that an individual is homozygous for any one of the possible alleles at this locus. Similarly, let $J_t(1)$ be the probability that two randomly chosen homologous genes in two adjacent individuals in the t^{th} generation share the same allele. In general, let $J_t(k)$ be the similar probability

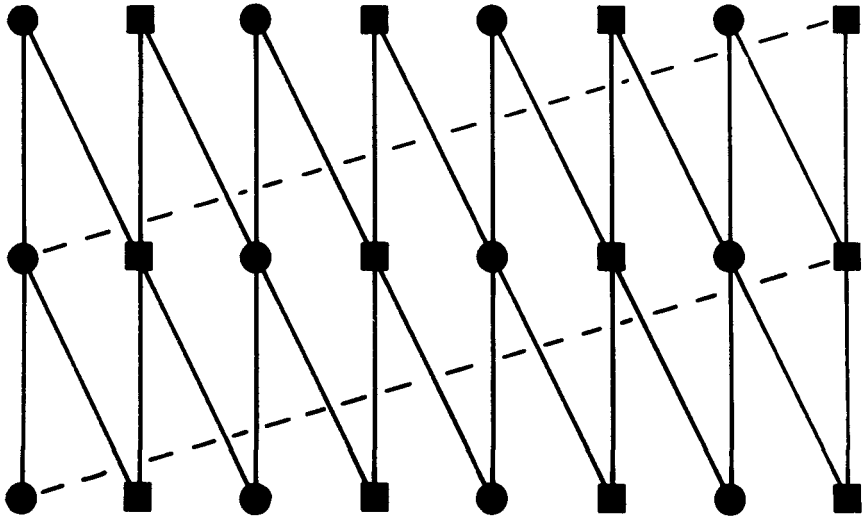


Fig. 2. Circular mating in a population of size 8.

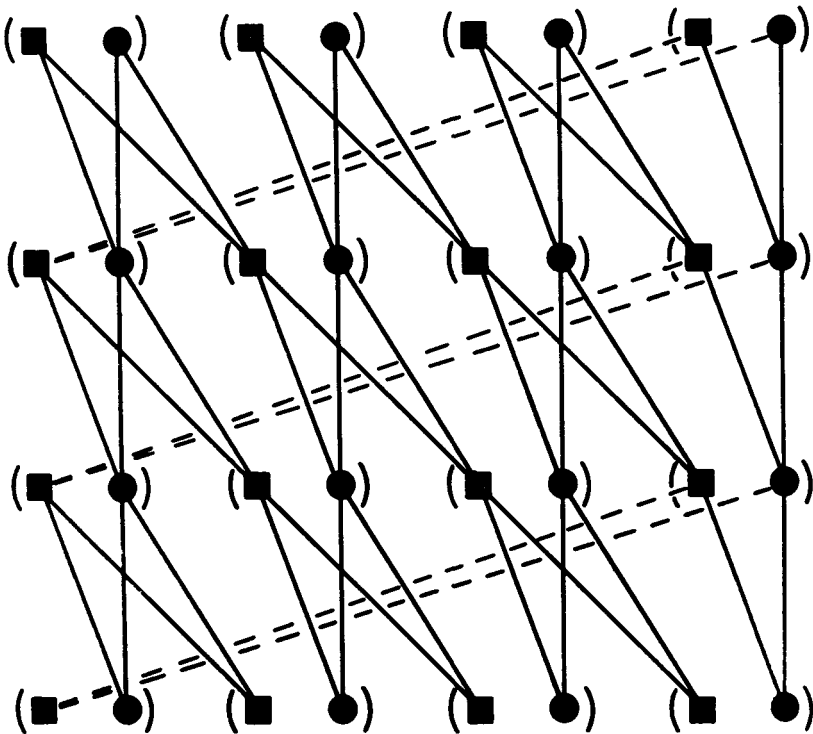


Fig. 3. Circular pair mating in a population of size 8 (4 pairs). Parentheses designate cages, and the animals are shown in the cages at the time of mating.

that two homologous genes in individuals k steps removed are identical ($k = 1, 2, \dots, 2n - 1$). Note that because of the circular arrangement $J_i(k) = J_i(2n - k)$. We then have:

$$I_t = J_{t-1}(1) \tag{2.1}$$

$$J_t(1) = \frac{1}{4}[\frac{1}{2}(1 + I_{t-1}) + 2J_{t-1}(1) + J_{t-1}(2)] \tag{2.2}$$

$$J_t(2) = \frac{1}{4}[J_{t-1}(1) + 2J_{t-1}(2) + J_{t-1}(3)] \tag{2.3}$$

$$J_t(k) = \frac{1}{4}[J_{t-1}(k-1) + 2J_{t-1}(k) + J_{t-1}(k+1)] \quad (n-1 \geq k \geq 2) \tag{2.4}$$

$$J_t(n-1) = \frac{1}{4}[J_{t-1}(n-2) + 2J_{t-1}(n-1) + J_{t-1}(n)] \tag{2.5}$$

$$J_t(n) = \frac{1}{2}[J_{t-1}(n-1) + J_t(n)] \tag{2.6}$$

The first relation (2.1) follows immediately from the fact that two homologous genes in an individual are derived from two adjacent individuals in the preceding generation. The second relation (2.2) is derived from the consideration that two homologous genes, taken one from each of the adjacent individuals, are derived from the same parent with probability 1/4, from two adjacent individuals with probability 1/2 and from two individuals two steps removed with probability 1/4. When they are derived from the same individual, they either come from the same gene or from two homologous genes with equal probability of 1/2. In the former case the probability is 1 that they share the same allele, while in the latter case, the probability is I_{t-1} by definition. Relations (2.3) to (2.5) are derived from similar considerations and (2.6) follows from (2.4) by putting $k = n$ and noting that $J_t(n-1) = J_t(n+1)$.

