GENERATION MATRIX METHOD OF STUDYING INBREEDING SYSTEM II

·BY

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SUMMARY

A study of correlation between the various full-sib pairs and parent-offspring pains by evolving joint distributions of relative pairs have been made. Sister-sister pair correlation is maximum at every generation of full-sib mating followed by mother-son and father-daughter correlation. The correlations between mother-son, pair and fatherdaughter pair are identical. The amount of correlation between father and son increases as the member of generations of inbreeding increases; but they are uncorrelated under random mating.

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1. INTRODUCTION

The problem of correlation between relatives in the case of sex-linked gene has been studied by several authors such as Fisher [1], Haldane [4], Li [6], Korde [5], George add Naraiu [3]. Fven though, Fisher, Haldane and Li derived the generation matrix for full-sib mating with sex-linked genes, it is in fact Korde and George, who made use of this generation matrix technique in studying the inbreeding systems. The problem of studying the various full-sib mating in the sex linked gene case has not been completely explored by any of these authors. In this paper a study of correlation between the various full-sib pairs-viz; (i) brother-sister, (ii) Sister-sister, (iii) brother-brother and various parent-offspring pairs-viz: (i) mother-daughter, (ii) mother-son, (iii) father-daughter (iv) father-son, under full-sib mating (sex-linked gene case) by evolving the joint distributions of the relative pairs, have been made.

2. CASE OF FULL-SIB PAIRS

2.1. Brother-Sister Correlation

Consider a male as heterogametic sex (A or a) and a female as homogametic sex (AA, Aa, aa). Now there will be six mating types in the case of sex-Linked genes, at a single locus with two alleles say A and a. They are $AA \times A$, $AA \times a$, $Aa \times A$, $Aa \times a$, $aa \times A$ and $aa \times a$. Let the frequencies at the initial generation of these six mating types be $V_{21}^{(o)}$, $V_{20}^{(o)}$, $V_{11}^{(o)}$, $V_{01}^{(o)}$, $V_{00}^{(o)}$ respectively.

The generation matrix of full-sib pairs (brother-sister pairs) are obtained as follows :

Mating types	Freq.	Brother-sister pairs with respective proportions
AA×A	$V_{21}^{(y)}$	(AA, A)
$AA \times a$	$V_{20}^{(o)}$	(Aa, A)
Aa×A	$V_{11}^{(e)}$	(AA, A), (AA, a), (Aa, A), (Aa, a)
Aa×a	V ^(o) 10	(Aa, A), (Aa, a), (Aa, A). (aa, a)
$aa \times A$	$V_{01}^{(o)}$	(<i>Aa</i> , <i>a</i>)
aa×a	V(0)	(a a, a)

Let the frequency of the six brother-sister pairs under random mating be denoted by $V_{21}^{(o)}$, $V_{20}^{(o)}$, $V_{11}^{(o)}$, $V_{10}^{(o)}$, $V_{01}^{(o)}$, $V_{00}^{(o)}$ respectively. These frequency can be worked out as follows:

 $V_{21}^{(o)} = V_{21}^{(o)} + \frac{1}{4}V_{11}^{(o)}$ $V_{20}^{(o)} = \frac{1}{3}V_{11}^{(o)}$ $V_{11}^{(o)} = V_{20}^{(o)} + \frac{1}{4}V_{11}^{(o)} + \frac{1}{4}V_{10}^{(o)}$ $V_{10}^{(o)} = \frac{1}{4}V_{11}^{(o)} + \frac{1}{4}V_{10}^{(0)} + V_{01}^{(o)}$ $V_{01}^{(o)} = \frac{1}{4}V_{10}^{(o)}$ $V_{00}^{(o)} = \frac{1}{4}V_{10}^{(o)} + V_{00}^{(o)}$

