

Pseudo-Random Mating Populations. In Celebration of the 80th Anniversary of the Hardy-Weinberg Law

C. C. Li

Graduate School of Public Health, University of Pittsburgh, Pittsburgh, Pennsylvania 15261

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ABSTRACT

That random mating leads to Hardy-Weinberg distribution of genotypes is well known. This report is to show that, if the deviations from random mating are of a certain pattern, the offspring generation will also be in Hardy-Weinberg proportions. This brings out the fact that random mating is a sufficient condition, not a necessary one, for the attainment of the Hardy-Weinberg proportions. Such nonrandom-mating populations are tentatively said to be pseudo-random mating. Pseudo-random-mating populations exist for both autosomal and sex-linked systems with two or multiple alleles. This report covers the basic case of a two-allele autosomal locus in detail, but the possible extension to two loci and cytonuclear systems have also been mentioned in discussion.

LET (p, q) be the frequency of the two alleles (A, a) and (f_2, f_1, f_0) be the frequency of the three genotypes (AA, Aa, aa) in a population. We use f_{ij} to denote the frequency of mating between a female genotype i and a male genotype j , where $i, j = AA, Aa, aa$, or simply 2, 1, 0. With this notation, random mating means $f_{ij} = f_i f_j$; and nonrandom mating means $f_{ij} = f_i f_j + d_{ij}$, where d_{ij} is the deviation from random-mating frequency.

The properties of panmixia are well known; we may mention a few: (i) the population is in equilibrium with $(f_2, f_1, f_0) = (p^2, 2pq, q^2)$; (ii) correlation (between mates) is $m = 0$; (iii) correlation (parent-child) = $1/2$; and (iv) correlation (sib-sib) = $1/2$. In the present report, I shall show that certain types of nonrandom mating ($f_{ij} = f_i f_j + d_{ij}$) have the same four properties of panmixia. In other words, random mating is a sufficient condition, not a necessary one, for such properties.

A NONRANDOM MATING POPULATION

As a concrete example, consider the type of deviations (d_{ij}) from random mating shown in Table 1A, with $d_{22} = h, d_{21} = -3h, d_{11} = 10h$, etc., where h is a constant, positive or negative. The deviations d_{ij} should of course sum to zero for each row and for each column, so that the marginal totals remain the same. The constant multiplier h should not be large enough to make any mating frequency f_{ij} negative or greater than unity. In the presence of d_{ij} , the population is no longer random mating.

With the nonrandom-mating frequencies shown in Table 1A, we may calculate the offspring generation in the usual manner, as shown in Table 1B. The resulting offspring generation is $(p^2, 2pq, q^2)$, identical with the result of true random mating. Such a

type of nonrandom mating may be called "pseudo-random mating."

We have established property (i) mentioned in the introductory paragraph. It is easy to establish property (ii) by noting that such deviations from random mating contribute nothing to the covariance of the parents. The contribution to covariance from the deviations (Table 1A) is:

$$(2)(2)h + (2)(1)(-3h) + (1)(2)(-4h) + (1)(1)10h = 0$$

so that the correlation between mates remains $m = 0$. In other words, the deviations d_{ij} do not alter the uncorrelated nature of the parents. The remaining two properties, (iii) and (iv), will be dealt with later when we know more about the deviation patterns.

The Hardy-Weinberg law may be viewed from another angle. The genotype frequencies ($p^2, 2pq, q^2$) imply random union of gametes. Hence, we wish to find the frequencies of the four types of uniting gametes ($A/A, A/a, a/A, a/a$) from the mating frequencies (f_{ij}) shown in Table 1A. Consider the case A/A . The frequency of this type of union is obviously equal to the following combination of mating frequencies:

$$A/A = (AA \times AA) + \frac{1}{2}(AA \times Aa) + \frac{1}{2}(Aa \times AA) + \frac{1}{4}(Aa \times Aa).$$

The frequency of the other three types of uniting gametes are calculated in a similar way. The results are shown in Table 2, which shows that there is indeed random union of gametes, as the deviations (terms involving h) sum to zero for each type of genetic union.