The heterozygosity at time t is proportional to $H_t = 1 - I_t$. From the above relations the proportion of heterozygosity can be worked out in successive generations. This was done by digital computer. The heterozygosity as a proportion of the initial value is shown for populations of size $N = 4, 8, 16,$ and 32 in Table 1, along with the corresponding changes for maximum avoidance and for circular pair mating. In each case it will be seen that circular mating has a more rapid initial loss of heterozygosity, but that eventually the rate of loss is much less.

Relations (2.1) through (2.6) may easily be expressed in matrix form by letting $H_t = 1 - I_t$ and $K_t(k) = 1 - J_t(k)$. This is given by

$$\begin{bmatrix} H_t \\ K_t(1) \\ K_t(2) \\ \vdots \\ K_t(n-2) \\ K_t(n-1) \\ K_t(n) \end{bmatrix} = \begin{bmatrix} 0 & 1 & 0 & 0 & 0 & \dots & 0 & 0 & 0 & 0 \\ \frac{1}{8} & \frac{1}{2} & \frac{1}{4} & 0 & 0 & \dots & 0 & 0 & 0 & 0 \\ 0 & \frac{1}{4} & \frac{1}{2} & \frac{1}{4} & 0 & \dots & 0 & 0 & 0 & 0 \\ \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots \\ \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots \\ 0 & 0 & 0 & 0 & 0 & \dots & \frac{1}{4} & \frac{1}{2} & \frac{1}{4} & 0 \\ 0 & 0 & 0 & 0 & 0 & \dots & 0 & \frac{1}{4} & \frac{1}{2} & \frac{1}{4} \\ 0 & 0 & 0 & 0 & 0 & \dots & 0 & 0 & \frac{1}{2} & \frac{1}{2} \end{bmatrix} \begin{bmatrix} H_{t-1} \\ K_{t-1}(1) \\ K_{t-1}(2) \\ \vdots \\ K_{t-1}(n-2) \\ K_{t-1}(n-1) \\ K_{t-1}(n) \end{bmatrix} \tag{2.7}$$

Table 1. Decrease in heterozygosity with maximum avoidance of inbreeding (M), circular pair mating (CP), and circular mating (C) in populations of size 4, 8, 16, and 32. The value given is H_t/H_0 , where H_t is the heterozygosity in generation t . $1 - \lambda$ is the asymptotic rate of decrease in heterozygosity per generation

t	$N = 4$		$N = 8$			$N = 16$			$N = 32$		
	M, CP	C	M	CP	C	M	CP	C	M	CP	C
0	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
1	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
2	1.000	0.875	1.000	1.000	0.875	1.000	1.000	0.875	1.000	1.000	0.875
3	0.875	0.813	1.000	0.938	0.813	1.000	0.938	0.813	1.000	0.938	0.813
4	0.813	0.750	0.938	0.906	0.758	1.000	0.906	0.758	1.000	0.906	0.758
5	0.750	0.695	0.906	0.875	0.715	0.969	0.879	0.715	1.000	0.879	0.715
10	0.492	0.477	0.755	0.732	0.577	0.891	0.777	0.577	0.953	0.777	0.577
15	0.324	0.327	0.628	0.614	0.494	0.817	0.709	0.499	0.915	0.711	0.499
20	0.213	0.224	0.522	0.514	0.432	0.750	0.655	0.446	0.878	0.662	0.446
25	0.140	0.154	0.434	0.431	0.379	0.688	0.608	0.407	0.842	0.623	0.407
30	0.092	0.105	0.361	0.361	0.334	0.632	0.566	0.377	0.808	0.592	0.377
40	0.040	0.050	0.250	0.254	0.259	0.532	0.490	0.333	0.744	0.542	0.333
50	0.017	0.023	0.173	0.178	0.202	0.448	0.424	0.300	0.685	0.503	0.302
70	0.003	0.005	0.083	0.088	0.122	0.318	0.318	0.252	0.581	0.443	0.259
100	0.000	0.000	0.027	0.030	0.057	0.190	0.207	0.199	0.454	0.374	0.219
150			0.004	0.005	0.016	0.080	0.101	0.136	0.301	0.287	0.180
200			0.000	0.001	0.004	0.034	0.049	0.092	0.199	0.220	0.156
300				0.000	0.000	0.006	0.012	0.043	0.087	0.130	0.123
400						0.001	0.003	0.020	0.038	0.077	0.099
500							0.001	0.009	0.017	0.045	0.080
$1 - \lambda$	0.0804	0.0727	0.0362	0.0347	0.0249	0.0170	0.0142	0.0076	0.0082	0.0053	0.0021

We designate this $(n + 1) \times (n + 1)$ matrix by A . Also we designate $|A - \lambda I|$ by $F_n(\lambda)$, so that the characteristic equation of A is written as

$$F_n(\lambda) = |A - \lambda I| = 0$$

The ultimate ratio by which the frequency of heterozygotes decreases from one generation to the next is given by the largest root of this equation. For $N = 2, 4, 6$ and 8 , the characteristic equations and the corresponding dominant roots are as follows:

$$N = 2; \quad F_1(\lambda) = \lambda^2 - \frac{1}{2}\lambda - \frac{1}{4} = 0$$

$$\lambda = 0.8090$$

$$N = 4; \quad F_2(\lambda) = -\lambda^3 + \lambda^2 - \frac{1}{16} = 0$$

$$\lambda = 0.9273$$

$$N = 6; \quad F_3(\lambda) = \lambda^4 - \frac{3}{2}\lambda^3 + \frac{7}{16}\lambda^2 + \frac{3}{32}\lambda - \frac{1}{64} = 0$$

$$\lambda = 0.9606$$

$$N = 8; \quad F_4(\lambda) = -\lambda^5 + 2\lambda^4 - \frac{9}{8}\lambda^3 + \frac{1}{16}\lambda^2 + \frac{1}{16}\lambda - \frac{1}{256} = 0$$

$$\lambda = 0.9751$$

The case with $N = 2$ is ordinary brother-sister mating with recurrence relation $H_t = \frac{1}{2}H_{t-1} + \frac{1}{4}H_{t-2}$ for heterozygote frequencies (Wright, 1921). To compute the dominant root for a larger n , a more general treatment of the characteristic equation is required and this can be done as follows.