These relation-ships in the matrix notation can be written as

$$\begin{bmatrix} V_{21}^{(o)} \\ V_{20}^{(o)} \\ V_{11}^{(o)} \\ V_{10}^{(o)} \\ V_{10}^{(o)} \\ V_{10}^{(o)} \\ V_{01}^{(o)} \\ V_{00}^{(o)} \end{bmatrix} = \begin{bmatrix} 1 & 0 & \frac{1}{4} & 0 & 0 & 0 \\ 0 & 0 & \frac{1}{4} & 0 & 0 & 0 \\ 0 & 0 & 0 & \frac{1}{4} & 3 & 1 \\ 0 & 0 & \frac{1}{4} & \frac{1}{5} & 1 & 0 \\ 0 & 0 & 0 & \frac{1}{4} & 0 & 0 \\ 0 & 0 & 0 & \frac{1}{4} & 0 & 1 \end{bmatrix} \begin{bmatrix} V_{21}^{(o)} \\ V_{20}^{(o)} \\ V_{20}^{(o)} \\ V_{20}^{(o)} \\ V_{11}^{(o)} \\ V_{10}^{(o)} \\ V_{10}^{(o)} \\ V_{00}^{(o)} \end{bmatrix}$$

i.e.:
$$V^{(0)} = A_{b-s} V^{(0)}$$

where A_{b-s} is called the generation matrix for full-sib (brother-sister) mating in the case of sex-linked gene.

Denoting the vector of frequencies for the n^{th} generation of full-sib mating in the case of sex-linked gene as $\underline{V}^{(n)}$, the recurrence relation for the vector of frequencies is given by

$$\underline{V}^{(n)} = A^{n}_{b-s} \underline{V}^{(0)} \qquad \dots (1)$$

where

 $V^{(o)^{1}} = \begin{bmatrix} V_{21}^{(o)} & V_{20}^{(o)} & V_{11}^{(o)} & V_{01}^{(o)} & V_{00}^{(o)} \end{bmatrix}$

and

$$\underline{V}^{(n)} = \begin{bmatrix} V_{21}^{(n)} & V_{20}^{(n)} & V_{11}^{(n)} & V_{01}^{(n)} & V_{00}^{(n)} \end{bmatrix}$$

Hence the frequency in the n^{th} generation can be worked out if one knows the matrix A_{b-s} as well as the initial vector.

Consider a single locus with two alleies 'A' and 'a' with proportion p and q (=1-p) respectively. Then $V^{(o)}$, the vector of frequencies of the six mating types under random mating in the sex-linked gene case would be $V^{(o)_1} = (p^3, p^2q, 2pq^2, pq^2, q^3)$. Now the vector of frequencies of the brother-sister pairs under random mating, 1st generation and 2nd generation of full-sib mating in the sex-linked

gene case, can be worked out as shown below, by using equation (1).

$\int \frac{1}{2} p^2 (1+p) -$		$\left(\frac{1}{8}p\left(1+5p+2p^2\right)\right)$		$f(2+5p+p^2)$
$\frac{1}{2}p^2q$		$\frac{1}{8}pq$ (1+2p)		1 8pq (1+p)
$\frac{1}{2}pq(1+2p)$	$V^{(1)} =$	$\frac{1}{2}pq$ (1+p)	$V^{(2)} =$	≵ pq (2+p)
$\frac{1}{2}pq(1+2q)$	<u> </u>	$\frac{1}{2}pq$ (1+p)	<u>v</u>	$\frac{1}{4}pq(2+q)$
$\frac{1}{2}pq^2$		$\frac{1}{8}pq$ (1+2p)		$\frac{1}{8}pq$ (I+q)
$\left(\frac{1}{2}p^2\left(1+q\right)\right)$) ($\frac{1}{8}q(1+5q+2q)$		$\left(\frac{1}{8}p\left(2+q+5q^2\right)\right)$

The joint distributian (correlation table) of brother-sister pair^s under the first generation of full-sib mating can be written as in Table 1.

TABLE 1

Joint distribution of brother-sister pairs in the first generation of full-sib mating.

			Total		
、		. AA	Aa	aa	TO(al
Ducthen	A	$\frac{p}{8}(1+5p+p^2)$	$\frac{pq}{2}(1+q)$	$\frac{pq}{8}(1+2q)$	р
Brother	а	$\frac{p}{8} (1+5p+p^2)$ $\frac{pq}{8} (1+2p)$	$\frac{pq}{2}$ (1+q)	$\frac{q}{8}\left(1+5q+q^2\right)$	q
Total		$\frac{p}{2} (1+3p)$	$\frac{3}{2}pq$	$\frac{q}{4}$ (1+3q)	1

The correlation coefficient $s_{BS}^{r(1)}$ between brother-sister pair in the first generation of full-sib mating is worked out directly from the joint distribution by assuming additive genic effects as $s_{B-S}^{r(1)} = 0.474$.