The correlation between uniting gametes is usually

TABLE 1

A. Nonrandom mating frequencies: $f_{ij} = f_i f_j + d_{ij}$

	AA, 2	Aa, 1	aa, 0	f_i
AA, 2	$p^4 + h$	$2p^3q - 3h$	$p^2q^2 + 2h$	p^2
Aa, 1	$2p^3q - 4h$	$4p^2q^2 + 10h$	$2pq^3 - 6h$	$2pq$
aa, 0	$p^2q^2 + 3h$	$2pq^3 - 7h$	$q^4 + 4h$	q^2
f_j	p^2	$2pq$	q^2	1.00

B. Offspring generation produced by matings of Part A

Parents mating	Offspring		
	AA	Aa	aa
AA ×	AA	$p^4 + 1.0h$	
	Aa	$p^3q - 1.5h$	$p^3q - 1.5h$
	aa		$p^2q^2 + 2.0h$
Aa ×	AA	$p^3q - 2.0h$	$p^3q - 2.0h$
	Aa	$p^2q^2 + 2.5h$	$2p^2q^2 + 5.0h$
	aa		$pq^3 - 3.0h$
aa ×	AA		$p^2q^2 + 3.0h$
	Aa		$pq^3 - 3.5h$
	aa		$q^4 + 4.0h$
Total	p^2	$2pq$	q^2

TABLE 2

Frequencies of uniting gametes based on mating frequencies (f_{ij}) of Table 1A

A	a
$p^4 + h + p^3q - 1.5h$ + $p^3q - 2h + p^2q^2 + 2.5h$ = p^2	$p^2q^2 + 2h + p^3q - 1.5h$ + $pq^3 - 3h + p^2q^2 + 2.5h$ = pq
$p^2q^2 + 3h + pq^3 - 3.5h$ + $p^3q - 2h + p^2q^2 + 2.5h$ = pq	$q^4 + 4h + pq^3 - 3.5h$ + $pq^3 - 3h + p^2q^2 + 2.5h$ = q^2

denoted by F . In Table 2, we have $F = 0$. Its general relationship with m is $F = m/(2 - m)$ in an equilibrium population [Wright (1921) using the method of path coefficients. For an algebraic proof, see LI (1953)]. Here we have produced an example in which $m = F = 0$ without being a truly random mating population. In other words, random union of gametes may be attained without random mating.

GENERAL AND ELEMENTAL PATTERNS

It is clear from the previous section that the pseudo-random-mating property depends solely on the coefficients of h . The random mating component ($f_i f_j$) of the matings will yield the usual results for a true random mating population. The constant multiplier h plays no part in the property of pseudo-random mating. Hence, in this section, we shall study the coefficients of h only. To shorten our language, we

use the word "pattern" to mean the 3×3 matrix of the nine coefficients of h . Also, it is to be understood that the rows and columns of the matrix are always in the order of AA, Aa, aa.

The deviation coefficients must add up to zero for each row and each column. This allows us to assign arbitrarily four values to the 3×3 elements; the remaining five will be determined automatically. Let us assign the four values (a, b, c, d) to the four corners of the pattern:

$$\begin{pmatrix} a & -a - b & b \\ -a - c & a + b + c + d & -b - d \\ c & -c - d & d \end{pmatrix}. \quad (1)$$

This arbitrary pattern (1), in general, will not have the pseudo-random-mating property. Our purpose is to find the condition under which it will have the desired property. The coefficients must be such that they add up to zero for each pair of uniting gametes, as exemplified in Table 2. The condition for A/A is then

$$a + \frac{1}{2}(-a - b) + \frac{1}{2}(-a - c) + \frac{1}{4}(a + b + c + d) = 0.$$

Upon simplification, this reduces to

$$a + d = b + c. \quad (2)$$

That is to say: the sums of opposite corner elements of (1) must be equal. Due to symmetry of (1), the other three conditions for A/a, a/A and a/a all reduce to (2). In other words, $a + d = b + c$ is the only requirement that (1) has to satisfy in order to possess the pseudo-random mating property. Hence, (1), conditioned by (2), can be regarded as the general form for all pseudo-random mating patterns. As a very simple numerical example, let us take (a, b, c, d) = (1, 2, 3, 4) with $a + d = b + c = 5$. Then the general form (1) becomes

$$\begin{pmatrix} 1 & -3 & 2 \\ -4 & 10 & -6 \\ 3 & -7 & 4 \end{pmatrix}$$

which, the reader will recognize, is the pattern we used for illustration in the previous section.