By expanding the determinant $|A - \lambda I|$ with respect to the first two and the last two rows, we get

$$F_n(\lambda) = -\lambda\left(\frac{1}{2} - \lambda\right)\left(\frac{1}{4}\right)^{n-1}\phi_{n-1}(2 - 4\lambda) + \left(\frac{\lambda}{4} - \frac{1}{16}\right)\left(\frac{1}{4}\right)^{n-2}\phi_{n-2}(2 - 4\lambda) + \left(\frac{1}{8}\right)^2\left(\frac{1}{4}\right)^{n-3}\phi_{n-3}(2 - 4\lambda), \tag{2.8}$$

where $\phi_n(\cdot)$ is an $n \times n$ determinant known as Wolstenholme's determinant, defined by

$$\phi_n(x) = \begin{vmatrix} x & 1 & 0 & 0 & \dots & 0 & 0 & 0 \\ 1 & x & 1 & 0 & \dots & 0 & 0 & 0 \\ 0 & 1 & x & 1 & \dots & 0 & 0 & 0 \\ \dots & \dots & \dots & \dots & \dots & \dots & \dots & \dots \\ \dots & \dots & \dots & \dots & \dots & \dots & \dots & \dots \\ 0 & 0 & 0 & 0 & \dots & 0 & 1 & x \end{vmatrix} \tag{2.9}$$

(cf. Rutherford, 1952). One of the important properties of this determinant is that if $x = -2 \cos \theta$, then

$$\phi_n(x) = (-1)^n \frac{\sin(n+1)\theta}{\sin \theta}. \tag{2.10}$$

Thus, if we put

$$2 - 4\lambda = -2 \cos \theta$$

or

$$\lambda = \frac{1}{2}(1 + \cos \theta) \tag{2.11}$$

then, (2.8) reduces to

$$F_n(\lambda) = \left(-\frac{1}{4}\right)^n [\sin \theta \sin n\theta - \cos n\theta]. \tag{2.12}$$

This shows that the dominant root and, indeed, all the roots of the characteristic equation are given by (2.11) with θ satisfying the equation.

$$\sin \theta = \frac{\cos n\theta}{\sin n\theta}. \tag{2.13}$$

Though (2.12) was derived by assuming $|A - \lambda I|$ has at least 4 rows, it turns out that (2.13) is valid for all $n \geq 1$.

For a large n , the following series expansion is useful to compute the dominant root:

$$\lambda = 1 - \frac{\pi^2}{16(n+1)^2} + \frac{\pi^4}{4!2^5(n+1)^4} + \dots \tag{2.14}$$

Since H_t is the probability that an individual in the t^{th} generation is heterozygous with respect to the locus under consideration, $1 - \lambda$ with λ given by (2.14) is equal to the rate of decrease of heterozygosity at the state of steady decay. As n becomes

large, the higher terms of the series decrease in absolute value very rapidly, so that for $n > 4$, the first two terms of the series are sufficient to evaluate the dominant root for any practical purpose. Thus we obtain

$$\lambda \approx 1 - \frac{\pi^2}{4(N+2)^2} \quad (N \rightarrow \infty) \tag{2.15}$$

Since it is known that $\lambda = 1 - (1/2N)$ for a randomly mating population of N breeding individuals, the above result shows that under circular individual mating the decrease of heterozygosity is extremely slow on a long-term basis. However it may be many generations before the superiority over other mating systems is manifest—so long that much of the heterozygosity is already lost.

For a monoecious organism, circular mating can be carried out among odd numbers of individuals, but we will not consider such a case in this paper.

3. CIRCULAR PAIR MATING

Although circular mating is extremely effective in slowing down the progress toward homozygosity in the long run, it is not a convenient mating system in practice because each individual has to be mated twice. A rather similar system is what we have called circular pair mating. This is illustrated for a population of 8 in Fig. 3. If the animals are thought of as being in four cages, indicated by parentheses, then in each generation a male is mated with a female in the cage to his right. This system, being monogamous, should be very convenient for insects or litter-bearing

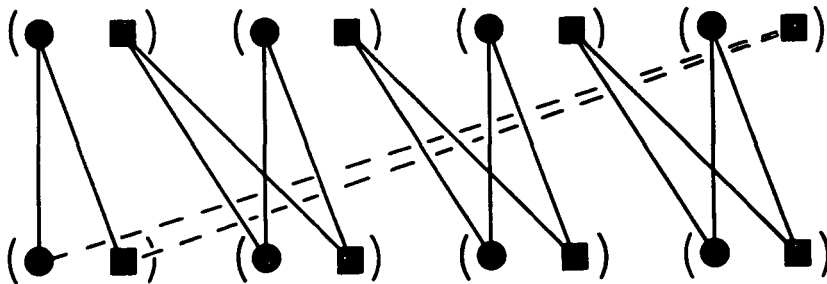


Fig. 4. Circular pair mating; same as Fig. 3 except that the animals are shown in cages at the time of birth.

mammals. It was suggested by J. B. S. Haldane in a personal communication to Professor Wright.

Figure 3 is drawn with the animals in their cages at the time of mating. For analytical purposes we have found it somewhat simpler to draw the pedigree with the animals in their positions at the time of birth, as shown in Fig. 4.

As before, let I_t be the probability that an individual in generation t is homozygous. Let $J_t(0)$ be the probability that the homologous genes taken one from each of the sibs born in the same cage in generation t are the same allele. Similarly, we will

denote by $J_t(k)$ the probability that two homologous genes taken one from each of two newly born individuals in cages k steps apart are identical alleles.