Similarly the joint distribution of the brother-sister pairs in the 2nd 3rd, etc., generation of full-sib mating can be obtained. The correlation coefficient between brother-sister pairs in ten generations of full-sib mating in the sex-linked gene case is as given in Table 8.

2.2. Sister-Sister Correlation

The vector of frequencies of sister-sister pairs can be either obtained by pairing the female offspring of full-sib mating within each of the mating types, or by multiplying the vector of frequencies of full-sib mating by the generation matrix A_{s-s} of sister-sister pairs, which is obtained in the similar lines as explained in 2.1 and A_{s-s} can be worked out as

	٦	1	0	1	0	0	0	٦
		<u></u>	0	1	0	0	0	
	}	0	0	0	0	0	0	
		0	0	14	0	0	0	
$A_{s-s} =$		0	1	14	1	1	0	
		.0	0	0	4	0	0	
		0	0	0	0·	0	0	
		0	0	0 -	$\frac{1}{4}$	0	0	
	L	0	0	0	$\frac{1}{4}$	0	1	J

Hence the joint distribution of sister-sister pairs under the first generation of full-sib mating (sex-linked gene case) can be written as shown in table 2.

TABLE	2
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Joint distribution of sister-sister pairs in the first generation of full-sib mating

	Sister II							
:	AA	Aa	aa	Total				
AA	$\frac{p}{8}(1+5p+2p^3)$	$\frac{pq}{8}(1+2p)$	0	$\frac{p}{4}(1+3p)$				
Sister I Aa	$\frac{pq}{8}(1+2p)$	pq	$\frac{pq}{8}$ (1+2q)	$\frac{3}{2}pq$				
aa	0	$\frac{pq}{8}(1+2q)$	$\frac{q}{8}(1+5q+2q^2)$	$\frac{q}{4}(1+3q)$				
Total	$\boxed{\frac{p}{4}(1+3p)}$	$\frac{3}{2}pq$	$\frac{q}{4}(1+3q)$	1				

The correlation coefficient $s_{s-s}^{r(1)}$ between the sister-sister pairs in the first generation of full-sib mating can be obtained directly from the joint distribution (assuming the additive genic effects) as $s_{s-s}^{r(1)} = 0.8$.

Similarly the joint distribution and correlation coefficient of sister-sister pairs in 2nd, 3-rd etc. generations of full-sib mating can be worked out. The correlation coefficient between sister-sister pairs in ten generations of full-sib mating is as given in table 8.

2.3. Brother-Brother Correlation

The joint distribution of brother-brother pairs can be obtained either by pairing the male-offspring of full-sib mating within each of the mating types, or by multiplying the vector of frequencies of fullsib mating by the generation matrix A_{b-b} of brother-brother pairs, which can be derived the same way as explained in section 2.1 and A_{b-b} can be obtained as

ſ	1	1	1	1 4	0	0	ן
$A_{b-b} =$	0 0	0		1	0	0	
~	0	0	ł	1	0	0	
Ĺ	0	. 0	14	$\frac{1}{4}$	I	1 _	J

Hence the joint distribution of brother-brother pairs in the first generation of full-sib mating (sex-linked gene case) can be worked out as shown an table 3.

TABLE 3

Join tdistribution of brother-brother pairs in the first generation of full-sib mating

Brother II

		A	a	Total
	A	$\frac{p}{8}$ (5+3p)	$\frac{3}{8}$ pq	р
Brother I	а	$\frac{3}{8}$ pq	$\frac{q}{8}$ (5+3q)	q
Total		p	q	1

The matrix $S_{B-B}^{M(1)}$ of conditional probabilities in this case can be written as

$$s_{-B-B}^{M(1)} = \begin{bmatrix} \frac{1}{8} (5+3p & \frac{3}{8}p \\ \frac{3}{8}p & \frac{1}{8} (5+3q) \end{bmatrix}$$

