

GENERATION MATRIX METHOD OF STUDYING INBREEDING SYSTEMS—I

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SUMMARY

The present study relates to the calculation of joint distribution of full-sib pairs and parent-offspring pairs under full-sib and parent-offspring mating systems by the generation matrix technique and also working out the correlation of these pairs there from. The method is tedious in the case of full-sib mating, but it is comparatively easier in the case of parent-offspring mating, as the conditional probability matrix in this case can be easily generated. The correlation between full-sib pairs and parent offspring pairs under full-sib and parent offspring mating systems were calculated for ten generations of continued mating of that particular system of mating and the trend of the correlation was properly interpreted.

1. INTRODUCTION

The problem of correlation between relatives under inbreeding systems was studied by several authors such as Fisher [1] [2] Wright [12], Haldane [5] [6], Kempthorne [8], Horner [7], Korde [10] and others. Fisher, Wright and Haldane gave a general treatment of the subject. Kempthorne and Horner worked with autosomal gene cases under full-sib mating and parent-offspring mating respectively, but Korde dealt with sex-linked gene case. Most of these workers used the generation matrix technique to evolve the joint distribution of the relatives under different systems of inbreeding. In this paper a study of correlation by generation matrix method with particular reference to full-sib mating and parent offspring mating under autosomal gene case is made.

2. FULL-SIB MATING

Fisher [2] was the first worker, who derived the generation matrix for full-sib mating by considering a single locus with two alleles 'A' and 'a'. However, he considered only the mating types

and did not make any distinction between the kinds of matings such as AAxAA and aaxaa. Kempthorne [8] however using the same method for continued full-sib mating system employed kind of matings rather than types, viz. mating types AAxAA was considered different from the kind of mating aaxaa. But he did not make any difference between mating types AAxAA and AaxAA as well as Aaxaa and aaxAa. Hence all the nine kinds of mating types, viz. AAxAA, AAxAa, AAxaa, AaxAA, AaxAa, Aaxaa, aaxAA, aaxAa, aaxaa are considered in this investigation. Let the frequencies in the initial generation be denoted by $U^{(0)}$'s as shown in table one.

TABLE 1

Mating types	Freq.	Full-sib mating types with respective proportion
AAxAA	$U_{22}^{(0)}$	(AAxAA) 1
AAxAa	$U_{21}^{(0)}$	(AAxAA), (AAxAa), (Aa x AA), (Aa x Aa) 1/4 (1/4 1/4 1/4
AAxaa	$U_{20}^{(0)}$	(Aa x Aa) 1
Aa x AA	$U_{12}^{(0)}$	(AAxAA), (AAxAa), (Aa x AA), (Aa x Aa) 1/4 1/4 1/4 1/4
Aa x Aa	$U_{11}^{(0)}$	(AAxAA), (AAxAa), (AAxaa), (Aa x AA), (Aa x Aa) 1/16 1/8 1/16 1/8 1/4 (Aa x aa), (aa x AA), (aa x Aa), (aa x aa) 1/8 1/16 1/8 1/16
Aa x aa	$U_{10}^{(0)}$	(Aa x Aa), (Aa x aa), (aa x Aa), (aa x aa) 1/4 1/4 1/4 1/4
aa x AA	$U_{02}^{(0)}$	(Aa x Aa) 1
aa x Aa	$U_{01}^{(0)}$	(Aa x Aa), (Aa x aa), (aa x Aa), (aa x aa) 1/4 1/4 1/4 1/4
aa x aa	$U_{00}^{(0)}$	(aa x aa) 1