In circular pair mating, the number of pairs may be either even or odd. In the former case we will denote the number of pairs by $2n$ and in the latter by $2n + 1$.

First consider the even case ($2n$ pairs) where the total number of individuals is $N = 4n$. The recurrence relation connecting the I and J 's in two consecutive generations are as follows:

$$I_t = J_{t-1}(1) \tag{3.1}$$

$$J_t(0) = \frac{1}{2}[\frac{1}{2}(I_{t-1} + 1) + J_{t-1}(1)] \tag{3.2}$$

$$J_t(k) = \frac{1}{4}[J_{t-1}(k-1) + 2J_{t-1}(k) + J_{t-1}(k+1)] \quad (1 \leq k \leq n-1) \tag{3.3}$$

$$J_t(n) = \frac{1}{2}[J_{t-1}(n-1) + J_{t-1}(n)] \tag{3.4}$$

These are readily derived by arguments very similar to the ones through which (2.1)-(2.6) were derived.

Let $H_t = 1 - I_t$ and $K_t(k) = 1 - J_t(k)$, $k = 0, 1, 2, \dots, n$, then we have

$$\begin{bmatrix} H_t \\ K_t(0) \\ K_t(1) \\ K_t(2) \\ \cdot \\ \cdot \\ K_t(n-1) \\ K_t(n) \end{bmatrix} = \begin{bmatrix} 0 & 0 & 1 & 0 & 0 & \cdot & \cdot & 0 & 0 & 0 \\ \frac{1}{4} & 0 & \frac{1}{2} & 0 & 0 & \cdot & \cdot & 0 & 0 & 0 \\ 0 & \frac{1}{4} & \frac{1}{2} & \frac{1}{4} & 0 & \cdot & \cdot & 0 & 0 & 0 \\ 0 & 0 & \frac{1}{4} & \frac{1}{2} & \frac{1}{4} & \cdot & \cdot & 0 & 0 & 0 \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ 0 & 0 & 0 & 0 & 0 & \cdot & \cdot & \frac{1}{4} & \frac{1}{2} & \frac{1}{4} \\ 0 & 0 & 0 & 0 & 0 & \cdot & \cdot & 0 & \frac{1}{2} & \frac{1}{2} \end{bmatrix} \begin{bmatrix} H_{t-1} \\ K_{t-1}(0) \\ K_{t-1}(1) \\ K_{t-1}(2) \\ \cdot \\ \cdot \\ K_{t-1}(n-1) \\ K_{t-1}(n) \end{bmatrix} \tag{3.5}$$

The characteristic equation of the above $(n + 2) \times (n + 2)$ matrix can again be expressed in terms of Wolstenholme's determinant $\phi_n(\cdot)$ as follows:

$$F_n(\lambda) = (\frac{1}{4})^n [4\lambda^2(\frac{1}{2} - \lambda)\phi_{n-1}(2 - 4\lambda) + 4(\frac{1}{8} - \lambda^2)\phi_{n-2}(2 - 4\lambda) - (\lambda + \frac{1}{2})\phi_{n-3}(2 - 4\lambda)] = 0. \tag{3.6}$$

This leads to

$$\left. \begin{aligned} \lambda &= \frac{1}{2}(1 + \cos \theta) \\ \sin \theta &= \frac{\cot n\theta}{2 + \cos \theta} \end{aligned} \right\} \tag{3.7}$$

For a large n , we obtain

$$\lambda = 1 - \frac{\pi^2}{16(n + 3)^2} \tag{3.8}$$

or, putting $n = N/4$,

$$\lambda = 1 - \frac{\pi^2}{(N + 12)^2} \tag{3.9}$$

Numerical values are given in Table 1.

In the case of odd $(2n + 1)$ pairs, the total number of individuals is $N = 4n + 2$ and the equation corresponding to (3.5) becomes

$$\begin{bmatrix} H_t \\ K_t(0) \\ K_t(1) \\ \cdot \\ \cdot \\ K_t(n-1) \\ K_t(n) \end{bmatrix} = \begin{bmatrix} 0 & 0 & 1 & 0 & \cdot & \cdot & 0 & 0 & 0 \\ \frac{1}{4} & 0 & \frac{1}{2} & 0 & \cdot & \cdot & 0 & 0 & 0 \\ 0 & \frac{1}{4} & \frac{1}{2} & \frac{1}{4} & \cdot & \cdot & 0 & 0 & 0 \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ 0 & 0 & 0 & 0 & \cdot & \cdot & \frac{1}{4} & \frac{1}{2} & \frac{1}{4} \\ 0 & 0 & 0 & 0 & \cdot & \cdot & 0 & \frac{1}{4} & \frac{3}{4} \end{bmatrix} \begin{bmatrix} H_{t-1} \\ K_{t-1}(0) \\ K_{t-1}(1) \\ \cdot \\ \cdot \\ K_{t-1}(n-1) \\ K_{t-1}(n) \end{bmatrix} \tag{3.10}$$

In this case, the equation giving λ turns out to be as follows:

$$\left. \begin{aligned} \lambda &= \frac{1}{2}(1 + \cos \theta) \\ \tan \frac{\theta}{2} &= \left(\frac{\cos^2 \theta + \cos \theta - 1}{\cos^2 \theta + 3 \cos \theta + 3} \right) \cot n\theta \end{aligned} \right\} \tag{3.11}$$

For a large n , we obtain

$$\lambda = 1 - \frac{\pi^2}{16} \frac{1}{(n + \frac{7}{2})^2}, \tag{3.12}$$

or, putting $n = (N - 2)/4$,

$$\lambda = 1 - \frac{\pi^2}{(N + 12)^2} \tag{3.13}$$

which fortunately is the same as (3.9). Comparison of (3.13) or (3.9) with (2.15) shows that asymptotically circular pair mating needs twice as many individuals as the circular individual mating to attain the same rate of decrease in heterozygosity.