This can be split as a function of I_{22} and o_{22} as

$$s^{M(1)}_{BBB} = \frac{5}{8}I_{22} + \frac{3}{8}O_{22}$$

Similarly the conditional probability matrix $s_{-B-B}^{M(2)}$ in the case of brother-brother pairs, under the 2nd generation of full-sib mating can be written as

$$s_{-B-B}^{M(2)} = \frac{11}{16} I_{22} + \frac{5}{16} o_{22}$$
$$I_{22} = \begin{bmatrix} 1 & 0 \\ 0 & 1 \end{bmatrix}$$

 $o_{22} = \begin{bmatrix} p & q \\ p & q \end{bmatrix}$

where

and

In general the matrix of conditional probabilities of brotherbrother pairs under full-sib mating can be written as

$$S_{-R-R}^{M(n)} = c_n I_{22} + (1 - c_n) o_{22} \qquad \dots (2)$$

 $c_n = \frac{1}{2}, \frac{5}{8}, \frac{11}{16}, \frac{24}{32}, \frac{51}{64}, \frac{107}{128}, \frac{222}{256}, \frac{457}{512}$ etc...(3)

for n the number of generation, is 0, 1, 2, 3 etc. The correlation between brother-brother pair can be calculated by using the technique explained by Li and Sacks [7] as

$$s_{B-B}^{r(n)} = c_n r_1 + (1 - c_n) r_o$$
 ...(4)

where c_n is as given in (3), and $r_I=1$, $r_o=0$, (for r_I and r_o are the correlation coefficients calculated from the two way tables obtained by multiplying the rows of $I_{22(n)}$ and o_{22} by p^2 , 2pq and q^2 repectively). Hence we get $s_{B-B}^{r(n)}=c_n$. The values of the correlation coefficients between brother-brother pairs under full-sib mating (sex-lined gene case) in ten generations are given in table 8.

where

3. _CASE OF PARENT-OFFSPRING PAIRS

3.1. Mother-daughter Correlation

The joint distribution of mother-daughter pairs in the first generation of full-sib mating can be obtained either by pairing the female parent and female offspring in the first generation of full-sib mating or by multiplying the vector of frequencies of full-sib mating by the generation matrix B_{m-d} of the mother-daughter pairs which can be derived in the similar lines as explained in section 2.1 and B_{m-d} can be worked out to be

	1	0	0	0	0	0	
	0	1	0	0	0	0	
	0	0	0	0	0	.0	
	0	0	$\frac{1}{2}$	0	0	0	
$\tilde{B}_{m-d} =$	0	0	$\frac{1}{2}$	$\frac{1}{2}$	0	0	
	0	0	0	12	0	0	
	0	0	0	0	0	0	
	0	0	0	0	1	0	
	0	0	0	0	0	1	

Hence the joint distribution of mother-daughter pairs under the 1st generation of full-sib mating can be written as shown in table 4.

		1 ABLE	4			
Correlation	table of	mother-daughter full-sib-ma	pairs, i ting	in the	e first	generation of

		· · · · · · · · · · · · · · · · · · ·	in sid mating						
			Daughter						
		AA	Aa	aa	Total				
	AA	$\frac{p^2}{2}(1+p)$ $\frac{pq}{4}(1+2p)$	$\frac{1}{2}p^{2}b$	0	p ²				
Mother	Aa	$\frac{pq}{4} (1+2p)$	Pq	$\frac{pq}{4}(1+2q)$	2 pq				
	aa	0	$\frac{1}{2} pq^2$	$\frac{pq}{4}(1+2q)$ $\frac{q^{a}}{2}(1+q)$	q^{a}				
Total		$\frac{q}{4}(1+3p)$	$\frac{3}{2}pq$	$\frac{q}{4}(1+3q)$	1				

The correlation coefficient $s_{M-D}^{r(1)}$ between the mother-daughter pairs in this case can be worked out directly by assuming additive genic effects as $s_{M-D}^{r(1)} = 0.670$.

Similarly the joint distribution and correlation coefficients of mother-daughter pairs in 2nd, 3rd, 4th, etc. generations of full-sib mating can be obtained. The correlation coefficients between motherdaughter pairs in ten generations of full-sib mating are worked out and is as shown in table 8.