We can write down the frequencies in the next generations;

$$U_{22}^{(1)} = U_{22}^{(0)} + \frac{1}{4} U_{21}^{(0)} + \frac{1}{4} U_{12}^{(0)} + \frac{1}{16} U_{11}^{(0)}$$

$$U_{21}^{(1)} = \frac{1}{4} U_{21}^{(0)} + \frac{1}{4} U_{12}^{(0)} + \frac{1}{8} U_{11}^{(0)}$$

$$U_{00}^{(1)} = \frac{1}{16} U_{11}^{(0)} + \frac{1}{4} U_{10}^{(0)} + \frac{1}{4} U_{01}^{(0)} + U_{00}^{(0)}$$

which can be expressed in the matrix form as:—

$$\begin{bmatrix} U_{22}^{(1)} \\ U_{21}^{(1)} \\ U_{20}^{(1)} \\ U_{12}^{(1)} \\ U_{11}^{(1)} \\ U_{10}^{(1)} \\ U_{02}^{(1)} \\ U_{01}^{(1)} \\ U_{00}^{(1)} \end{bmatrix} = \begin{bmatrix} 1 & \frac{1}{4} & 0 & \frac{1}{4} & \frac{1}{16} & 0 & 0 & 0 & 0 \\ 0 & \frac{1}{4} & 0 & \frac{1}{4} & \frac{1}{8} & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & \frac{1}{16} & 0 & 0 & 0 & 0 \\ 0 & \frac{1}{4} & 0 & \frac{1}{4} & \frac{1}{8} & 0 & 0 & 0 & 0 \\ 0 & \frac{1}{4} & 1 & \frac{1}{4} & \frac{1}{4} & \frac{1}{4} & 1 & \frac{1}{4} & 0 \\ 0 & 0 & 0 & 0 & \frac{1}{8} & \frac{1}{4} & 0 & \frac{1}{4} & 0 \\ 0 & 0 & 0 & 0 & \frac{1}{16} & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & \frac{1}{8} & \frac{1}{4} & 0 & \frac{1}{4} & 0 \\ 0 & 0 & 0 & 0 & \frac{1}{16} & \frac{1}{4} & 0 & \frac{1}{4} & 1 \end{bmatrix} \begin{bmatrix} U_{22}^{(0)} \\ U_{21}^{(0)} \\ U_{20}^{(0)} \\ U_{12}^{(0)} \\ U_{11}^{(0)} \\ U_{10}^{(0)} \\ U_{02}^{(0)} \\ U_{01}^{(0)} \\ U_{00}^{(0)} \end{bmatrix}$$

$$\underline{U}^{(1)} = \underline{A} \underline{U}^{(0)}$$

where \underline{A} is called the generation matrix for full-sib mating.

Denoting the vector of frequencies for the n^{th} generation as $\underline{U}^{(n)}$ the recurrence relation for the vector of frequencies is given by

$$\underline{U}^{(n)} = \underline{A}^{(n)} \underline{U}^{(0)} \dots(1)$$

where

$$\underline{U}^{(0)} = \begin{bmatrix} U_{22}^{(0)} & U_{21}^{(0)} & U_{20}^{(0)} & U_{12}^{(0)} & U_{11}^{(0)} & U_{10}^{(0)} & U_{02}^{(0)} & U_{01}^{(0)} & U_{00}^{(0)} \end{bmatrix}$$

and

$$\underline{U}^{(n)} = \begin{bmatrix} U_{22}^{(n)} & U_{21}^{(n)} & U_{20}^{(n)} & U_{12}^{(n)} & U_{11}^{(n)} & U_{10}^{(n)} & U_{02}^{(n)} & U_{01}^{(n)} & U_{00}^{(n)} \end{bmatrix}$$

Hence the frequencies in the n^{th} generation can be worked out if one knows the Matrix \underline{A} as well as the initial vector $\underline{U}^{(0)}$. However, when \underline{A} is of large order and n is also large, it may not be easy to obtain \underline{A}^n by direct multiplication. In such cases \underline{A}^n is calculated

with the help of diagonalisation. Consider a single locus with two alleles 'A' and 'a' with proportions p and q ($=1-p$). Then $U^{(0)}$ the vector of frequencies of the nine mating types under random mating population in equilibrium would be $U^{(0)} = [p^4 \ 2p^3q \ p^2q^2 \ 2p^2q \ 4p^2q^2 \ 2pq^3 \ p^2q^2 \ 2pq^3 \ q^4]$. Now the vector of frequencies of the full-sib pairs from this nine matings can be obtained as $U^{(1)} = AU^{(0)}$.