4. CIRCULAR SUBPOPULATION MATING

Under some circumstances it may be convenient to have several parents in a single cage. It is natural to extend the circular mating system to include this possibility. For example, each generation the male progeny could be transferred one cage to the right.

Let the number of cages be $2n$ (or $2n + 1$ if the number is odd) and in each cage let m^* be the number of males and m^{**} be the number of females. Figure 5 illustrates an example where $2n = 4$, $m^* = 2$, and $m^{**} = 3$.

We assume that mating within a cage or subpopulation is random and that each parent of a given sex has the same expectation of progeny. As before, we denote by I the probability that an individual in the t^{th} generation is homozygous with respects to any of the alleles, A_1, A_2 , etc. Let $J_t(k)$ be the probability that two homologous genes taken one from each of two newly born individuals coming from subpopulations k steps apart are identical. In particular, $J_t(0)$ stands for the probability of two homologous genes taken one from each of two newly born individuals within a subpopulation are the same allele.

In the case of an even number of subpopulations, if $2n$ is the number of subpopulations such that the total number of breeding individuals is

$$N = 2n(m^* + m^{**}),$$

we have the following recurrence relations:

$$I_t = J_{t-1}(1) \tag{4.1}$$

$$J_t(0) = \frac{1}{2} \left\{ \frac{1}{2} \left[\frac{1}{m^*} \left(\frac{1+I_{t-1}}{2} \right) + \left(1 - \frac{1}{m^*} \right) J_{t-1}(0) \right] + \frac{1}{2} \left[\frac{1}{m^{**}} \left(\frac{1+I_{t-1}}{2} \right) + \left(1 - \frac{1}{m^{**}} \right) J_{t-1}(0) \right] \right\} + \frac{1}{2} J_{t-1}(1) \tag{4.2}$$

$$J_t(k) = \frac{1}{4} [J_{t-1}(k-1) + 2J_{t-1}(k) + J_{t-1}(k+1)] \quad (1 \leq k \leq n-1) \tag{4.3}$$

$$J_t(n) = \frac{1}{2} [J_{t-1}(n-1) + J_{t-1}(n)] \tag{4.4}$$

These relations are similar to (3.1)–(3.4) and only (4.2) requires explanation: Two homologous genes, taken one from each of two individuals within a sub-

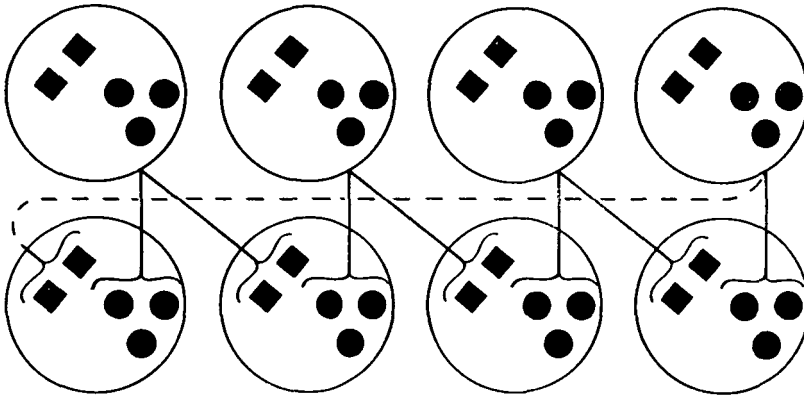


Fig. 5. Circular population mating for 4 populations, each with 2 males and 3 females.

population, are either derived from the same parental subpopulation or from two adjacent parental subpopulations with equal probability of $1/2$. In the former case, they are either derived from a male, or a female, with equal probability of $1/2$. If paternal, they are derived from the same male with probability $1/m^*$, and from different males with probability $1 - 1/m^*$. Similarly, if maternal, they are derived from the same female with probability $1/m^{**}$ and different females with probability $1 - 1/m^{**}$. Irrespective of whether they are derived from male or female, the probability of the two homologous genes sharing the same allele is $(1 + I_{t-1})/2$ if they are derived from the same individual and $J_{t-1}(0)$ if they are derived from different individuals originated from the same subpopulation. On the other hand, if they are derived from adjacent parental subpopulations, the probability that they share the same allele is $J_{t-1}(1)$.

Let $H_t = 1_t - I_t$ and $K_t(k) = 1 - J_t(k)$, $k = 0, 1, 2, \dots, n$. Then

$$\begin{bmatrix} H_t \\ K_t(0) \\ K_t(1) \\ \cdot \\ \cdot \\ K_t(n-1) \\ K_t(n) \end{bmatrix} = \begin{bmatrix} 0 & 0 & 1 & 0 & \cdot & \cdot & 0 & 0 & 0 \\ \frac{1}{4m} & \left(\frac{1}{2} - \frac{1}{2m}\right) & \frac{1}{2} & 0 & \cdot & \cdot & 0 & 0 & 0 \\ 0 & \frac{1}{4} & \frac{1}{2} & \frac{1}{4} & \cdot & \cdot & 0 & 0 & 0 \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ 0 & 0 & 0 & 0 & \cdot & \cdot & \frac{1}{4} & \frac{1}{2} & \frac{1}{4} \\ 0 & 0 & 0 & 0 & \cdot & \cdot & 0 & \frac{1}{2} & \frac{1}{2} \end{bmatrix} \begin{bmatrix} H_{t-1} \\ K_{t-1}(0) \\ K_{t-1}(1) \\ \cdot \\ \cdot \\ K_{t-1}(n-1) \\ K_{t-1}(n) \end{bmatrix} \tag{4.5}$$

where m is the harmonic mean of the number of males and females;

$$m = 2 / \left(\frac{1}{m^*} + \frac{1}{m^{**}} \right) \tag{4.6}$$

Performing the calculation as before, the characteristic equation giving λ becomes

$$\left. \begin{aligned} \lambda &= \frac{1}{2}(1 + \cos \theta) \\ \sin \theta &= \frac{\cot n\theta}{m(1 + \cos \theta) + 1} \end{aligned} \right\} \tag{4.7}$$

