Agronomy 615
Statistical Genetics
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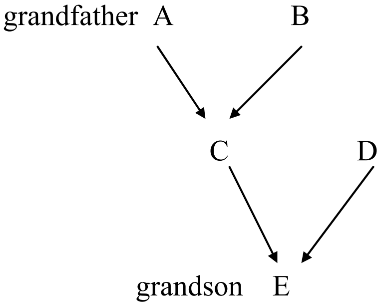
SOLUTIONS TO EXERCISES FOR CHAPTER 4

Exercise 4.1.

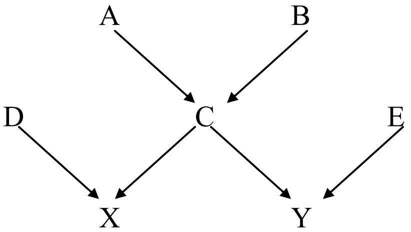


$$\theta_{AE} = \theta_{A(CD)} = \tfrac{1}{2}\left(\theta_{AC} + \theta_{AD}\right) = \tfrac{1}{2}\left[\theta_{A(AB)} + \theta_{AD}\right]$$

$$= \tfrac{1}{2}\left[\tfrac{1}{2}\left(\theta_{AA} + \theta_{AB}\right) + 0\right] = \tfrac{1}{4}\left(\theta_{AA} + 0\right) = \tfrac{1}{4}\theta_{AA} = \tfrac{1}{4}\left(\frac{1+F_A}{2}\right) = \tfrac{1}{8}$$

Exercise 4.2.

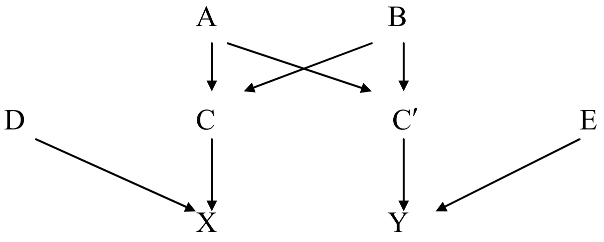
The simplest pedigree diagram is to represent the two monozygotic twins as one individual *C*:



$$\theta_{XY} = \theta_{(DC)(CE)} = \tfrac{1}{4}\left(\theta_{DC} + \theta_{DE} + \theta_{CC} + \theta_{CE} +\right) = \tfrac{1}{4}\left(0 + 0 + \frac{1+F_C}{2} + 0\right) = \tfrac{1}{4}\left(\frac{1+F_C}{2}\right) = \frac{1+0}{8} = \tfrac{1}{8}$$

The coancestry between *X* and *Y* is the same as that for half sibs.

An alternative pedigree depicting the two monozygotic twins as two separate individuals, *C* and C', is also possible.



$$\theta_{XY} = \theta_{X(C'E)} = \tfrac{1}{2}\left(\theta_{XC'} + \theta_{XE}\right) = \tfrac{1}{2}\left(\theta_{(DC)C'} + \theta_{(DC)E}\right)$$

$$= \tfrac{1}{2}\left[\tfrac{1}{2}\left(\theta_{DC'} + \theta_{CC'}\right) + \tfrac{1}{2}\left(\theta_{DE} + \theta_{CE}\right)\right] = \tfrac{1}{4}\left(0 + \theta_{CC'} + 0 + 0\right)$$

Since C and C′ are the same genotype being monozygotic twins, $\theta_{CC'}$ is equal to the coancestry of an individual with itself.

$$\theta_{XY} = \tfrac{1}{4}\left(\frac{1+F_C}{2}\right) = \tfrac{1}{8}$$

Exercise 4.3.

a. The coefficients of coancestry between all individuals in the pedigree are (see Example 4.1, pp. 4.33 to 4.38)

	A	B	C	D	E	F
	- -	- A	A -	- B	C -	D E
A	$\frac{1}{2}$	$\frac{1}{4}$	$\frac{1}{4}$	$\frac{1}{8}$	$\frac{1}{8}$	$\frac{1}{8}$
B		$\frac{1}{2}$	$\frac{1}{8}$	$\frac{1}{4}$	$\frac{1}{16}$	$\frac{5}{32}$
C			$\frac{1}{2}$	$\frac{1}{16}$	$\frac{1}{4}$	$\frac{5}{32}$
D				$\frac{1}{2}$	$\frac{1}{32}$	$\frac{17}{64}$
E					$\frac{1}{2}$	$\frac{17}{64}$
F						$\frac{33}{64}$

b. The coefficient of inbreeding of individual *F* as given in the table is $F_F = \theta_{DE} = \frac{1}{32}$.

c. Obtaining the coefficient of inbreeding of individual *F* by expanding backwards in the pedigree, we have

$$F_F = \theta_{DE} = \theta_{(-B)(C-)} = \tfrac{1}{4}\left(\theta_{-C} + \theta_{--} + \theta_{BC} + \theta_{B-}\right) = \tfrac{1}{4}\left(0 + 0 + \theta_{BC} + 0\right)$$

$$= \tfrac{1}{4}\left(\theta_{(-A)(A-)}\right) = \tfrac{1}{4}\left(\tfrac{1}{4}\theta_{AA}\right) = \tfrac{1}{16}\left(\frac{1+F_A}{2}\right) = \tfrac{1}{32}$$

d. Obtaining the coefficient of inbreeding of individual *F* by using equation (4.60), we have

$$F_F = \left(\tfrac{1}{2}\right)^5 \left(1 + F_A\right) = \tfrac{1}{32}$$

Exercise 4.4.

a. The coefficients of coancestry between all individuals in the pedigree are (see Example 4.1, pp. 4.33 to 4.38)

	A	B	C	D	E	F
	- -	- A	A -	- B	C -	D E
A	$\frac{3}{4}$	$\frac{3}{8}$	$\frac{3}{8}$	$\frac{3}{16}$	$\frac{3}{16}$	$\frac{3}{16}$
B		$\frac{1}{2}$	$\frac{3}{16}$	$\frac{1}{4}$	$\frac{3}{32}$	$\frac{11}{64}$
C			$\frac{1}{2}$	$\frac{3}{32}$	$\frac{1}{4}$	$\frac{11}{64}$
D				$\frac{1}{2}$	$\frac{3}{64}$	$\frac{35}{128}$
E					$\frac{1}{2}$	$\frac{35}{128}$
F						$\frac{67}{128}$

b. The coefficient of inbreeding of individual *F* as given in the table is $F_F = \theta_{DE} = \frac{3}{64}$.

c. Obtaining the coefficient of inbreeding of individual *F* by expanding backwards in the pedigree, we have

$$F_F = \theta_{DE} = \theta_{(-B)(C-)} = \tfrac{1}{4}\left(\theta_{-C} + \theta_{--} + \theta_{BC} + \theta_{B-}\right) = \tfrac{1}{4}\left(0 + 0 + \theta_{BC} + 0\right)$$

$$= \tfrac{1}{4}\left(\theta_{(-A)(A-)}\right) = \tfrac{1}{4}\left(\tfrac{1}{4}\theta_{AA}\right) = \tfrac{1}{16}\theta_{AA} = \tfrac{1}{16}\left(\frac{1+F_A}{2}\right) = \tfrac{1}{16}\left(\frac{1+\frac{1}{2}}{2}\right) = \frac{3}{64}$$

d. Obtaining the coefficient of inbreeding of individual *F* by using equation (4.60), we have

$$F_F = \left(\tfrac{1}{2}\right)^5 (1 + F_A) = \left(\tfrac{1}{2}\right)^5 \left(1 + \tfrac{1}{2}\right) = \frac{3}{64}$$

Exercise 4.5.