3.2. Mother-Son Correlation

The joint distribution of the mother-son pairs in the first generation of full-sib mating can be obtained, either by pairing the female parent and male offspring from the first generation of full-sib mating or by multiplying the vector of frequencies of full-sib mating by the generation matrix B_{m-s} of mother daughter pairs, which can be derived in the similar lines as explained in section 2.1 and B_{m-s} can be worked out as

	[1	1	0	0	0	0]
$B_{m-s} =$	0	0	0	0	0	0
	0	0	$\frac{1}{2}$	$\frac{1}{2}$	0	0
$\tilde{B}_{m-s} =$	0	1 0 0 0 0	$\frac{1}{2}$	12	0	0
	0	0	0	0 -	0	0
	Lo	0	0	0	1	ز 1

Hence the joint distribution of mother-son pairs under the 1st generation of full-sib mating can be written as shown in table 5.

The correlation coefficient $s_{M-S}^{r(1)}$, between the mother-daughter pairs in this case can be worked out directly by assuming additive genic effects as

$$s_{M-S}^{r(1)} = 0.790$$

Similarly the joint distribution and correlation coefficients of the mother-son pairs in the 2nd, 3rd etc., generations of full-sib mating can de obtained. The correlation coefficients between mother and son in ten generations of full-sib mating is as given in table 8.

	<u> </u>	Son			
		A	a	Total	
	AA	$\frac{p}{4}(1+3p)$	0	$\frac{p}{4}(1+3p)$	
Mother	Aa	$\frac{3}{4}pq$	$\frac{1}{4} pq$	$\frac{3}{2}pq$	
	aa	0	$\frac{q}{4}(1+3q)$	$\frac{q}{4}(1+3q)$	
Total		р	q	1	

TABLE 5

Correlation table of the mother-son pairs in the first generation of full-sib mating

3.3. Father-Daughter Correlation

The joint distribution of father-daughter pairs in the first generation of full-sib mating can be obtained either by pairing the male parent and female offspring from the first generation of full-sib mating or by multiplying the vector of frequencies in the first generation of full-sib mating by the generation matrix B_{f-d} of father-daughter pairs, which can be derived in the similar lines as explained in the section 2.1 and B_{f-d} can be worked out as

Hence the joint distribution of father-daughter pairs under the 1st generation of full-sib mating can be written as shown in table 6

TABLE 6

Joint distribution of father-daughter pairs in the first generation of full-sib mating

		Daughter					
		AA	Aa	aa	Total		
	A	$\frac{p}{4}$ (1+3p)	$\frac{3}{4}pq$	0	р		
Fath e r	a	0	$\frac{3}{4}pq$	$\frac{q}{4}(1+3q)$	q		
Total		$\frac{p}{4}(1+3p)$	$\frac{3}{2}pq$	$\frac{q}{4} (1+3q)$	1		

The correlation coefficient $s_{F-D}^{r(1)}$, between the father-daughter pairs in this case can be worked out directly by assuming additive genic effects as

$$s_{R-n}^{r(1)} = 0.790$$

Similarly the joint distribution and correlation coefficients of the father-daughter pair in the 2nd, 3rd etc. generations of full-sib mating can be obtained. The correlation coefficients between father and daughter in ten generations of full-sib mating is given in table 8.

It is interesting to note that these joint distributions and the correlation coefficients are exactly same as that of mother-son pair case.

3.4. Father-Son Correlation

The joint distribution of father-son pairs in the first generation of full-sib mating of either obtained by pairing the male parent and male offspring in that mating or by multiplying the vector of frequencies in the first generation of full-sib mating by the generation

matrix B_{f-s} of father-son pair, which can be derived in the similar lines as explained in the section 2.1 and B_{f-s} can be worked out as

$\underline{B}_{f-s} =$		0	$\frac{1}{2}$	0	0	[0
	0	0	1	0	1	0
	0	1	0	12	. 0	0
	0	0	0	$\frac{1}{2}$	0	IJ

Hence the joint distribution of father-son pairs under the 1st generation of full-sib mating can be written as shown in table 7.