Let us call the upper left corner of (1) the first corner, the upper right the second corner, the lower left the third, and the lower right the fourth. If there are four numbers written as (X_1, X_2, X_3, X_4), it is understood to mean that X_1 is to be placed in the first corner, X_2 in the second corner, etc. With any given four numbers, a, b, c, d , with the restriction $a + d = b + c$, there are four choices to be X_1 . Having fixed X_1 , there are two choices to be X_2 . Then the remaining two corners are automatically determined. It follows that pseudo-random mating patterns occur

in sets of eight:

$$\begin{aligned} &(a, b, c, d) (b, a, d, c) \\ &(a, c, b, d) (b, d, a, c) \\ &(c, a, d, b) (d, b, c, a) \\ &(c, d, a, b) (d, c, b, a) \end{aligned}$$

which means: if you find one pattern, you find eight. If $a = d$ or $b = c$, there are only four distinct patterns.

The restriction $a + d = b + c$ means that there are three independent arbitrary numbers in the pattern. Any one of the four letters may be eliminated and hence there are four ways of expressing (1) in terms of three letters. Due to symmetry, no form has any advantage over the other three, so let us eliminate d by substituting $d = -a + b + c$ and express (1) in terms of a, b, c :

$$\begin{pmatrix} a & -a - b & b \\ -a - c & 2(b + c) & a - 2b - c \\ c & a - b - 2c & -a + b + c \end{pmatrix}. \quad (3)$$

This form permits us to decompose the pattern into three elementary patterns which would help us to understand the results of parent-child and sib-sib distributions in a pseudo-random mating population in later sections.

When reciprocal crosses have the same frequency, the general pattern will be symmetrical. Putting $b = c$, the general form (3) becomes

$$\begin{pmatrix} a & -a - b & b \\ -a - b & 4b & a - 3b \\ b & a - 3b & -a + 2b \end{pmatrix} \quad (4)$$

which is the general form of all symmetrical patterns.

Three elemental patterns (E_1, E_2, E_3) are shown in the first row of Table 3. It is important to note that each elemental pattern itself has the pseudo-random mating property, because the sums of its opposite corner elements are equal. Any linear combination of two or three elemental patterns is also a pattern with pseudo-random mating property. E_1 is symmetrical; and E_2 is the transpose of E_3 , so $E_2 + E_3$ is symmetrical (second row of Table 3). A pattern can have at most three zero elements. Any row, any column, or any diagonal can be zero. All of these patterns have been shown in Table 3 to exhibit the extreme patterns possible for pseudo-random mating. The last pattern $E_1 + 2E_2 + 3E_3$ is the one we used for illustration previously. In terms of these elemental patterns, we see that

$$\text{General form (3)} = aE_1 + bE_2 + cE_3$$

$$\text{Symmetrical form (4)} = aE_1 + b(E_2 + E_3).$$

Since there are an infinite number of possible pseudo-random mating patterns, we cannot be sure that none of them exists in nature.

TABLE 3

Elemental patterns and some of their linear combinations

E_1 $\begin{pmatrix} 1 & -1 & 0 \\ -1 & 0 & 1 \\ 0 & 1 & -1 \end{pmatrix}$	E_2 $\begin{pmatrix} 0 & -1 & 1 \\ 0 & 2 & -2 \\ 0 & -1 & 1 \end{pmatrix}$	E_3 $\begin{pmatrix} 0 & 0 & 0 \\ -1 & 2 & -1 \\ 1 & -2 & 1 \end{pmatrix}$
$E_2 + E_3$ $\begin{pmatrix} 0 & -1 & 1 \\ -1 & 4 & -3 \\ 1 & -3 & 2 \end{pmatrix}$	$E_1 + E_3$ $\begin{pmatrix} 1 & -1 & 0 \\ -2 & 2 & 0 \\ 1 & -1 & 0 \end{pmatrix}$	$E_1 + E_2$ $\begin{pmatrix} 1 & -2 & 1 \\ -1 & 2 & -1 \\ 0 & 0 & 0 \end{pmatrix}$
$E_2 - E_3$ $\begin{pmatrix} 0 & -1 & 1 \\ 1 & 0 & -1 \\ -1 & 1 & 0 \end{pmatrix}$	$E_1 - E_2 + E_3$ $\begin{pmatrix} 1 & 0 & -1 \\ -2 & 0 & 2 \\ 1 & 0 & -1 \end{pmatrix}$	$E_1 + E_2 - E_3$ $\begin{pmatrix} 1 & -2 & 1 \\ 0 & 0 & 0 \\ -1 & 2 & -1 \end{pmatrix}$
$-E_1 + E_2 + E_3$ $\begin{pmatrix} -1 & 0 & 1 \\ 0 & 4 & -4 \\ 1 & -4 & 3 \end{pmatrix}$	$E_1 + E_2 + E_3$ $\begin{pmatrix} 1 & -2 & 1 \\ -2 & 4 & -2 \\ 1 & -2 & 1 \end{pmatrix}$	$E_1 + 2E_2 + 3E_3$ $\begin{pmatrix} 1 & -3 & 2 \\ -4 & 10 & -6 \\ 3 & -7 & 4 \end{pmatrix}$