The table of coefficients of coancestry is

	A	B	C	D	E	F	G
	- -	- -	- -	A B	C D	B C	E F
A	$\frac{1}{2}$	0	0	$\frac{1}{4}$	$\frac{1}{8}$	0	$\frac{1}{16}$
B	0	$\frac{1}{2}$	0	$\frac{1}{4}$	$\frac{1}{8}$	$\frac{1}{4}$	$\frac{3}{16}$
C	0	0	$\frac{6}{10}$	0	$\frac{3}{10}$	$\frac{3}{10}$	$\frac{3}{10}$
D	$\frac{1}{4}$	$\frac{1}{4}$	0	$\frac{1}{2}$	$\frac{1}{4}$	$\frac{1}{8}$	$\frac{3}{16}$
E	$\frac{1}{8}$	$\frac{1}{8}$	$\frac{3}{10}$	$\frac{1}{4}$	$\frac{1}{2}$	$\frac{17}{80}$	$\frac{57}{160}$
F	0	$\frac{1}{4}$	$\frac{3}{10}$	$\frac{1}{8}$	$\frac{17}{80}$	$\frac{1}{2}$	$\frac{57}{160}$
G	$\frac{1}{16}$	$\frac{3}{16}$	$\frac{3}{10}$	$\frac{3}{16}$	$\frac{57}{160}$	$\frac{57}{160}$	$\frac{97}{160}$

$\theta_{CC} = \frac{1+F_C}{2} = \frac{1+\frac{1}{5}}{2} = \frac{6}{10}$ which is inserted in the table above.
The inbreeding coefficient of individual G is
$F_G = F_{(EF)} = \theta_{EF} = \frac{17}{80}$
or to check that value by an alternative method of counting individuals in chains of coancestry [see equation (4.60)]

$$F_G = \theta_{EF} = \left(\frac{1}{2}\right)^3 (1+F_C) + \left(\frac{1}{2}\right)^4 (1+F_B) = \frac{1}{8}\left(1+\frac{1}{5}\right) + \frac{1}{16} = \frac{6}{40} + \frac{1}{16} = \frac{12+5}{2 \cdot 5 \cdot 8} = \frac{17}{80}$$

Recommend D × G $\left(\theta_{DG} = F_{(DG)} = \frac{3}{16}\right)$, because inbreeding would be less than C × G $\left(\theta_{CG} = F_{(CG)} = \frac{3}{10}\right)$.

Exercise 4.6.

a. The coefficients of coancestry between all individuals in the pedigree are

	A	B	C	D	E	F	G	I
	- -	- -	A B	A B	A D	C E	C E	F G
A	$\frac{1}{2}$	0	$\frac{1}{4}$	$\frac{1}{4}$	$\frac{3}{8}$	$\frac{5}{16}$	$\frac{5}{16}$	$\frac{5}{16}$
B		$\frac{1}{2}$	$\frac{1}{4}$	$\frac{1}{4}$	$\frac{1}{8}$	$\frac{3}{16}$	$\frac{3}{16}$	$\frac{3}{16}$
C			$\frac{1}{2}$	$\frac{1}{4}$	$\frac{1}{4}$	$\frac{3}{8}$	$\frac{3}{8}$	$\frac{3}{8}$
D				$\frac{1}{2}$	$\frac{3}{8}$	$\frac{5}{16}$	$\frac{5}{16}$	$\frac{5}{16}$
E					$\frac{5}{8}$	$\frac{7}{16}$	$\frac{7}{16}$	$\frac{7}{16}$
F						$\frac{5}{8}$	$\frac{13}{32}$	$\frac{33}{64}$
G							$\frac{5}{8}$	$\frac{33}{64}$
I								$\frac{45}{64}$

b. The coefficient of inbreeding of individual *I* as given in the table is $F_I = \theta_{FG} = \frac{13}{32}$.

c. Obtaining the coefficient of inbreeding of individual *I* by expanding backwards in the pedigree, we have

$$F_I = \theta_{FG} = \theta_{(CE)(CE)} = \tfrac{1}{4}\left(\theta_{CC} + 2\theta_{CE} + \theta_{EE}\right) = \frac{1}{4}\left[\left(\frac{1+\theta_{AB}}{2}\right) + 2\theta_{C(AD)} + \left(\frac{1+\theta_{AD}}{2}\right)\right]$$

$$= \frac{1}{4}\left[\tfrac{1}{2} + 2\cdot\tfrac{1}{2}\left(\theta_{CA} + \theta_{CD}\right) + \frac{1+\theta_{A(AB)}}{2}\right]$$

$$= \tfrac{1}{8}\left[1 + 2\left(\theta_{(AB)A} + \theta_{(AB)(AB)}\right) + 1 + \tfrac{1}{2}\left(\theta_{AA} + \theta_{AB}\right)\right]$$

$$= \tfrac{1}{8}\left\{1 + 2\left[\tfrac{1}{2}\left(\theta_{AA} + \theta_{AB}\right) + \tfrac{1}{4}\left(\theta_{AA} + 2\theta_{AB} + \theta_{BB}\right)\right] + 1 + \tfrac{1}{2}\left(\frac{1+F_A}{2} + 0\right)\right\}$$

$$= \tfrac{1}{8}\left\{2 + \frac{1+F_A}{2} + 0 + \tfrac{1}{2}\left(\frac{1+F_A}{2} + 0 + \frac{1+F_B}{2}\right) + \tfrac{1}{2}\left(\frac{1+F_A}{2}\right)\right\}$$

$$= \tfrac{1}{8}\left\{2 + \tfrac{1}{2} + \tfrac{1}{4} + \tfrac{1}{4} + \tfrac{1}{4}\right\}$$

$$= \tfrac{1}{8}\left\{\tfrac{13}{4}\right\} = \tfrac{13}{32}$$

d. We obtain the coefficient of inbreeding of individual *I* by using equation (4.60). The common ancestors are E, C, A, and B. The inbreeding of the common ancestors are $F_E = \frac{1}{4}, F_C = F_A = F_B = 0$

Common ancestor	Chain of coancestry	
E	$F\underline{E}G$	$\left(\tfrac{1}{2}\right)^3\left(1+F_E\right) = \dfrac{1+\frac{1}{4}}{8} = \tfrac{5}{4}\tfrac{1}{8} = \tfrac{5}{32}$
C	$F\underline{C}G$	$\left(\tfrac{1}{2}\right)^3\left(1+F_C\right) = \tfrac{1}{8}$
A	$FC\underline{A}EG$	$\left(\tfrac{1}{2}\right)^5\left(1+F_A\right) = \tfrac{1}{32}$
	$FC\underline{A}DEG$	$\left(\tfrac{1}{2}\right)^6\left(1+F_A\right) = \tfrac{1}{64}$
	$FE\underline{A}CG$	$\left(\tfrac{1}{2}\right)^5\left(1+F_A\right) = \tfrac{1}{32}$
	$FED\underline{A}CG$	$\left(\tfrac{1}{2}\right)^6\left(1+F_A\right) = \tfrac{1}{64}$
B	$FC\underline{B}DEG$	$\left(\tfrac{1}{2}\right)^6\left(1+F_B\right) = \tfrac{1}{64}$
	$FED\underline{B}CG$	$\left(\tfrac{1}{2}\right)^6\left(1+F_B\right) = \tfrac{1}{64}$
Total		$\tfrac{26}{64} = \tfrac{13}{32}$

Exercise 4.7.

	A	B	C	D	E	F	G	H	I
	- -	- -	A B	A -	- C	C -	B D	E F	G H
A	$\frac{1}{2}$	0	$\frac{1}{4}$	$\frac{1}{4}$	$\frac{1}{8}$	$\frac{1}{8}$	$\frac{1}{8}$	$\frac{1}{8}$	$\frac{1}{8}$
B		$\frac{1}{2}$	$\frac{1}{4}$	0	$\frac{1}{8}$	$\frac{1}{8}$	$\frac{1}{4}$	$\frac{1}{8}$	$\frac{3}{16}$
C			$\frac{1}{2}$	$\frac{1}{8}$	$\frac{1}{4}$	$\frac{1}{4}$	$\frac{3}{16}$	$\frac{1}{4}$	$\frac{7}{32}$
D				$\frac{1}{2}$	$\frac{1}{16}$	$\frac{1}{16}$	$\frac{1}{4}$	$\frac{1}{16}$	$\frac{5}{32}$
E					$\frac{1}{2}$	$\frac{1}{8}$	$\frac{3}{32}$	$\frac{5}{16}$	$\frac{13}{64}$
F						$\frac{1}{2}$	$\frac{3}{32}$	$\frac{5}{16}$	$\frac{13}{64}$
G							$\frac{1}{2}$	$\frac{3}{32}$	$\frac{19}{64}$
H								$\frac{9}{16}$	$\frac{21}{64}$
I									$\frac{35}{64}$

$$F_I = \theta_{GH} = \frac{3}{32}$$

$$F_I = 2\theta_{II} - 1 = 2\left(\frac{35}{64}\right) - 1 = \frac{3}{32}$$

By the chain method:

$HEC\underline{A}DG$ $\quad \left(\frac{1}{2}\right)^6 (1+F_A) = \frac{1}{64}$

$HFC\underline{A}DG$ $\quad \left(\frac{1}{2}\right)^6 (1+F_A) = \frac{1}{64}$

$HEC\underline{B}G$ $\quad \left(\frac{1}{2}\right)^5 (1+F_B) = \frac{1}{32}$

$HFC\underline{B}G$ $\quad \left(\frac{1}{2}\right)^5 (1+F_B) = \underline{\frac{1}{64}}$

Total $\quad \frac{6}{64} = \frac{3}{32}$

Exercise 4.8.

a. For autosomal locus, using Method 1, a tabular coancestry approach

	A	B	C	D	E	F	G	H	I	J	K
	- -	- A	- -	A -	- C	C -	D -	E F	B H	G H	I J
A	$\frac{1}{2}$	$\frac{1}{4}$	0	$\frac{1}{4}$	0	0	$\frac{1}{8}$	0	$\frac{1}{8}$	$\frac{1}{16}$	$\frac{3}{32}$
B		$\frac{1}{2}$	0	$\frac{1}{8}$	0	0	$\frac{1}{16}$	0	$\frac{1}{4}$	$\frac{1}{32}$	$\frac{9}{64}$
C			$\frac{1}{2}$	0	$\frac{1}{4}$	$\frac{1}{4}$	0	$\frac{1}{4}$	$\frac{1}{8}$	$\frac{1}{8}$	$\frac{1}{8}$
D				$\frac{1}{2}$	0	0	$\frac{1}{4}$	0	$\frac{1}{16}$	$\frac{1}{8}$	$\frac{3}{32}$
E					$\frac{1}{2}$	$\frac{1}{8}$	0	$\frac{5}{16}$	$\frac{5}{32}$	$\frac{5}{32}$	$\frac{5}{32}$
F						$\frac{1}{2}$	0	$\frac{5}{16}$	$\frac{5}{32}$	$\frac{5}{32}$	$\frac{5}{32}$
G							$\frac{1}{2}$	0	$\frac{1}{32}$	$\frac{1}{4}$	$\frac{9}{64}$
H								$\frac{9}{16}$	$\frac{9}{32}$	$\frac{9}{32}$	$\frac{9}{32}$
I									$\frac{1}{2}$	$\frac{10}{64}$	$\frac{42}{128}$
J										$\frac{1}{2}$	$\frac{42}{128}$
K											$\frac{74}{128}$

$F_K = \theta_{IJ} = \frac{10}{64} = \frac{5}{32}$ or $F_K = 2\theta_{KK} - 1 = 2\left(\frac{74}{128}\right) - 1 = \frac{74}{64} - \frac{64}{64} = \frac{10}{64} = \frac{5}{32}$

For autosomal locus, Method 2, chain of coancestry method

i	j		
1	1	$IB\underline{A}DGJ$	$\theta_{(IJ)_A} = \left(\frac{1}{2}\right)^6 (1 + F_A) = \frac{1}{64}$
2	1	$I\underline{H}J$	$\theta_{(IJ)_H} = \left(\frac{1}{2}\right)^3 (1 + F_H)$
			$= \left(\frac{1}{2}\right)^3 \left[1 + \left(\frac{1}{2}\right)^3\right]$
			$= \frac{1}{8}\left[1 + \frac{1}{8}\right] \quad = \frac{9}{64}$
Total			$\frac{10}{64} = \frac{5}{32}$

$F_K = \theta_{IJ} = \frac{10}{64} = \frac{5}{32}$

Exercise 4.9.

a. Using a tabular method for an autosomal locus, the coefficients of coancestry are

	A	B	C	D	E	F	G	H	I
	- -	- -	A B	A B	B -	D -	C -	E F	G H
A	$\frac{1}{2}$	0	$\frac{1}{4}$	$\frac{1}{4}$	0	$\frac{1}{8}$	$\frac{1}{8}$	$\frac{1}{16}$	$\frac{3}{32}$
B		$\frac{1}{2}$	$\frac{1}{4}$	$\frac{1}{4}$	$\frac{1}{4}$	$\frac{1}{8}$	$\frac{1}{8}$	$\frac{3}{16}$	$\frac{5}{32}$
C			$\frac{1}{2}$	$\frac{1}{4}$	$\frac{1}{8}$	$\frac{1}{8}$	$\frac{1}{4}$	$\frac{1}{8}$	$\frac{3}{16}$
D				$\frac{1}{2}$	$\frac{1}{8}$	$\frac{1}{4}$	$\frac{1}{8}$	$\frac{3}{16}$	$\frac{5}{32}$
E					$\frac{1}{2}$	$\frac{1}{16}$	$\frac{1}{16}$	$\frac{9}{32}$	$\frac{11}{64}$
F						$\frac{1}{2}$	$\frac{1}{16}$	$\frac{9}{32}$	$\frac{11}{64}$
G							$\frac{1}{2}$	$\frac{1}{16}$	$\frac{9}{32}$
H								$\frac{17}{32}$	$\frac{19}{64}$
I									$\frac{17}{32}$

b. The inbreeding coefficient of I is

$$F_I = \theta_{GH} = \tfrac{1}{16} \quad \text{or} \quad F_I = 2\theta_{II} - 1 = 2\left(\tfrac{17}{32}\right) - 1 = \tfrac{34}{32} - \tfrac{32}{32} = \tfrac{2}{32} = \tfrac{1}{16}$$

Exercise 4.10.

We need to calculate the coefficients of coancestry between the wealthy man *G* and the son *I* of his cousin and between *G* and the grandson *K* of his half sister.

$$\theta_{GI} = \left(\tfrac{1}{2}\right)^6 (1+F_A) + \left(\tfrac{1}{2}\right)^6 (1+F_B) = 2\left(\tfrac{1}{2}\right)^6 = 2\tfrac{1}{64} = \tfrac{1}{32} \quad \text{[see equation (4.60)]}$$

$$\theta_{GK} = \left(\tfrac{1}{2}\right)^5 (1+F_E) = \tfrac{1}{32}$$

The degree of relationship of the wealthy man to each of the two candidates is the same, so I suppose that the money would need to be divided between the two candidates.

Exercise 4.11.

a. The coefficient of coancestry between X and Y is

$$\theta_{XY} = \theta_{(AB)(AB)} = \tfrac{1}{4}\left[\theta_{AA} + 2\theta_{AB} + \theta_{BB}\right] \qquad \text{equation (4.42)}$$

$$= \frac{1}{4}\left[\frac{1+F_A}{2} + 0 + \frac{1+F_B}{2}\right] = \frac{1}{4}\left[\frac{1+\frac{1}{2}}{2} + \frac{1+\frac{3}{4}}{2}\right] = \frac{1}{4}\left[\frac{3}{4} + \frac{7}{8}\right] = \frac{1}{4}\left[\frac{13}{8}\right] = \frac{13}{32}$$

b. The inbreeding coefficient of an offspring from *A* by *X* is

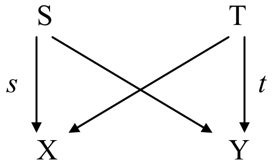
$$F_{(AX)} = \theta_{AX} = \theta_{A(AB)} = \tfrac{1}{2}\left(\theta_{AA} + \theta_{AB}\right) = \tfrac{1}{2}\left(\frac{1+F_A}{2} + 0\right) = \frac{1+F_A}{4} = \frac{1+\frac{1}{2}}{4} = \frac{3}{8}$$

c. The probability that the genotype for a single locus in *X* is identical by descent to the genotype in *Y* is given by the coefficient of dominance coancestry for full sibs in Table 9.5 (p. 9.52)

$$\delta_{dXY}=\frac{(1+F_A)(1+F_B)}{4}=\frac{\left(1+\frac{1}{2}\right)\left(1+\frac{3}{4}\right)}{4}=\frac{\frac{3}{2}\left(\frac{7}{4}\right)}{4}=\frac{21}{32}$$

Exercise 4.12.