The column vector of the frequencies of the full-sib pairs after the first generation of full-sib mating can be obtained in a similar manner as $U^{(2)} = AU^{(1)}$

$$\underline{U}^{(1)} = \begin{bmatrix} \frac{p^2}{4} (1+p)^2 \\ \frac{p^2q^2}{2} (1+p) \\ \frac{p^2q^2}{4} \\ \frac{p^2q}{2} (1+p) \\ pq (1+pq) \\ \frac{pq^2}{2} (1+q) \\ \frac{p^2q^2}{4} \\ \frac{pq^2}{2} (1+q) \\ \frac{q^2}{4} (1+q)^2 \end{bmatrix} \quad \underline{U}^{(2)} = \begin{bmatrix} \frac{p}{16} (1+6p+6p^2+p^3) \\ \frac{pq}{8} (1+3p+p^2) \\ \frac{pq}{16} (1+pq) \\ \frac{pq}{8} (1+3p+p^2) \\ \frac{pq}{4} (3+pq) \\ \frac{pq}{8} (1+3q+q^2) \\ \frac{pq}{16} (1+pq) \\ \frac{pq}{8} (1+3q+q^2) \\ \frac{q}{16} (1+8q+6q^2+q^3) \end{bmatrix}$$

Hence the joint distribution (correlation table) of full-sib pairs after the first generation of full-sib mating is written as in table 2.

TABLE 2

Correlation table for full-sib pairs after the first generation of full-sib mating

<i>SIB-II</i>			
<i>AA</i>	<i>Aa</i>	<i>aa</i>	<i>Total</i>
<i>AA</i> $\frac{p}{16} (1+8p+6p^2+p^3)$	$\frac{pq}{8} (1+3p+p^2)$	$\frac{pq}{16} (1+pq)$	$\frac{p}{4} (1+3p)$
SI B-I			
<i>Aa</i> $\frac{pq}{8} (1+3p+p^2)$	$\frac{pq}{4} (3+pq)$	$\frac{pq}{8} (1+3q+q^2)$	$\frac{3}{2} pq$
<i>aa</i> $\frac{pq}{16} (1+pq)$	$\frac{pq}{8} (1+3q+q^2)$	$\frac{q}{16} (1+8q+6q^2+q^3)$	$\frac{q}{4} (1+3q)$
Total $\frac{p}{4} (1+3p)$	$\frac{3}{2} pq$	$\frac{q}{4} (1+3q)$	1

The correlation coefficient between full-sib pairs after first generation of full-sib mating is worked out directly from the correlation table assuming additive genic effects as

$$\begin{matrix} Sr^{(1)} \\ \text{F.S.} \end{matrix} = 0.600$$

Similarly the correlation table for full-sib pairs after the 2nd, 3rd...etc. generations of full-sib mating are worked out. The correlation coefficient of full-sib pairs in first ten generations of full-sib mating is as given in table 9.

2.2. Parent-Offspring Correlation Under Full-Sib Mating

The joint distribution of parent and offspring after the first generation of full-sib mating with single locus with two alleles 'A' and 'a' with proportion *p* and *q* ($=1-p$) can be obtained by pairing out of the parents with an offspring obtained from a respective mating out of nine types of full-sib mating, whose frequencies are given by the elements of the vector $U^{(1)}$ as in table 3.

TABLE 3
Correlation table for parent-offspring pairs after the first
generation of full-sib mating
Offspring

		AA	Aa	aa	Total
Parent	AA	$\frac{p^2}{2}(1+p)$	$\frac{1}{2}P^2q$	0	p^2
	Aa	$\frac{pq}{4}(1+2p)$	pq	$\frac{pq}{4}(1+2q)$	$2pq$
	aa	0	$\frac{1}{2}pq^2$	$\frac{q^2}{2}(1+q)$	q^2
Total	1	$\frac{p}{4}(1+3p)$	$\frac{3}{2}pq$	$\frac{q}{2}(1+3q)$	1

Hence the correlation coefficient $S^{r(1)} p-o$ between parent and offspring after the first generation of full-sib mating is obtained directly from the correlation table assuming the additive genic effect as

$$S^{r(1)} p-o=0.670$$

In a similar manner we can find the joint distribution and correlation of the parents and offspring pairs after the second generation of full-sib mating by using the vector of frequencies $U^{(2)}$ of the second generation of full-sib mating as in table 4.