For a large value of n , the dominant root may be calculated from

$$\lambda = 1 - \frac{\pi^2}{16(n + 2m + 1)^2} \tag{4.8}$$

If the number of subpopulations is odd, say $2n + 1$, the matrix of transformation corresponding to (4.5) should be modified slightly such that the last row is $(0, \dots, 0, \frac{1}{4}, \frac{3}{4})$ rather than $(0, \dots, 0, \frac{1}{2}, \frac{1}{2})$. The characteristic equation may be worked out as in the case of even numbers of subpopulations.

5. COMPARISON OF VARIOUS MATING SYSTEMS WITH RESPECT TO THE RATE OF DECREASE OF HETEROZYGOSITY

It has been shown by Wright (1931) that in a random-mating population of N breeding individuals equally divided between males and females, the rate of decrease of heterozygosity is approximately $1/(2N)$ per generation, i.e.

$$1 - \lambda \sim \frac{1}{2N} \tag{5.1}$$

With N breeding individuals, but under 'maximum avoidance' of consanguineous mating, the ultimate rate of decrease of heterozygosity is asymptotically $1/(4N)$ per generation (see Wright, 1951), i.e.

$$1 - \lambda \sim \frac{1}{4N} \tag{5.2}$$

From the common notion that the decrease of heterozygosity is directly related to the intensity of inbreeding, these results seem to show that $1/4N$ is the minimum rate of decrease of heterozygosity that can possibly be attained with N breeding individuals per generation. Furthermore, Wright (1931) has shown that if each individual leaves exactly two offspring per generation, the effective size of population is approximately twice the actual size. In other words, we again have relation (5.2). Thus it is natural to infer that in addition to keeping the number of offspring equal between different individuals, if matings between close relatives are avoided, 'the inbreeding coefficient in any generation is slightly lower and is more uniform between the individuals in the generation than if matings between close relatives are allowed; but the rate of inbreeding is the same' (Falconer, 1960).

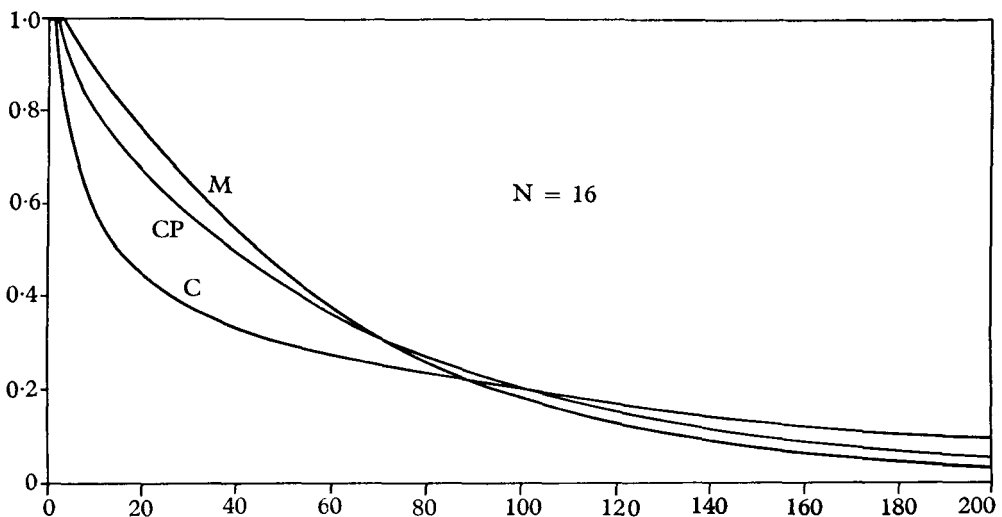


Fig. 6. Decrease of heterozygosity in a population of size 16 for circular mating (C), circular pair mating (CP), and maximum avoidance of inbreeding (M). Ordinate: heterozygosity as a fraction of initial heterozygosity; abscissa: time in generations.

Actually, an inquiry on this point from Dr Y. Yamada to one of us (M.K.) provided the stimulus to work on the problem. Thus the general result that, under circular mating, the ultimate rate of decrease in heterozygosity is proportional to $1/N^2$ rather than to $1/N$ was quite an unexpected one.

The processes of change in heterozygote frequencies under circular matings and the 'maximum avoidance of inbreeding' are illustrated in Figs. 6 and 7 for $N = 16$ and 32.

They show that the decrease of heterozygosity is always more rapid in the circular matings than in the maximum avoidance system during the earlier stages of inbreeding, after which the latter starts to lose heterozygosity more rapidly. The point at which this transition occurs depends on the population size as well as the type of circular mating.

The practical utility of circular mating systems for maintaining heterozygosity is

limited by the fact that much of the heterozygosity is lost before the circular mating systems become advantageous. The point of transition is difficult to determine analytically, but some idea of the numerical values can be gotten from Figs. 6 and 7 and Table 1.