TABLE 7

Joint distribution of father-son pairs in the first generation of full-sib mating

	.	Son				
	-	A	а	Total		
Father	 	$\frac{1}{4}p(1+3p)$	₹ pq	p		
	a	₹ pq	$\frac{1}{4}q(1+3q)$	q		
Total				1		

The matrix $s_{F-S}^{M(1)}$ of conditional probabilities of father-son pairs in this case is obtained as

$$s_{-F-S}^{M(1)} = \begin{bmatrix} \frac{1}{4} (1+3p) & \frac{3}{4}q \\ \frac{3}{4}p & \frac{1}{4} (1+3q) \end{bmatrix}$$

This can be split into a function of I_{22} and o_{22} as

$$s_{-F-S}^{M(1)} = \frac{1}{4}I_{22} + \frac{3}{4}o_{22}$$

Similarly the matrix of conditional probabilities $s_{F-S}^{M(2)}$ of father-son pairs in the case of second generation of full-sib mating can be expressed as a function of I_{22} and o_{22} as

$$S_{-F-S}^{M(2)} = \frac{3}{8} I_{22} + \frac{5}{8} o_{22}$$

In general the matrix of conditional probabilities of father-son pairs under full-sib mating can be written as

$$s_{\tau F \to S}^{M(n)} = D_n I_{22} + (1 - D_n) o_{22}$$

where

$$D_n=0, \frac{1}{4}, \frac{3}{8}, \frac{8}{16}, \frac{19}{22}, \frac{43}{64}$$
 ...(6)

for, n, the number of generation, is 0, 1, 2, 3 etc. The correlation between father-son pairs can be calculated by using the technique explained by Li and Sacks (1954) as

$$s_{F-S}^{r(n)} = D_n r_I + (1 - D_n) r_o$$

where $r_I = 1$ and $r_o = 0$ as explained in section 2.3. The values of the correlation coefficients between father-son pairs under full-sib mating (Sex-linked gene case) is as given in table 8.

4. CONCLUSION

From table 8, it is intersting to not that sister-sister pair correlation is maximum at every generation of full-sib mating followed by mother-son and father-daughter correlations. It is also interesting to note that the correlation between mother-son pair and father-daughter pair are identical. Another important point worth mentioning is that father and the sons are uncorrelated under random mating but as the inbreeding starts the pairs become correlated and the amuont of correlation increases as the number of generations of inbreeding increases. Another point worth mentioning is that, even though the brother-brother correlation and mother-daughter correlations, under random mating are the same the correlation increases at a rapid rate in the case of mother daughter pairs than that of brother-brother pair. It can also be concluded from the table 8, that the correlation coefficients of all these seven types of pairs will be tending to unity as the number of generations of inbreeding increases indefinitely.

From the present study one can conclude that the joint distributions and correlation coefficients of brother-brother pairs and father-son pairs can be easily worked out with the help of the equation (2), (4), (5) and (7).

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TABLE	8
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Correlation between full-sib pairs and parent-offspring pairs in ten generations of full-sib mating (sex-linked gene case)

, Generation	Full-sib pairs				Parent offspring pairs		
	Brother sister pairs	Sister sister pairs	Brother brother pairs	Mother daughter pairs	Mother Son pairs	Father daughter pairs	Father son pairs
0	0.354	0,750	0,500	0.500	0.707	0.707	0.000
1	0.274	0.800	0.625	0.670	0.79 0	0.790	0.250
2	0.603	0.863	0.687	0.762	0.829	0.829	0.375
3	0.686	0.895	0.750	0.826	0.866	0.866	0.500
4	0.752	0.921	0.796	0.868	0.892	0.892	0.593
5	0.853	0.939	0.835	0.899	0.914	0.914	0.671
6	0.843	0.942	0.867	0.921	0.931	0.931	0.734
7	0.874	0.962	0,892	0,941	0.944	0.944	0.785
8	0.899	0,970	0.213	0.949	0.955	0.955	0.826
9	0.919	0.976	0.936	0,960	0,964	0.964	0.859
10	0.935	0.981	0,946	0.968	0.971	0.971	0.866

Note: 0-th generation stands for random mating.

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