TABLE 4
Correlation table of parent and offspring for the second
generation of full-sib mating.
Offspring

		AA	Aa	aa	Total
Parent	AA	$\frac{p}{8}(1+5p+2p^2)$	$\frac{pq}{8}(1+2p)$	0	$\frac{p}{4}(1+3p)$
	Aa	$\frac{pq}{4}(1+p)$	$\frac{3}{4}pq$	$\frac{pq}{4}(1+q)$	$\frac{3}{2}pq$
	aa	0	$\frac{pq}{8}(1+2q)$	$\frac{q}{8}(1+5q+2q^2)$	$\frac{q}{4}(1+3q)$
Total	1	$\frac{p}{8}(3+5p)$	$\frac{5}{4}pq$	$\frac{q}{8}(3+5q)$	1

The correlation $S^{r(2)} p-o$ between parent and offspring in this case is calculated directly by assuming additive genic effects as

$$S^{r(2)} p-o=0.762$$

Hence the generation matrix can be written as :

$$A^* = \begin{bmatrix} 1 & \frac{1}{2} & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & \frac{1}{2} & 1 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & \frac{1}{2} & \frac{1}{4} & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & \frac{1}{2} & \frac{1}{2} & \frac{1}{2} & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & \frac{1}{2} & \frac{1}{2} & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 1 & \frac{1}{2} & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & \frac{1}{2} & 1 \end{bmatrix}$$

With the help of this generation matrix the vector of frequencies after n -th generation of parent-offspring mating can be calculated as in (1) as $\underline{U}^{(n)*} = A^n \underline{U}^{(0)}$ —(2)

3.1. Full-Sib Correlation under Parent-Offspring Mating

As in the case of full-sib mating system, the parent offspring mating system is also developed from the nine mating types from the equilibrium random mating population. Now the vector of frequencies $\underline{U}^{(1)*}$ of the nine parent-offspring mating types can be obtained as

$$\underline{U}^{(1)*} = A^* \underline{U}^{(0)}$$

Thus we can write down

$$\underline{U}^{(1)*} = [p^3, p^2q, 0, p^2q, pq, pq,^2, 0, pq,^2, q^3]$$

Now the joint distribution of full-sib pairs under the first generation of parent-offspring mating can be obtained by pairing offspring in the first generation of the parent-offspring mating within each of these nine mating types whose frequencies are given by the vector $\underline{U}^{(1)}$ as given in table 6.

TABLE 6

Correlation table for the full sib pairs in the First Generation of Parent Offspring Mating

<i>SIB II</i>				
<i>AA</i>	<i>Aa</i>	<i>aa</i>	<i>Total</i>	
<i>AA</i>	$\frac{p}{16}(1+7p+8p^2)$	$\frac{pq}{8}(1+4p)$	$\frac{1}{16}pq$	$\frac{p}{4}(1+3p)$
<i>Aa</i>	$\frac{pq}{8}(1+4p)$	$\frac{3}{8}pq$	$\frac{pq}{8}(1+4q)$	$\frac{3}{4}pq$
Sib I <i>aa</i>	$\frac{1}{16}pq$	$\frac{pq}{8}(1+4q)$	$\frac{q}{16}(1+7q+8q^2)$	$\frac{q}{4}(1+3q)$
Total	$\frac{p}{4}(1+3p)$	$\frac{3}{2}pq$	$\frac{q}{4}(1+3p)$	1