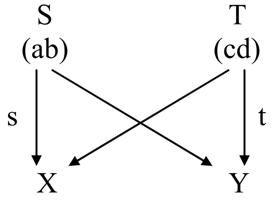
a.



(*s* denotes a random gene from *S*, and likewise for *t*)

$\gamma_{\ddot{X}Y}$ means that the two genes in *X* and a random gene from *Y* are all identical by descent. The two genes in *X* must be a random one from *S*, i.e., *s*, and the other gene must be a random one from *T*, i.e., *t*. Since these two genes can never be identical by descent, given that $\theta_{ST}=0$, then $\gamma_{\ddot{X}Y}$ must be zero. What the third gene is is irrelevant because the first two can never be identical. The third gene is *s* $\frac{1}{2}$ of the time and is *t* $\frac{1}{2}$ of the time. Hence, $\gamma_{\ddot{X}Y}=\frac{1}{2}\gamma_{sts}+\frac{1}{2}\gamma_{stt}$.

b.



(s denotes a random gene from S, and likewise for t)

Let *S* have genes *a* and *b* and *T* have genes *c* and *d*. γ_{XXY} means two random genes are drawn independently from *X* and one from *Y*. The first random gene drawn from *X* maybe 1/2 *a* or 1/2 *b*. Likewise, the second random gene from *X* maybe 1/2 *a* or 1/2 *b*, so we have probability of 1/4 of obtaining two *a* genes (*a*, *a*) and probability of 1/4 of obtaining two *b* genes (*b*, *b*). Then the random one from *Y* is 1/2 *s* or 1/2 *t*, i.e.,

$\frac{1}{2}s\rightarrow\frac{1}{2}\left(\frac{1}{2}a,\frac{1}{2}b\right)=\frac{1}{4}a,\frac{1}{4}b$ and

$\frac{1}{2}t\rightarrow\frac{1}{2}\left(\frac{1}{2}c,\frac{1}{2}d\right)=\frac{1}{4}c,\frac{1}{4}d$

Putting this together, we have

	1/4 *a*	1/4 *b*	1/4 *c*	1/4 *d*
1/4 *aa*	1/16 *aaa*			
1/4 *bb*		1/16 *bbb*		

--the total is 1/8, the probability of all three genes being identical by descent

Alternatively, following the labeling in the notes (p. 4.66) we have two random genes, *a* and *b*, from *X* and a single random gene, *c*, from *Y*, i.e., $\overset{X}{(ab)}\downarrow\overset{Y}{c}$. Thus, we may express γ_{XXY} as (also see derivation of Rule 8, pp. 4.83 and 4.84, with somewhat different notation—I have not been entirely consistent)

$$\begin{aligned}\gamma_{XXY} &= \tfrac{1}{4}\left[P(a\equiv a\equiv c)+P(a\equiv b\equiv c)+P(b\equiv a\equiv c)+P(b\equiv b\equiv c)\right]\\ &= \tfrac{1}{4}\left[P(a\equiv c)+2P(a\equiv b\equiv c)+P(b\equiv c)\right]\\ &= \tfrac{1}{4}\left[P(a\equiv c)+P(b\equiv c)+2P(a\equiv b\equiv c)\right]\\ &= \tfrac{1}{4}\left[2\theta_{XY}+2\gamma_{\ddot{X}Y}\right] \qquad \text{substitute equation (4.75)}\\ &= \tfrac{1}{2}\left(\theta_{XY}+0\right) \qquad \text{(coefficient of coancestry for full sibs is 1/4)}\\ &= \tfrac{1}{2}\left(\tfrac{1}{4}\right)=\tfrac{1}{8}\end{aligned}$$

γ_{XXY} in this part (b) differs from $\gamma_{\ddot{X}Y}$ in part (a) in that with γ_{XXY} there is a chance that the two random genes drawn from *X* can be identical since they are drawn from the same individual *X*. We have sampling with replacement. This is in contrast to $\gamma_{\ddot{X}Y}$ which involves the probability of the two random genes which *X* carries being identical by descent. This depends upon pedigree relations.

Exercise 4.13.

The table of coefficients of coancestry is (see Example 4.4, pp. 4.44 to 4.45):

	A	B	C	D	X	Y
	- -	- -	A B	C C	D D	D D
A	$\frac{1}{2}$	0	$\frac{1}{4}$	$\frac{1}{4}$	$\frac{1}{4}$	$\frac{1}{4}$
B		$\frac{1}{2}$	$\frac{1}{4}$	$\frac{1}{4}$	$\frac{1}{4}$	$\frac{1}{4}$
C			$\frac{1}{2}$	$\frac{1}{2}$	$\frac{1}{2}$	$\frac{1}{2}$
D				$\frac{3}{4}$	$\frac{3}{4}$	$\frac{3}{4}$
X					$\frac{7}{8}$	$\frac{3}{4}$
Y						$\frac{7}{8}$

The quantities required for calculating the condensed coefficients of identity are given in equation (4.81):

R9 R14 (4.86) R1 A

(1) $\delta_{\ddot{X}\ddot{Y}}=\delta_{(DD)(DD)}=\delta_{DDDD}=\tfrac{1}{8}\left(1+7F_{\ddot{D}}\right)=\tfrac{1}{8}\left(1+7\theta_{CC}\right)=\tfrac{1}{8}\left[1+7\left(\tfrac{1}{2}\right)\left(1+\theta_{AB}\right)\right]$

$=\tfrac{1}{8}\left[1+7\left(\tfrac{1}{2}\right)(1+0)\right]=\tfrac{1}{8}\tfrac{9}{2}=\tfrac{9}{16}$

Comment for (1) above: In applying Rule 9, as well as many other similar rules, the important idea to keep in mind is the parental origin of the genes in *X* and *Y*. The parental origin of each of the two genes in *X* is a random one from *D*, and likewise for each of the two genes in *Y*. Hence, we translate or equate $\delta_{\ddot{X}\ddot{Y}}$ to δ_{DDDD}.

R18 R22 see (1) above

(2) $\Delta_{\ddot{X}\cdot\ddot{Y}}=\Delta_{(DD)\cdot(DD)}=\Delta_{DD\cdot DD}=\tfrac{1}{4}\left(1+3F_{\ddot{D}}\right)=\tfrac{1}{4}\left(1+3\left(\tfrac{1}{2}\right)\right)=\tfrac{1}{4}\left(\tfrac{2+3}{2}\right)=\tfrac{5}{8}$

R28 R32 see (2) above

(3) $\Delta_{\ddot{X}+\ddot{Y}}=\Delta_{(DD)+(DD)}=\Delta_{DD+DD}=\tfrac{1}{4}\left(1+3F_{\ddot{D}}\right)=\tfrac{1}{4}\left(1+3\left(\tfrac{1}{2}\right)\right)=\tfrac{1}{4}\left(\tfrac{2+3}{2}\right)=\tfrac{5}{8}$

R3 R7 see (2) above

(4) $\gamma_{\ddot{X}Y} = \gamma_{(DD)D} = \gamma_{DDD} = \frac{1}{4}\left(1+3F_{\ddot{D}}\right) = \frac{1}{4}\left(1+3\left(\frac{1}{2}\right)\right) = \frac{1}{4}\left(\frac{2+3}{2}\right) = \frac{5}{8}$

Comment for (4) above: The parental origin of each of the two genes in X is a random one from D, and again the random gene in Y is a random gene from D. Hence, we translate or equate $\delta_{\ddot{X}Y}$ to γ_{DDD}.