PARENT-CHILD PAIR DISTRIBUTION

Now we come to study the third property mentioned in the introductory paragraph, viz., the parent-child (PC) correlation in a random mating population is 1/2. Before we show the general result from a pseudo-random mating population, let us go back to Table 1B, and see what the result is for this particular example. The parent-child distribution is obtained by pooling the first three rows for parent AA, the next three rows for parent Aa, and the last three rows for parent aa. The result is shown in Table 4. In this table the first term in each cell (p^3, p^2q , etc.) is the standard result for a true random mating population. The terms involving h are caused by the deviations from random mating. The results of Table 4 may be written as (PC) + (dPC), where

$$\begin{aligned} \text{(PC)} &= \begin{pmatrix} p^3 & p^2q & 0 \\ p^2q & pq & pq^2 \\ 0 & pq^2 & q^3 \end{pmatrix} \text{ and} \\ \text{(dPC)} &= \begin{pmatrix} -0.5 & 0.5 & 0 \\ 0.5 & 0 & -0.5 \\ 0 & -0.5 & 0.5 \end{pmatrix} h. \end{aligned}$$

The (PC) part will remain the same whatever the pattern of deviations, because it is determined by the random mating component $f_i f_j$ of f_{ij} . Hence, from now on, we shall study the deviation pattern only, i.e. (dPC) without writing out the common multiplier h .

Comparing the pattern in (dPC) above with the elemental pattern E_1 of Table 3, we see that the pattern is equal to $-\frac{1}{2}E_1$. All the patterns shown in Table 3 have the pseudo-random mating property;

TABLE 4

Parent-child correlation table obtained from the example in Table 1B

		Child			Total
		AA	Aa	aa	
Parent	AA	$p^3 - 0.5h$	$p^2q + 0.5h$		p^2
	Aa	$p^2q + 0.5h$	pq	$pq^2 - 0.5h$	$2pq$
	aa		$pq^2 - 0.5h$	$q^3 + 0.5h$	q^2
Total		p^2	$2pq$	q^2	1.00

that means they contribute nothing to the covariance of a genetic correlation table. It follows that the parent-child correlation of Table 4 is the same as the correlation determined by (PC) which is 1/2, as well known.

It remains to understand why in this particular example the deviation pattern from (PC) should be $-\frac{1}{2}E_1$. As indicated by the last pattern shown in Table 3, the deviation pattern in the parental mating for this particular example is $E_1 + 2E_2 + 3E_3$. This shows we need to study the properties of the general pattern (3) = $aE_1 + bE_2 + cE_3$. This is done in Table 5. The upper portion of Table 5 lists the results of all nine matings. Pooling the three rows for each given parent, we obtain the parent-child table, shown in the lower half of Table 5.

The lower portion of Table 5 gives the general pattern of (dPC). A remarkable feature of the pattern is the total absence of c ; it means the E_3 component of the general pattern (3) does not contribute to (PC) deviations. Thus, the patterns $aE_1 + bE_2 + cE_3$ and $aE_1 + bE_2$ will have the same (dPC) deviations. Next, we note the deviations from (PC) may be written in the general form:

$$(dPC) = a(\frac{1}{2}E_1) + b(-\frac{1}{2}E_1) = \frac{1}{2}(a - b)E_1. \quad (5)$$

In our previous numerical example, $a = 1, b = 2$, and $(dPC) = \frac{1}{2}(1 - 2)E_1 = -\frac{1}{2}E_1$ correctly. All deviation patterns in the parental mating type of the form $a(E_1 + E_2) + cE_3$ yields $(dPC) = 0$; that is, the PC distribution of a pseudo-random mating population is identical with (PC) of a true random mating population. The important point is that even when $(dPC) \neq 0$, the PC correlation remains 1/2, because (dPC) contributes nothing to PC covariance.