Thus the correlation coefficient $p-o$ $r^{(1)}$ F.S, between full-sib pairs under the first generation of parent-offspring mating is obtained directly by assuming additive genic effects as

$$p-o r^{(1)} F.S. = 0.600$$

In a similar manner the column vector $\underline{U}^{(2)*}$ of the frequencies of the nine parent-offspring mating types in the second generation of parent offspring can be obtained as

$$\underline{U}^{(2)*} = \underline{A}^* \underline{U}^{(1)}$$

Hence we can write down

$$\underline{U}^{(2)*} = [\frac{1}{2}p^2(1+p) \frac{1}{2}pq^2 \ 0 \ \frac{1}{2}pq(1+2p) \ pq \ \frac{1}{2}pq(1+2q) \ 0 \ \frac{1}{2}pq^2 \ \frac{1}{2}p^2(1+q)]$$

Now as in the previous case by pairing and pooling the frequencies of respective full-sib pairs from the offspring the second generation of parent-offspring mating, the joint distribution of full-sib pairs in the 2nd generation of parent-offspring mating can be obtained as given in table 7.

TABLE 7

Correlation Table for Full-Sib pairs in the 2nd Generation of Parent-Offspring Mating

<i>SIB II</i>			
<i>AA</i>	<i>Aa</i>	<i>aa</i>	<i>Total</i>
<i>AA</i> $\frac{p}{8}(1+5p+2p^2)$	$\frac{pq}{16}(3+4p)$	$\frac{pq}{16}$	$\frac{p}{8}(3+5p)$
<i>Aa</i> $\frac{pq}{16}(3+4p)$	$\frac{5}{8}pq$	$\frac{pq}{16}(3+4q)$	$\frac{5}{4}pq$
<i>SIB I aa</i> $\frac{pq}{16}$	$\frac{pq}{16}(3+4q)$	$\frac{q}{8}(1+5q+2q^2)$	$\frac{q}{8}(3+5q)$
<i>Total</i> $\frac{p}{8}(3+5p)$	$\frac{5}{4}pq$	$\frac{q}{8}(3+5q)$	1

The correlation coefficient $p-o r^2$ F.S. between full-sib pairs after the 2-nd generation of parent-offspring mating is obtained directly as $p-o r^{(2)}$ F.S. = 0.717

Similarly the joint distribution and correlation coefficient for the full-sib pairs in the 3rd, 4th, . . . etc. generations of parent-offspring mating can be worked out. The correlation coefficient between full sib pairs upto ten generations of parent-offspring mating is given in table 9.

3.2. Parent-Offspring Correlation under Parent-offspring Mating.

It is seen from section 3.1 that the column vector of frequencies of the parent-offspring pairs from an equilibrium random mating population can be calculated as $\underline{U}^{(1)*}, \underline{U}^{(2)*}$. . . for the 1st, 2nd etc. generation of parent-offspring mating respectively. Hence we can write down the correlation table of parent-offspring pairs in the first generation of parent-offspring mating as given in table 8

TABLE 8
Correlation Table between Parent and Offspring pairs in the First Generation of Parent-Offspring Mating

		Offspring			
		AA	Aa	aa	Total
Parent	AA	$\frac{1}{2}p^2(1+p)$	$\frac{1}{2}p^2q$	0	p^2
	Aa	$\frac{1}{2}pq(1+2p)$	pq	$\frac{1}{2}pq(1+2q)$	$2pq$
	aa	0	$\frac{1}{2}pq^2$	$\frac{1}{2}q^2(1+p)$	q^2
Total		$\frac{1}{2}p(1+3p)$	$\frac{3}{2}pq$	$\frac{1}{2}q(1+3q)$	1

The matrix $p-o_{-}^{M(1)}(p-o)$ of conditional probabilities of parent-offspring relationship after the first generation of parent-offspring mating can be conveniently written down as function of F and T as

$$p-o_{-}^{M(1)}(p-o) = \frac{1}{2}F_{-} + \frac{1}{2}T_{-}$$

where $F_{-} = \begin{bmatrix} 1 & 0 & 0 \\ \frac{1}{2} & \frac{1}{2} & \frac{1}{2} \\ 0 & 0 & 1 \end{bmatrix}$ and $T_{-} = \begin{bmatrix} p & q & 0 \\ \frac{1}{2}p & \frac{1}{2} & \frac{1}{2}p \\ p & q & q \end{bmatrix}$