R3 R7 see (2) above

(5) $\gamma_{X\ddot{Y}} = \gamma_{D(DD)} = \gamma_{DDD} = \frac{1}{4}\left(1+3F_{\ddot{D}}\right) = \frac{1}{4}\left(1+3\left(\frac{1}{2}\right)\right) = \frac{1}{4}\left(\frac{2+3}{2}\right) = \frac{5}{8}$

eq. (4.13), table

(6) $F_{\ddot{X}} = \theta_{DD} = \frac{3}{4}$

eq. (4.13), table

(7) $F_{\ddot{Y}} = \theta_{DD} = \frac{3}{4}$

table

(8) $\theta_{XY} = \frac{3}{4}$

The condensed coefficients of identity are calculated as given in equation (4.82):

$\Delta_1 = \delta_{\ddot{X}\ddot{Y}} = \frac{9}{16}$

$\Delta_2 = 2\left(\gamma_{\ddot{X}Y} - \delta_{\ddot{X}\ddot{Y}}\right) = 2\left(\frac{5}{8} - \frac{9}{16}\right) = \frac{1}{8}$

$\Delta_3 = 2\left(\gamma_{X\ddot{Y}} - \delta_{\ddot{X}\ddot{Y}}\right) = 2\left(\frac{5}{8} - \frac{9}{16}\right) = \frac{1}{8}$

$\Delta_4 = \Delta_{\ddot{X}\cdot\ddot{Y}} - \delta_{\ddot{X}\ddot{Y}} = \frac{5}{8} - \frac{9}{16} = \frac{1}{16}$

$\Delta_5 = 2\left(\Delta_{\ddot{X}+\ddot{Y}} - \delta_{\ddot{X}\ddot{Y}}\right) = 2\left(\frac{5}{8} - \frac{9}{16}\right) = \frac{1}{8}$

$\Delta_6 = F_{\ddot{X}} - \Delta_{\ddot{X}\cdot\ddot{Y}} - 2\left(\gamma_{\ddot{X}Y} - \delta_{\ddot{X}\ddot{Y}}\right) = \frac{3}{4} - \frac{5}{8} - 2\left(\frac{5}{8} - \frac{9}{16}\right) = \frac{1}{8} - \frac{1}{8} = 0$

$\Delta_7 = F_{\ddot{Y}} - \Delta_{\ddot{X}\cdot\ddot{Y}} - 2\left(\gamma_{X\ddot{Y}} - \delta_{\ddot{X}\ddot{Y}}\right) = \frac{3}{4} - \frac{5}{8} - 2\left(\frac{5}{8} - \frac{9}{16}\right) = \frac{1}{8} - \frac{1}{8} = 0$

$\Delta_8 = 4\left(\theta_{XY} - \Delta_{\ddot{X}+\ddot{Y}} - \gamma_{\ddot{X}Y} - \gamma_{X\ddot{Y}} + 2\delta_{\ddot{X}\ddot{Y}}\right) = 4\left[\frac{3}{4} - \frac{5}{8} - \frac{5}{8} - \frac{5}{8} + 2\left(\frac{9}{16}\right)\right] = 4\left(\frac{15}{8} - \frac{15}{8}\right) = 0$

$\Delta_9 = 1 - F_{\ddot{X}} - F_{\ddot{Y}} - 4\theta_{XY} + \Delta_{\ddot{X}\cdot\ddot{Y}} + 2\Delta_{\ddot{X}+\ddot{Y}} + 4\gamma_{\ddot{X}Y} + \gamma_{X\ddot{Y}} - 6\delta_{\ddot{X}\ddot{Y}}$

$= 1 - \frac{3}{4} - \frac{3}{4} - 4\left(\frac{3}{4}\right) + \frac{5}{8} + 2\left(\frac{5}{8}\right) + 4\left(\frac{5}{8}\right) + 4\left(\frac{5}{8}\right) - 6\left(\frac{9}{16}\right) = 0$

Check:

$\Delta_1 + \Delta_2 + \Delta_3 + \Delta_4 + \Delta_5 + \Delta_6 + \Delta_7 + \Delta_8 + \Delta_9 = \frac{9}{16} + \frac{1}{8} + \frac{1}{8} + \frac{1}{16} + \frac{1}{8} + 0 + 0 + 0 + 0 = 1$

Exercise 4.14.

This topic is not discussed in the present notes, but it is discussed by D. S. Falconer and T. F. C. Mackay, 1996, Introduction to Quantitative Genetics, Longman, pp. 94-96.

$$F^{*} = F^{'} + (1-F^{'})F = F + (1-F)F^{'}$$
$$= 0.11 + (0.89)(0.29) = 0.3681$$

where $F^{'}$ = old inbreeding of the population, F = new inbreeding of the population, and F*.= newly calculated inbreeding coefficient relative to the more remote population.

Exercise 4.15.

a. We can deduce the inbreeding coefficient of the selfed (or random-mated) offspring from a cross between two unrelated, fully inbred lines from elementary considerations as follows: Suppose inbred *A* carries two copies of gene *a* both identical by descent, and likewise inbred *B* carries two copies of gene *b* both identical by descent. Then the cross *C* would carry the two genes *a* and *b*. Then upon selfing or random mating of the cross itself we would have:

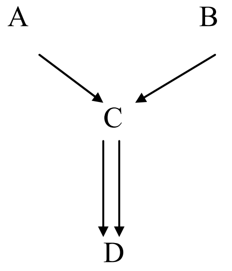
		Female side	
		a ½	b ½
Male side	a ½	aa ¼	ab ¼
	b ½	ab ¼	bb ¼

Each cell has a frequency of ¼ . The genotypes in the upper left and lower right are identical homozygotes, and the genotypes in the upper right and lower left are nonidentical genotypes because inbred A and B are unrelated. Thus the inbreeding coefficient of the selfed offspring or that of the two-way cross random mated is

$$F(\text{two-way cross random mated}) = \tfrac{1}{4}\left[P(a \equiv a) + P(a \equiv b) + P(b \equiv a) + P(b \equiv b)\right] = \tfrac{1}{4}(1+0+0+1) = \tfrac{1}{2}$$

The elements in a pedigree are normally individuals. If an element in a pedigree denotes a group of individuals, one should theoretically employ group measures (pp. 6.142 to 6.151). However, it seems that for certain situations simple pedigrees can give the correct answers.

i. The first simple pedigree representing this situation and its table of coancestry are as follows:

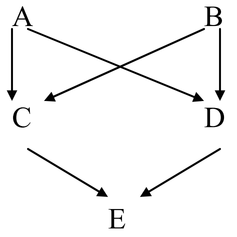


The table of coefficients of coancestry is $(F_A = F_B = 1)$:

	A	B	C	D
	- -	- -	A B	C C
A	1	0	$\frac{1}{2}$	$\frac{1}{2}$
B		1	$\frac{1}{2}$	$\frac{1}{2}$
C			$\frac{1}{2}$	$\frac{1}{2}$
D				$\frac{3}{4}$

The inbreeding coefficient of D is $F_D = \theta_{CC} = \frac{1}{2}$

ii. The second simple pedigree representing this situation and its table of coancestry are as follows:



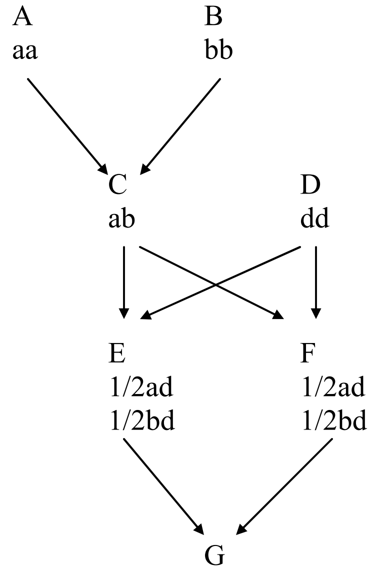
The table of coefficients of coancestry is $\left(F_A = F_B = 1\right)$:

	A	B	C	D	E
	- -	- -	A B	A B	C D
A	1	0	$\frac{1}{2}$	$\frac{1}{2}$	$\frac{1}{2}$
B		1	$\frac{1}{2}$	$\frac{1}{2}$	$\frac{1}{2}$
C			$\frac{1}{2}$	$\frac{1}{2}$	$\frac{1}{2}$
D				$\frac{1}{2}$	$\frac{1}{2}$
E					$\frac{3}{4}$

The inbreeding coefficient of E is $F_E = \theta_{CD} = \frac{1}{2}$. Both simple diagrams give the same inbreeding coefficient as that from elementary considerations.