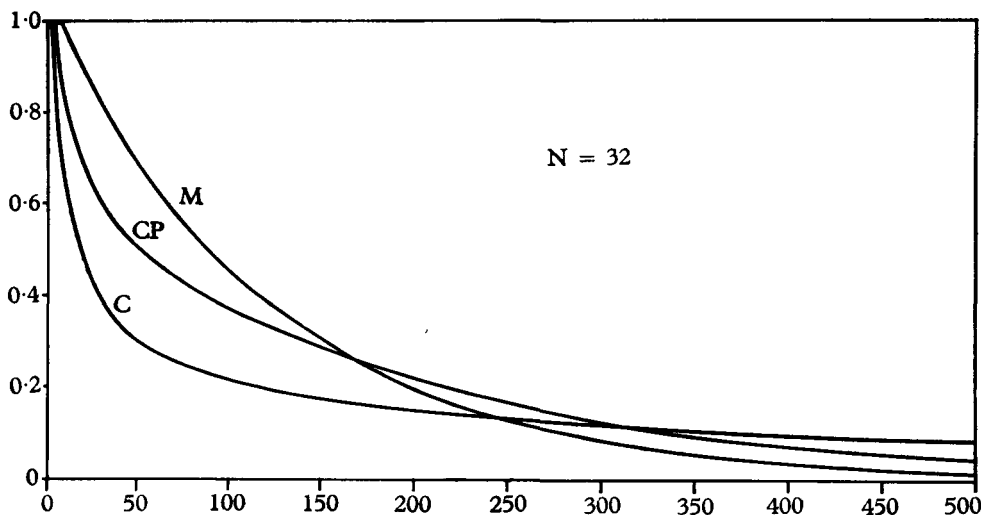


Fig. 7. Decrease of heterozygosity in a population of size 32.

Although the ultimate rate of decrease in heterozygosity, $1 - \lambda$, may not be very important in judging the merit of various mating systems for practical use, it is of considerable theoretical interest. A problem that immediately comes up is whether there is any mating system that gives a smaller value of $1 - \lambda$ than circular mating for the same population size. We have not found any that is applicable to populations that have separate sexes. For example, Fig. 8 shows a system suggested by Dr Y.

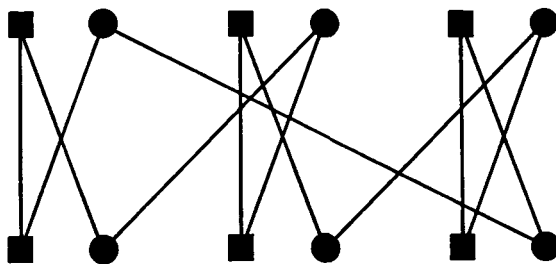


Fig. 8. A mating system that combines circular and circular pair systems.

Yamada that is a mixture of circular and circular pairs. For the case of $N = 6$, the equation determining λ is

$$-(4\lambda)^6 + 3(4\lambda)^5 + 5(4\lambda)^4 - (4\lambda)^3 - 23(4\lambda)^2 - 6(4\lambda) + 12 = 0$$

from which we get $1 - \lambda = 0.0465$ as the ultimate rate of decrease in heterozygosity. Since the corresponding values for the circular individual and the circular pair

matings are respectively $1 - \lambda = 0.0395$ and 0.0494 , this system is intermediate between these two circular mating systems with respect to the ultimate rate of decrease in heterozygosity.

For a monoecious population in which self-fertilization is allowed, it is possible to produce an example which gives a smaller value of $1 - \lambda$ than circular individual mating (for equal N). Figure 9 illustrates a mating scheme in which selfing and sib-mating are systematically mixed among three monoecious individuals compared

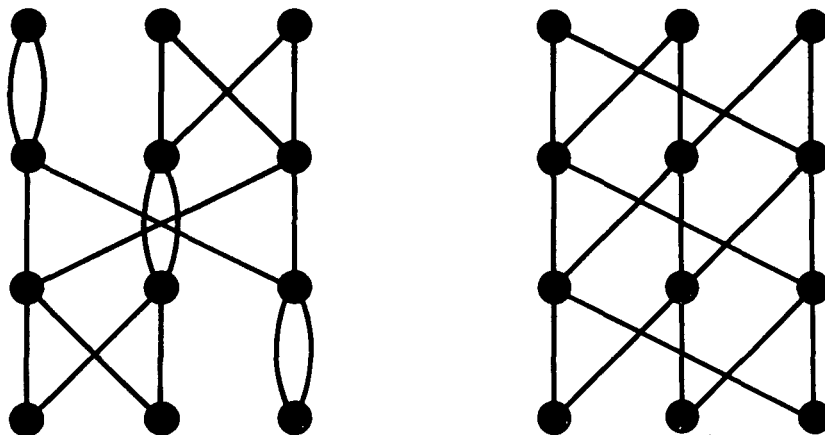


Fig. 9. Partial self-fertilization without subdivision into lines for $N = 3$ compared to circular mating.

with circular mating involving three monoecious individuals. In the former case, the equation determining λ turns out to be

$$32\lambda^4 - 15\lambda^3 - 8\lambda^2 - 2\lambda - 1 = 0$$

from which we get $1 - \lambda = 0.1013$. In the latter case,

$$8\lambda^2 - 6\lambda - 1 = 0$$

and the ultimate rate of decrease in heterozygosity is $1 - \lambda = 0.1096$.

Thus, more intense inbreeding of individuals within the line produces a lower ultimate rate of decrease in heterozygosity, provided there is no permanent splitting of the population into isolated lines. An extreme example would be a system of self-fertilization or sib-mating for several generations, with random mating interspersed. By lengthening the interval between the random matings the ultimate rate of decrease in heterozygosity could be made as small as desired. Conversely, a system that avoids mating of relatives for as long as possible does so at the expense of a more rapid final approach to homozygosity.

The circular and circular pair systems have the same mating pattern each generation, as do the maximum avoidance systems. Among such systems it would appear that circular mating has the slowest ultimate rate of approach to homozygosity.

It is interesting to note that circular mating and circular pair mating for populations of infinite size have already been worked out, although they are usually not thought of in this sense. The half sib mating scheme of Wright (1921, p. 138) would be equivalent to circular mating if the right and left ends of the pedigree were joined. Likewise, Wright's first cousin mating scheme (p. 140) is equivalent to circular pair mating in a population of infinite size. As expected, the heterozygosity change in the first few generations of our systems agree with those of Wright.