SIB-SIB PAIR DISTRIBUTION

The fourth property mentioned in the introductory paragraph is that the sib-sib (SS) correlation in a pseudo-random mating population remains 1/2, the same as that in a true random mating population. We shall show that this is so by the same procedure employed in the previous section. Let the SS distribution in a pseudo-random mating population be

written as (SS) + (dSS), where

$$(SS) = \begin{pmatrix} \frac{1}{4}p^2(1+p)^2 & \frac{1}{2}p^2q(1+p) & \frac{1}{4}p^2q^2 \\ \frac{1}{2}p^2q(1+p) & pq(1+pq) & \frac{1}{2}pq^2(1+q) \\ \frac{1}{4}p^2q^2 & \frac{1}{2}pq^2(1+q) & \frac{1}{4}q^2(1+q)^2 \end{pmatrix}.$$

This is the standard result obtained by using the random mating frequency $f_i f_j$. We now want to find (dSS) by using the general pattern (3) of deviations from random mating. This is done in Table 6 which is analogous to Table 5 for (PC) except that the entries of (3) are written in a single column to save space.

The nine column headings of Table 6 denote the genotypes of the two siblings; the genotype above the line is the first child; that below the second child. To find the frequency of AA/AA sibpairs, we use the conditional probabilities in the first column, each multiplied by its deviation coefficients on the left and then find the sum of such products. Thus, for the AA/AA sibpair,

$$a + \frac{1}{4}(-a - b) + \frac{1}{4}(-a - c) + \frac{1}{16}(2b + 2c) = \frac{1}{2}a - \frac{1}{8}b - \frac{1}{8}c.$$

This is the first entry of (dSS) shown in the lower half of Table 6. The frequency of the other eight types of sibpairs are found in a similar way.

The lower portion of Table 6 is then (dSS). First, we note that the E_1 component contributes $a(\frac{1}{2}E_1)$, just like in the case of (PC). Second, we note that b and c always appear together and have the same sign. This means that the E_2 and E_3 components contribute to (dSS) the same way. Their coefficients are

$$\frac{1}{8} \begin{pmatrix} -1 & 0 & 1 \\ 0 & 4 & -4 \\ 1 & -4 & 3 \end{pmatrix} = \frac{1}{8}(-E_1 + E_2 + E_3)$$

as may be seen from the bottom row of Table 3. The general expression for (dSS) is then

$$(dSS) = \frac{1}{2}aE_1 + \frac{1}{8}(b + c)(-E_1 + E_2 + E_3). \quad (6)$$

As a special example, consider the doubly symmetrical pattern $E_1 + E_2 + E_3$ for which $(a, b, c, d) = (1, 1, 1, 1)$ as shown in the bottom row of Table 3. We have already seen that for this pattern (dPC) = 0 by (5). Now we see that its (dSS) = $\frac{1}{4}(E_1 + E_2 + E_3)$ by (6), exactly a quarter of the mating pattern. This may be readily verified by direct calculation.

These algebraic details may not be too important; the main point is that both (dPC) and (dSS) are linear functions of the elemental patterns which contribute nothing to the covariance of a genetic correlation table. It is this property that causes the parent-child and sib-sib correlations to remain 1/2 in a pseudo-random mating population.

TABLE 5

Derivation of the parent-child distribution of deviation coefficients from the general pattern (3)

Mating	Child			Total
	AA	Aa	aa	
AA × $\begin{cases} AA \\ Aa \\ aa \end{cases}$	$\begin{matrix} a \\ -0.5a - 0.5b \end{matrix}$	$\begin{matrix} -0.5a - 0.5b \\ b \end{matrix}$	0	
Aa × $\begin{cases} AA \\ Aa \\ aa \end{cases}$	$\begin{matrix} -0.5a & -0.5c \\ 0.5b + 0.5c \end{matrix}$	$\begin{matrix} -0.5a & -0.5c \\ b + c \\ 0.5a - b - 0.5c \end{matrix}$	$\begin{matrix} 0.5b + 0.5c \\ 0.5a - b - 0.5c \end{matrix}$	
aa × $\begin{cases} AA \\ Aa \\ aa \end{cases}$	0	$\begin{matrix} c \\ 0.5a - 0.5b - c \end{matrix}$	$\begin{matrix} 0.5a - 0.5b - c \\ -a + b + c \end{matrix}$	
AA	0.5a - 0.5b	-0.5a + 0.5b	0	0
Aa	-0.5a + 0.5b	0	0.5a - 0.5b	0
aa	0	0.5a - 0.5b	-0.5a + 0.5b	0
Total	0	0	0	0