Simple diagrams can represent random mating because the hybrid individual *C* in the first simple pedigree (or *C* and *D*, in the case of the second pedigree) will be the same genotype whether or not there is one or two or more *C* individuals. This is true because *A* and *B* are fully inbred, i.e., all loci are homozygous. Hence, any number of *C*s can only be heterogygous at all loci. This means that only *C*s can intermate.

b. The inbreeding coefficient for the open-pollinated progeny of a three-way hybrid or that from random mating of a three-way cross, deduced from elementary considerations, is as follows: We construct the following pedigree and label the genes contained therein.



		Female side		
		a ¼	b ¼	d ½
Male side	a ¼	aa 1/16	ab 1/16	ad 1/8
	b ¼	ab 1/16	bb 1/16	bd 1/8
	d ½	ad 1/8	bd 1/8	dd ¼

Thus, from elementary considerations the inbreeding coefficient of the three-way cross random mated is

$$F(\text{three-way cross random mated}) = \tfrac{1}{16}\left[P(a \equiv a) + P(b \equiv b)\right] + \tfrac{1}{4}P(d \equiv d) = \tfrac{1}{16}[1+1] + \tfrac{1}{4}\cdot 1 = \tfrac{3}{8}$$

Using the above pedigree, the table of coefficients of coancestry is:

	A	B	C	D	E	F	G
	- -	- -	A B	- -	C D	C D	E F
A	1	0	$\frac{1}{2}$	0	$\frac{1}{4}$	$\frac{1}{4}$	$\frac{1}{4}$
B		1	$\frac{1}{2}$	0	$\frac{1}{4}$	$\frac{1}{4}$	$\frac{1}{4}$
C			$\frac{1}{2}$	0	$\frac{1}{4}$	$\frac{1}{4}$	$\frac{1}{4}$
D				1	$\frac{1}{2}$	$\frac{1}{2}$	$\frac{1}{2}$
E					$\frac{1}{2}$	$\frac{3}{8}$	$\frac{7}{16}$
F						$\frac{1}{2}$	$\frac{7}{16}$
G							$\frac{11}{16}$

The inbreeding coefficient of G is $F_G = \theta_{EF} = \frac{3}{8}$. This simple diagram gives the same inbreeding coefficient as that from elementary considerations.

Exercise 4.16.

a. The table of coancestries is the same as that given in the solution for Exercise 4.15.b.

	A	B	C	D	E	F	G
	- -	- -	A B	- -	C D	C D	E F
A	1	0	$\frac{1}{2}$	0	$\frac{1}{4}$	$\frac{1}{4}$	$\frac{1}{4}$
B		1	$\frac{1}{2}$	0	$\frac{1}{4}$	$\frac{1}{4}$	$\frac{1}{4}$
C			$\frac{1}{2}$	0	$\frac{1}{4}$	$\frac{1}{4}$	$\frac{1}{4}$
D				1	$\frac{1}{2}$	$\frac{1}{2}$	$\frac{1}{2}$
E					$\frac{1}{2}$	$\frac{3}{8}$	$\frac{7}{16}$
F						$\frac{1}{2}$	$\frac{7}{16}$
G							$\frac{11}{16}$

One can represent the amount of inbreeding of the offspring from random mating among equal proportions of *E* and *F* individuals by the inbreeding of individual *G* because the coefficient of inbreeding is a probability and is an expected value. Since individual *E* is a random individual from the cross *C* by *D*, it may have genes *ad* or *bd* with equal chance. Similarly, individual *F* is another random individual from the same cross *C* by *D* with the same genes *ad* or *bd* with equal chance. Hence, the inbreeding of the random mating of the cross (*A* × *B*) × *D* can be represented by the cross between the two individuals *E* and *F*.

			F			
			1/2		1/2	
			a	d	b	d
E	1/2	a	aa*	ad	ab	ad
		d	ad	dd*	bd	dd*
	1/2	b	ab	bd	bb*	bd
		d	ad	dd*	bd	dd*

*IBD

$$F_{E\times F} = F_G = \frac{6}{16} = \frac{3}{8}$$

Another way to think about this is that *E* could be *ad* or *bd*, each with probability of 1/2, and similarly *F* could be *ad* or *bd*, each with equal probability. Then you get the above diagram.

No, the inbreeding coefficient of *G* does not change. The *F* value remains the same even if only one individual of *E* and one of *F* are intercrossed because *F* is an expected value or probability.

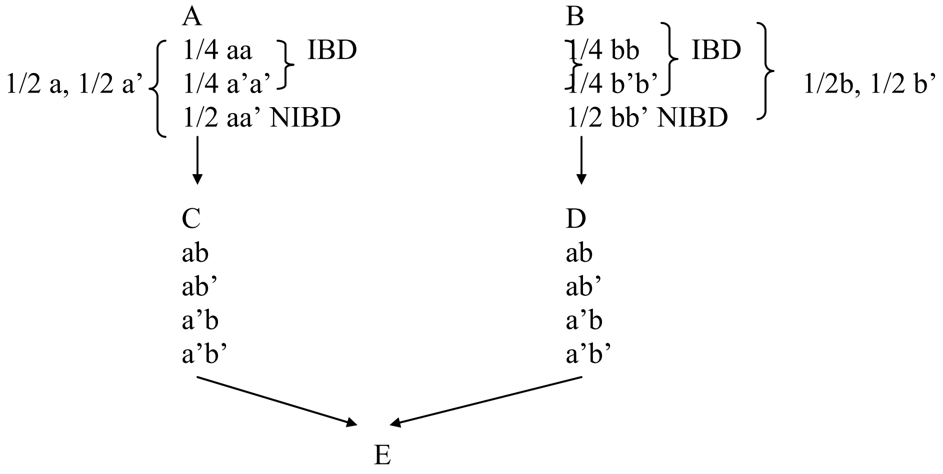
The thing that is different is that the variance of *F* for any single locus is much greater when *E*, *F*, and *G* are individuals than the case when a large number of individuals are used. When a large number of individuals are used, the variance of the inbreeding coefficient σ_F^2 would be essentially zero. The variance of *F* for the one-individual by one-individual case would be as follows: First, we calculate the distribution of the *F* values for the offspring *G* of *E* by *F*.

If *E* is *ad* and *F* is *ad* with frequency 1/4, $F_G = 1/2$.
If *E* is *ad* and *F* is *bd* with frequency 1/4, $F_G = 1/4$.
If *E* is *bd* and *F* is *ad* with frequency 1/4, $F_G = 1/4$.
If *E* is *bd* and *F* is *bd* with frequency 1/4, $F_G = 1/2$.

One half of the time the inbreeding of F_G would be 1/2, and one half of the time the inbreeding of F_G would be 1/4, so the variance of F_G would be

$$\sigma_F^2 = \frac{1}{2}\left(\frac{1}{2}-\frac{3}{8}\right)^2 + \frac{1}{2}\left(\frac{1}{4}-\frac{3}{8}\right)^2 = \frac{1}{2}\left(\frac{1}{8}\right)^2 + \frac{1}{2}\left(-\frac{1}{8}\right)^2 = \frac{1}{64}$$

b. In the cross between two S_1 lines, we deduce the inbreeding coefficient of *E* as follows: Even though one half of the individuals in each line would carry genes identical by descent, the cross is still the union between two equally frequency genes, *a* and *a*’, from line *A* and two equally frequency genes, *b* and *b*’, from line *B*.