6. MATING SYSTEMS THAT MINIMIZE RANDOM GENE FREQUENCY DRIFT

It is frequently desirable to keep the gene frequencies of a population as constant as possible, as for example in a control population for a selection experiment.

In considering mating systems that minimize gene frequency drift it is clear that the first requisite for such a system is that the number of progeny per parent be constant. Assuming that each individual leaves exactly two offspring, the variance in the change in frequency of a particular allele *A* from generation *t* to generation *t* + 1 is given by $H_t/8N$, where H_t is the proportion of heterozygotes in generation *t*. This is because each heterozygote contributes two genes, randomly chosen, and hence with variance $2 \times \frac{1}{2} \times \frac{1}{2} = \frac{1}{2}$. With *N* parents there are NH_t heterozygotes, with a variance in number of *A* alleles contributed of $NH_t/2$. Thus, among the $2N$ genes contributed, the variance in *A* allele frequency is $NH_t/2 \div 4N^2$, or $H_t/8N$.

Therefore, the gene frequency variance after *T* generations is

$$V_T = \frac{1}{8N} \sum_{t=0}^{T-1} H_t$$

that is, the total random drift is proportional to the sum of the heterozygote frequencies in all previous generations. If there are *L* isolated lines, each with *N* individuals, the variance in average gene frequency becomes $1/L$ of the above value. Thus it is desirable to adopt a mating system in which heterozygosity decreases rapidly and the population breaks up into as many lines as possible.

For a randomly mating population of *N* monoecious individuals and constant number of progeny per parent $H_t = \lambda H_{t-1}$ where $1 - \lambda = 1/(4N - 2)$ (see Kimura & Crow, 1963), so that

$$V_\infty = \frac{1}{8N} \sum_{t=0}^{\infty} H_0 \lambda^t = \frac{H_0}{8N(1-\lambda)} = \frac{H_0}{8N} (4N - 2) \tag{6.2}$$

If, instead, the population is split into *N* self-fertilizing lines, $\lambda = \frac{1}{2}$ in each line and

$$V_\infty = \frac{1}{N} \cdot \frac{H_0}{8(1-\lambda)} = \frac{2H_0}{8N} \tag{6.3}$$

thus by splitting into *N* selfing lines the total accumulated variance is reduced to $1/(2N - 1)$ of the value in a randomly mated population.

If there are separate sexes the change of heterozygosity is given by

$$H_t = (1 - P_t) H_{t-1} + \frac{P_t}{2} H_{t-2}$$

where P_t is the probability that two homologous genes in generation t come from the same individual in generation $t-2$ (Wright, 1951; Kimura & Crow, 1963). If each parent leaves the same number of progeny (which implies equal numbers of male and female parents), $P_t = 1/(2N-2)$ and we have

$$H_t = \frac{2N-3}{2N-2} H_{t-1} + \frac{1}{4N-4} H_{t-2}$$

$$\sum_{t=0}^{\infty} H_t = H_0(4N-2)$$

$$V_{\infty} = \frac{H_0}{8N} (4N-2) \quad (6.4)$$

Note that (6.2) and (6.4) are the same; i.e. the situation is not changed by having separate sexes.

If the population is split into $N/2$ sib-mated lines

$$V_{\infty} = \frac{6H_0}{8N}$$

and the drift variance is decreased to $3/(2N-1)$ of the value with random mating.

These examples clearly show that in order to keep the total drift to a minimum, the population should be split into as many lines as possible.

If the population is not split into lines the system that has the least total heterozygosity over the generations considered is preferred. From Figs. 6 and 7 it is clear that circular mating is the best of the systems considered, since for any particular generation the area under this curve to the left of the generation is least.

If we ask for the limit, each of these systems (or any other that does not lead to population subdivision) leads to the same result, for eventually one allele will become fixed. Therefore

$$V_{\infty} = p(1-p) \quad (6.5)$$

where p is the initial frequency of the allele under consideration.

This can be verified by noting that, with random mating in a finite population,

$$H_0 = 2p(1-p)(1-\alpha)$$

$$\alpha = \frac{-1}{2N-1} \quad (\text{Kimura \& Crow, 1963})$$

Substituting these into (6.2) or (6.4) leads to (6.5).

The relationship between minimum gene frequency drift and minimum ultimate decrease in heterozygosity can now be seen. Minimization of random drift is accomplished by intense inbreeding in the early generations and subdivision of the population into as many lines as possible; for example, self-fertilization if this is possible. By crossing such lines at random a population can be reconstituted and the final approach to homozygosity of such populations, successively reconstituted, will be minimal.

7. SUMMARY

Mating systems in which the least related individuals are mated have been designated by Wright as having maximum avoidance of inbreeding. For such systems the initial rate of decrease in heterozygosity is minimum. However, some other systems have a lower rate of decrease in later generations.

Circular mating, in which each individual is mated with the one to his right and to his left, leads to an asymptotic rate of decrease in heterozygosity of $1 - \lambda \sim \pi^2/(2N + 4)^2$ compared with $1/4N$ for maximum avoidance systems. Circular pair mating, in which for example each male progeny is moved one cage to the right, leads to $1 - \lambda \sim \pi^2/(N + 12)^2$. Other similar systems are discussed.

For minimum gene frequency drift, a mating system should have a constant number of progeny per parent and the population should be broken up as rapidly as possible into the maximum number of lines. The gene frequency variance at generation T within a line is

$$V_T = \frac{1}{8N} \sum_{t=0}^{T-1} H_t$$

where N is the number in the line and H_t is the proportion of heterozygotes in generation t . Although the three mating systems, circular, circular pair, and maximum avoidance (and many others) have the same amount of random drift ultimately, at any generation circular mating has the smallest drift variance, V_T , and circular pair next smallest.

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