TABLE 6

Derivation of the sib-sib distribution of deviation coefficients from the general pattern (3)

Mating deviation type coefficient	Conditional probabilities of sib-sib pairs								
	$\frac{AA}{AA}$	$\frac{AA}{Aa}$	$\frac{AA}{aa}$	$\frac{Aa}{AA}$	$\frac{Aa}{Aa}$	$\frac{Aa}{aa}$	$\frac{aa}{AA}$	$\frac{aa}{Aa}$	$\frac{aa}{aa}$
AA × $\begin{cases} AA & a \\ Aa & -a - b \\ aa & b \end{cases}$	1	$\frac{1}{4}$		$\frac{1}{4}$	$\frac{1}{4}$	1			
Aa × $\begin{cases} AA & -a & -c \\ Aa & 2b + 2c \\ aa & a - 2b - c \end{cases}$	$\frac{1}{4}$	$\frac{1}{4}$	$\frac{1}{16}$	$\frac{1}{4}$	$\frac{1}{4}$	$\frac{2}{16}$	$\frac{2}{16}$	$\frac{1}{16}$	$\frac{1}{16}$
aa × $\begin{cases} AA & c \\ Aa & a - b - 2c \\ aa & -a + b + c \end{cases}$				$\frac{1}{4}$	$\frac{1}{4}$			$\frac{1}{4}$	1
Sib-sib distribution of deviations									
	AA				Aa				
AA	$\frac{1}{2}a - \frac{1}{8}b - \frac{1}{8}c$				$-\frac{1}{2}a$				
Aa	$-\frac{1}{2}a$				$\frac{1}{2}b + \frac{1}{2}c$				
aa	$\frac{1}{8}b + \frac{1}{8}c$				$\frac{1}{2}a - \frac{1}{2}b - \frac{1}{2}c$				
						$\frac{1}{8}b + \frac{1}{8}c$			
						$\frac{1}{2}a - \frac{1}{2}b - \frac{1}{2}c$			
						$-\frac{1}{2}a + \frac{3}{8}b + \frac{3}{8}c$			

SEX-LINKED SYSTEM

On the assumption that males are (A, a) and females are (AA, Aa, aa), there are only six types of mating (instead of nine) but there are five types of children (instead of three). Due to these restrictions, only one elemental pseudo-random mating pattern has been found, viz.,

$$E_0 = \begin{pmatrix} 1 & -2 & 1 \\ -1 & 2 & -1 \end{pmatrix}$$

This is the pattern employed in Table 7A. The total daughters and sons produced by the six types of

mating (Table 7B) show that the equilibrium population is indistinguishable from that of true random mating.

The parent-child (Table 7C) distributions are easily found from Table 7B by pooling the offspring of fathers or the offspring of mothers. There are four types of parent-child pairs for a sex-linked locus. An examination of Table 7C shows that:

$$(\text{mother-daughter}) = (\text{PC}) + E_1$$

where (PC) is the same (PC) for parent-child pairs for an autosomal locus. The other three types of parent-child pairs have exactly the same distribution

TABLE 7
A pseudo-random-mating population for a sex-linked locus

A. Mating frequency						
		AA	Aa	aa	Total	
	A	$p^3 + h$	$2p^2q - 2h$	$pq^2 + h$	p	
	a	$p^2q - h$	$2pq^2 + 2h$	$q^3 - h$	q	
	Total	p^2	$2pq$	q^2	1.00	

B. Total offspring						
Mother	Father	Daughters			Sons	
		AA	Aa	aa	A	a
AA	× A	$p^3 + h$			$p^3 + h$	
AA	× a		$p^2q - h$		$p^2q - h$	
Aa	× A	$p^2q - h$	$p^2q - h$		$p^2q - h$	$p^2q - h$
Aa	× a		$pq^2 + h$	$pq^2 + h$	$pq^2 + h$	$pq^2 + h$
aa	× A		$pq^2 + h$			$pq^2 + h$
aa	× a			$q^3 - h$		$q^3 - h$
	Total	p^2	$2pq$	q^2	p	q

C. Parent-child						
		Daughters			Sons	
		AA	Aa	aa	A	a
Mother	AA	$p^3 + h$	$p^2q - h$		p^2	0
	Aa	$p^2q - h$	pq	$pq^2 + h$	pq	pq
	aa		$pq^2 + h$	$q^3 - h$	0	q^2
Father	A	p^2	pq	0	p^2	pq
	a	0	pq	q^2	pq	q^2

as in a true random-mating population, without any deviations.