			D		
		a	a’	b	b’
		1/4	1/4	1/4	1/4
	1/4 a	aa*	aa’	ab	ab’
C	1/4 a’	aa’	a’a’*	a’b	a’b’
	1/4 b	ab	a’b	bb*	bb’
	1/4 b’	ab’	a’b’	bb’	b’b’*

*IBD

$F_{C\times D} = F_E = 1/4$

If we assumed that each element in the pedigree were an individual, we would have the following table of coancestries:

	A	B	C	D	E
	- -	- -	A B	A B	C D
A	$\frac{3}{4}$	0	$\frac{3}{8}$	$\frac{3}{8}$	$\frac{3}{8}$
B		$\frac{3}{4}$	$\frac{3}{8}$	$\frac{3}{8}$	$\frac{3}{8}$
C			$\frac{1}{2}$	$\frac{3}{8}$	$\frac{7}{16}$
D				$\frac{1}{2}$	$\frac{7}{16}$
E					$\frac{11}{16}$

The coefficient of inbreeding of individual *E* obtained by the tabular method of coancestries is 3/8, which is not equal to that obtained by a definitional approach. The definitional approach has given us the correct inbreeding coefficient for *E*. The results are not the same, because we regarded each individual in the pedigree as an individual. For example, for *A* as an individual, the $\theta_{AA} = \frac{3}{4}$, but if *A* were a line $\theta_{AAl} = \frac{1}{2}$ [see Section 6.5.1(3), pp. 148-151]. Hence, if we modify the table accordingly, we obtain

	A	B	C	D	E
	- -	- -	A B	A B	C D
A	$\frac{1}{2}$	0	$\frac{1}{4}$	$\frac{1}{4}$	$\frac{1}{4}$
B		$\frac{1}{2}$	$\frac{1}{4}$	$\frac{1}{4}$	$\frac{1}{4}$
C			$\frac{1}{2}$	$\frac{1}{4}$	$\frac{3}{8}$
D				$\frac{1}{2}$	$\frac{3}{8}$
E					$\frac{5}{8}$

Now we obtain $F_E = \theta_{CD} = \frac{1}{4}$ so the results seem to agree with the definitional approach. The conclusion seems to be that we need coefficients of group coancestry in this situation. I do not currently profess to fully understand this situation and the use of group coancestries. The reader is referred to pp. 6.142 to 6.204 and the paper by C.C. Cockerham, 1967, Group inbreeding and coancestry. Genetics 56:88-104.

Exercise 4.17.

A four-gene probability is the probability associated with one of 15 possible, mutually exclusive states of identity by descent involving four genes at the same locus.

A four-gene probability for which only three genes are identical by descent is the probability of one of the 15 states of identity for which three genes, say a, b, and c, are identical and the fourth gene is not identical to the other three genes. In contrast, the three-gene probability for which all three genes, say a, b, and c, are identical is the probability of one of the five possible states of identity by descent involving three genes at the same locus. The three-gene probability γ_{abc} is equal to the probability of the union of the two disjoint four-gene states of identity, $a \equiv b \equiv c$ and $a \equiv b \equiv c \equiv d$ [see equation (4.77)].

Exercise 4.18.

R9 R13 R3 R8 A A

$$(1)\quad \delta_{\ddot{X}\ddot{Y}} = \delta_{\ddot{X}(XT)} = \delta_{\ddot{X}XT} = \gamma_{\ddot{X}T} = \gamma_{(ST)T} = \gamma_{STT} = \tfrac{1}{2}\left(\theta_{ST} + \gamma_{S\ddot{T}}\right) = \tfrac{1}{2}(0+0) = 0$$

R18 R21 R3 (see (1) above) R8 A A

$$(2)\quad \Delta_{\ddot{X}\cdot\ddot{Y}} = \Delta_{\ddot{X}\cdot XT} = \gamma_{\ddot{X}T} = \gamma_{(ST)T} = \gamma_{STT} = \tfrac{1}{2}\left(\theta_{ST} + \gamma_{S\ddot{T}}\right) = \tfrac{1}{2}(0+0) = 0$$

R28 R31 R2 R3 (see (1) above) A R1 R8

$$(3)\quad \Delta_{\ddot{X}+\ddot{Y}} = \Delta_{\ddot{X}+(XT)} = \Delta_{\ddot{X}+XT} = \tfrac{1}{2}\left(\theta_{XT} + \gamma_{\ddot{X}T}\right) = \tfrac{1}{2}\left(\theta_{(ST)T} + \gamma_{(ST)T}\right) = \tfrac{1}{2}\left[\tfrac{1}{2}\left(\theta_{ST} + \theta_{TT}\right) + \gamma_{STT}\right]$$

A A A

$$= \tfrac{1}{2}\left[\tfrac{1}{2}\left(0 + \frac{1+F_T}{2}\right) + \tfrac{1}{2}\left(\theta_{ST} + \gamma_{S\ddot{T}}\right)\right] = \tfrac{1}{2}\left[\tfrac{1}{2}\left(\tfrac{1}{2}\right) + \tfrac{1}{2}(0+0)\right] = \tfrac{1}{8}$$

R4 R6 R3 (see (1) above) R8 A R8

$$(4)\quad \gamma_{\ddot{X}Y} = \gamma_{\ddot{X}(XT)} = \tfrac{1}{2}\left(\gamma_{\ddot{X}X} + \gamma_{\ddot{X}T}\right) = \tfrac{1}{2}\left(F_{\ddot{X}} + \gamma_{(ST)T}\right) = \tfrac{1}{2}\left(\theta_{ST} + \gamma_{STT}\right)$$

$$= \tfrac{1}{2}\left[0 + \tfrac{1}{2}\left(\theta_{ST} + \gamma_{S\ddot{T}}\right)\right] = \tfrac{1}{2}\left[0 + \tfrac{1}{2}(0+0)\right] = 0$$

R3 R8 R2 R3 (see (1) above) A R1 R8

$$(5)\quad \gamma_{X\ddot{Y}} = \gamma_{X(XT)} = \gamma_{XXT} = \tfrac{1}{2}\left(\theta_{XT} + \gamma_{\ddot{X}T}\right) = \tfrac{1}{2}\left(\theta_{(ST)T} + \gamma_{(ST)T}\right) = \tfrac{1}{2}\left[\tfrac{1}{2}\left(\theta_{ST} + \theta_{TT}\right) + \gamma_{STT}\right]$$

A A A

$$=\tfrac{1}{2}\left[\tfrac{1}{2}\left(0+\frac{1+F_T}{2}\right)+\tfrac{1}{2}\left(\theta_{ST}+\gamma_{S\ddot{T}}\right)\right]=\tfrac{1}{2}\left[\tfrac{1}{4}+\tfrac{1}{2}(0+0)\right]=\tfrac{1}{8}$$

eq. (4.86)

(6) $F_{\ddot{X}}=\theta_{ST}=0$

eq. (4.86) R2 A

(7) $F_{\ddot{Y}}=\theta_{XT}=\theta_{(ST)T}=\tfrac{1}{2}\left(\theta_{ST}+\theta_{TT}\right)=\tfrac{1}{2}\left[0+\frac{1+F_T}{2}\right]=\tfrac{1}{2}\left[0+\tfrac{1}{2}\right]=\tfrac{1}{4}$

R2 R1 R2 (see (7) above) A

(8) $\theta_{XY}=\theta_{X(XT)}=\tfrac{1}{2}\left(\theta_{XX}+\theta_{XT}\right)=\tfrac{1}{2}\left[\frac{1+\theta_{ST}}{2}+\theta_{(ST)T}\right]=\tfrac{1}{2}\left[\tfrac{1}{2}+\tfrac{1}{2}\left(\theta_{ST}+\theta_{TT}\right)\right]=\tfrac{1}{2}\left[\tfrac{1}{2}+\tfrac{1}{2}\left(0+\frac{1+F_T}{2}\right)\right]$

$$=\tfrac{1}{2}\left[\tfrac{1}{2}+\tfrac{1}{2}\left(\tfrac{1}{2}\right)\right]=\tfrac{1}{2}\left[\tfrac{1}{2}+\tfrac{1}{4}\right]=\tfrac{3}{8}$$

The condensed coefficients of identity for *X* and *Y* from equation (4.82) are

$\Delta_1=\delta_{\ddot{X}\ddot{Y}}=0$

$\Delta_2=2\left(\gamma_{\ddot{X}Y}-\delta_{\ddot{X}\ddot{Y}}\right)=2(0-0)=0$

$\Delta_3=2\left(\gamma_{X\ddot{Y}}-\delta_{\ddot{X}\ddot{Y}}\right)=2\left(\tfrac{1}{8}-0\right)=\tfrac{1}{4}$

$\Delta_4=\Delta_{\ddot{X}\cdot\ddot{Y}}-\delta_{\ddot{X}\ddot{Y}}=0-0=0$

$\Delta_5=2\left(\Delta_{\ddot{X}+\ddot{Y}}-\delta_{\ddot{X}\ddot{Y}}\right)=2\left(\tfrac{1}{8}-0\right)=\tfrac{1}{4}$