Similarly from the correlation table of parent-offspring pairs under the second generation of parent-offspring mating one can write the matrix of condition probabilities $p-o_{-}^{M(2)}(p-o)$ as

$$p-o_{-}^{M(2)}(p-o) = \frac{1}{2}(1 + \frac{1}{2})F_{-} + (\frac{1}{2})^2 T_{-}$$

In general the matrix of conditional probabilities $p-o_{-}^{M(n)}(p-o)$ of parent-offspring relation in the n -th generation of parent-offspring mating can be obtained as

$$p-o_{-}^{M(n)}(p-o) = [1 - (\frac{1}{2})^n] F_{-} + (\frac{1}{2})^n T_{-} \quad \dots(3)$$

where n is the number of generation.

The joint distribution between parent and offspring in any generation of parent-offspring mating can be obtained from the matrix of conditional probabilities by multiplying the elements of the 1st, 2nd, 3rd rows by p^2 , $2pq$ and q^2 respectively.

The correlation between parent and offspring can be calculated by using the technique explained by Li and Sacks [11] as

$$p-o^{r(n)} p-o = C_F r_F + C_T r_T$$

where $C_F = 1 - (\frac{1}{2})^n$, $C_T = (\frac{1}{2})^n$, $r_F = 1$ and $r_T = \frac{1}{2}$ (r_F and r_T are the correlation coefficients, calculated from the two-way tables obtained by multiplying the rows of F and T by $(p^2, 2pq$ and q^2 respectively)

Hence we get $p-o^{r(n)} p-o = 1 - (\frac{1}{2})^n + (\frac{1}{2})^n \frac{1}{2} = 1 - (\frac{1}{2})^{n+1}$ —(4)

where n is the number of generations of parent-offspring mating. The values of the correlation coefficients at the different generations of mating can be obtained by putting $n=0, 1, 2, \dots etc.$ The correlation coefficient between parent and offspring in ten generations of parent offspring mating is given in table 9.

TABLE 9

Correlation between full-sib pairs and parent-offspring pairs in ten generations of full-sib and parent-offspring mating systems

Generation	Full-sib mating system		Parent-offspring mating system	
	Full sib-pairs	Parent-offspring pairs	Full-sib pairs	Parent-offspring pairs
0	0.500	0.500	0.500	0.500
1	0.600	0.670	0.600	0.750
2	0.727	0.762	0.717	0.875
3	0.791	0.826	0.734	0.938
4	0.843	0.868	0.742	0.969
5	0.878	0.899	0.746	0.934
6	0.905	0.921	0.748	0.992
7	0.925	0.941	0.749	0.996
8	0.942	0.949	0.749	0.998
9	0.954	0.960	0.749	0.999
10	0.967	0.968	0.750	0.999

Note : 0-th generation stands for random mating.

The results of full-sib pairs and parent offspring pairs under parent-offspring mating in table 9 are fully in agreement with the results given by George and Narayan [4] when k , the member of

offspring is one. Also the values of the correlations of parent-offspring and full-sibs under full-sib mating in table 9 are in fully agreement with values given by Wright [12] when $t=0,2,\dots,10$ (where t is the number of generations).

4. CONCLUSION

Under full-sib mating system the correlation table for full-sib pairs and parent offspring pairs are comparatively difficult to calculate. But in the case of parent-offspring mating system the correlation table for the parent-offspring pairs can be easily calculated from the conditional probability matrix as given in relation (3) and the correlation as given in relation (4).

From the table 9, one can easily observe that the correlation increases as the number of generation increases and ultimately reaches the limit unity when the number of generation increases indefinitely large. It is interesting to observe that the parent-offspring correlation is higher in magnitude than that of the full-sib correlation under both the systems of mating, eventhough the correlation in all the four cases are equal to 0.5 under random mating. The parent-offspring correlation under parent-offspring mating increases at a rapid rate than all the other three types of correlations even at the first generation of parent-offspring mating and become almost unity at the tenth generation.

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