There are three types of sib-sib pairs for a sex-linked system. The calculations are routine, following the same general procedure of Table 6. We omit the detailed tabulation of such calculations and give only the deviation patterns, $d(\text{sib/sib})$, from the standard random mating results:

$$d(\text{sister/sister}) = \frac{1}{2}E_1$$

$$d(\text{brother/sister}) = \frac{1}{2}E_0$$

$$d(\text{brother/brother}) = 0.$$

The distribution for the three types of sib pairs and their correlations for a true random mating population may be found in several elementary texts [e.g., Li (1976), p. 141]. To summarize, the eight correlations (one for mates, four for parent-child, and three for sib-sib) will all remain the same as those of a true random mating population.

MULTIPLE ALLELES

Multiple alleles would greatly increase the number of patterns of deviations for pseudo-random mating

populations. When there are three alleles, there will be six genotypes and the deviation pattern is given by a 6×6 matrix of 36 coefficients. Due to the large amount of algebra involved, no attempt has been made to find the most general form of the desired patterns. In principle, it may be found by the criterion of random union of gametes which involves nine equations. However, some elemental and symmetrical patterns may be obtained quite easily. One elemental and one symmetrical form are shown in Table 8 as examples. The purpose is merely to show the existence of pseudo-random mating populations for multiple alleles.

Multiple alleles also permit more flexibility for sex-linked systems. Again, one example for three alleles is shown in the bottom portion of Table 8 where a and b are arbitrary numbers.

DISCUSSION

An infinite number of patterns of deviations from random mating exists for autosomal loci that would make a population pseudo-random mating. This could be a contributing factor to the robustness of the Hardy-Weinberg law. The usual "tests for ran-

TABLE 8

Three alleles: examples of patterns of deviations from random mating that would make the population pseudo-random mating

	A_1A_1	A_1A_2	A_1A_3	A_2A_2	A_2A_3	A_3A_3
A_1A_1	2	-1	-1	0	0	0
A_1A_2	-1	0	0	1	0	0
A_1A_3	-1	0	0	0	0	1
A_2A_2	0	1	0	1	-2	0
A_2A_3	0	0	0	-2	0	2
A_3A_3	0	0	1	0	2	-3
A_1A_1	10	-7	-7	1	2	1
A_1A_2	-7	4	4	-7	4	2
A_1A_3	-7	4	4	2	4	-7
A_2A_2	1	-7	2	10	-7	1
A_2A_3	2	4	4	-7	4	-7
A_3A_3	1	2	-7	1	-7	10

Sex-linked system						
A_1	a	$-a$	$-a$	a	$-a$	a
A_2	b	$-b$	$-b$	b	$-b$	b
A_3	$-a - b$	$a + b$	$a + b$	$-a - b$	$a + b$	$-a - b$

dom mating" are actually only tests for random union of gametes which yields the Hardy-Weinberg law, whatever the mating pattern in the population. The situation described in this report makes the study of the mating pattern of a population a worthwhile subject.

If two pairs of genes are independently distributed in a population and each locus has its own deviation pattern, it is possible that pseudo-random mating populations also exist for two loci. However, if there are "interactions" between the two patterns, so that

the 9×9 deviation pattern must be taken as one overall pattern, the situation would be much more complicated than indicated here. I leave this problem to other investigators.

Similarly, pseudo-random mating populations may exist for a cytonuclear system as well. A cytonuclear system is one that involves a pair of nuclear autosomal genes and a cytoplasmic gene, such as the gene (M or m) residing in mitochondria in the cytoplasm. Whether the nuclear and cytoplasmic genes are distributed independently or not in a population, pseudo-random mating populations are possible.

In view of all these possibilities with respect to autosomal loci, sex-linked loci, cytoplasmic genes, and two or multiple alleles, when we observe reasonable agreement with random mating expectations from a sample, we really could not be sure what the mating pattern might be in the population.

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