$\Delta_6=F_{\ddot{X}}-\Delta_{\ddot{X}\cdot\ddot{Y}}-2\left(\gamma_{\ddot{X}Y}-\delta_{\ddot{X}\ddot{Y}}\right)=0-0-2(0-0)=0$

$\Delta_7=F_{\ddot{Y}}-\Delta_{\ddot{X}\cdot\ddot{Y}}-2\left(\gamma_{X\ddot{Y}}-\delta_{\ddot{X}\ddot{Y}}\right)=\tfrac{1}{4}-0-2\left(\tfrac{1}{8}-0\right)=0$

$\Delta_8=4\left(\theta_{XY}-\Delta_{\ddot{X}+\ddot{Y}}-\gamma_{\ddot{X}Y}-\gamma_{X\ddot{Y}}+2\delta_{\ddot{X}\ddot{Y}}\right)=4\left[\tfrac{3}{8}-\tfrac{1}{8}-0-\tfrac{1}{8}+2(0)\right]=4\left(\tfrac{1}{8}\right)=\tfrac{1}{2}$

$\Delta_9=1-F_{\ddot{X}}-F_{\ddot{Y}}-4\theta_{XY}+\Delta_{\ddot{X}\cdot\ddot{Y}}+2\Delta_{\ddot{X}+\ddot{Y}}+4\gamma_{\ddot{X}Y}+4\gamma_{X\ddot{Y}}-6\delta_{\ddot{X}\ddot{Y}}$

$\quad=1-0-\tfrac{1}{4}-4\cdot\tfrac{3}{8}+0+2\cdot\tfrac{1}{8}+4\cdot 0+4\cdot\tfrac{1}{8}-6\cdot 0$

$\quad=1-\tfrac{1}{4}-\tfrac{3}{2}+\tfrac{1}{4}+\tfrac{1}{2}=0$

Check:

$\Delta_1+\Delta_2+\Delta_3+\Delta_4+\Delta_5+\Delta_6+\Delta_7+\Delta_8+\Delta_9=0+0+\tfrac{1}{4}+0+\tfrac{1}{4}+0+0+\tfrac{1}{2}+0=1$

Exercise 4.19.

This exercise was subsequently inserted in my notes as Example 4.12A (see pp. 4.112 to 4.115), so the solution is given therein.

Exercise 4.20.

The quantities calculated for any two individuals, say *X* and *Y*, from any pedigree used to calculate the condensed coefficients of identity are given in equation (4.81).

First, we consider the full-sib individuals, *F* and *G*. The values for the required quantities in equation (4.81) for *F* and *G* are given in Example 4.10, p. 4.108 and 4.109, by simply replacing *X* with *F* and replacing *Y* with *G*, namely,

(1) $\delta_{\ddot{F}\ddot{G}}=0$, (2) $\Delta_{\ddot{F}\cdot\ddot{G}}=0$, (3) $\Delta_{\ddot{F}+\ddot{G}}=\tfrac{1}{8}$, (4) $\gamma_{\ddot{F}G}=0$, (5) $\gamma_{F\ddot{G}}=0$, (6) $F_{\ddot{F}}=0$, (7) $F_{\ddot{G}}=0$, (8) $\theta_{FG}=\tfrac{1}{4}$

Next, we consider individuals *M* and *N*:

(1) For the quantity $\delta_{\ddot{M}\ddot{N}}$ one can apply rule 9 and then apply rule 10 repeatedly, expanding backward in the pedigree to obtain a function of four-gene probabilities with a random gene from each of four ancestors *A*, *B*, *E*, and *H* all being identical by descent. By assumptions stated in the exercise all four-gene probabilities in which all four genes are identical by descent are equal to zero, namely, $\delta_{EAAH} = \delta_{EABH} = \delta_{EBAH} = \delta_{EBBH} = 0$. This expansion backwards in the pedigree is shown below

R9 R10b R10b R10b

(1) $\delta_{\ddot{M}\ddot{N}} = \delta_{(EF)(GH)} = \delta_{E(AB)GH} = \frac{1}{2}\left(\delta_{EAGH} + \delta_{EBGH}\right) = \frac{1}{2}\left(\delta_{EA(AB)H} + \delta_{EB(AB)H}\right)$

$= \frac{1}{2}\left[\frac{1}{2}\left(\delta_{EAAH} + \delta_{EABH}\right) + \frac{1}{2}\left(\delta_{EBAH} + \delta_{EBBH}\right)\right] = \frac{1}{4}\left[(0+0) + (0+0)\right] = 0$

However, if one gives a little thought to the meaning of $\delta_{\ddot{M}\ddot{N}}$, one does not need to do all of this detailed backward expansion in the pedigree. The meaning of $\delta_{\ddot{M}\ddot{N}}$ is given in equation (4.81) and Table 4.8, pp. 4.68 to 4.69. Its meaning is that all four genes are identical by descent—two genes in *M* and two genes in *N*. Alternatively, one may simply relabel the two genes in *M* and the two genes in *N* in terms of the parental origin of the genes in *M* and *N*, namely, $\delta_{\ddot{M}\ddot{N}} = \delta_{(EF)(GH)} = \delta_{EFGH}$ Finally, we may set the expression $\delta_{\ddot{M}\ddot{N}}$ equal to zero, because by a simple examination of the pedigree we know that the two genes in *M*, for example, from *E* and *F* are unrelated and that a random gene from *E* can never be identical by descent to a random gene from *F*, so $\delta_{\ddot{M}\ddot{N}} = 0$.

(2) Likewise by similar reasoning from the definition of $\Delta_{\ddot{M}\cdot\ddot{N}}$, given in equation (4.81) and Table 4.8, and inspection of the pedigree, one can set it equal to zero because the two genes in either *M* or *N* can never be identical, namely,

$\Delta_{\ddot{M}\cdot\ddot{N}} = \Delta_{(EF)\cdot(GH)} = 0$

(3) Again from the definition of $\Delta_{\ddot{M}+\ddot{N}}$ given in equation (4.81) and Table 4.8 we can write

$2\Delta_{\ddot{M}+\ddot{N}} = \Delta_{ac\cdot bd} + \Delta_{ad\cdot bc} = 2\delta_{abcd} + \delta_{ac\cdot bd} + \delta_{ad\cdot bc}$

where the random genes in *M* are *a* and *b* and those in *N* are *c* and *d* (bottom of p. 4.73). Since the parents of *M* are *E* and *F*, we may relabel *a* as *E* and *b* as *F*. Similarly since the parents of *N* are *G* and *H*, we may relabel *c* as *G* and *d* as *H*. Thus, we can rewrite the above in terms of parents *E*, *F*, *G*, and *H*:

$2\Delta_{\ddot{M}+\ddot{N}} = 2\Delta_{(EF)+(GH)} = \Delta_{EG\cdot FH} + \Delta_{EH\cdot FG} = 2\delta_{EFGH} + \delta_{EG\cdot FH} + \delta_{EH\cdot FG} = 2(0) + 0 + 0 = 0$

The second term $\delta_{EG\cdot FH}$ is equal to zero because *E* is unrelated to *G*, or *F* is unrelated to *H*. Similarly the third term $\delta_{EH\cdot FG}$ is equal to zero because *E* and *H* are unrelated.

(4) For the three-gene probability $\gamma_{\ddot{M}N}$ we can write

$2\gamma_{\ddot{M}N} = \gamma_{abc} + \gamma_{abd} = 2\delta_{abcd} + \delta_{abc} + \delta_{abd}$

Labeling *a*, *b*, *c*, and *d* as *E*, *F*, *G*, and *H*, we have

$2\gamma_{\ddot{M}N} = \gamma_{EFG} + \gamma_{EFH} = 2\delta_{EFGH} + \delta_{EFG} + \delta_{EFH} = 2(0) + 0 + 0 = 0$

(5) For the three-gene probability $\gamma_{M\ddot{N}}$ we can write

$2\gamma_{M\ddot{N}} = \gamma_{acd} + \gamma_{bcd} = 2\delta_{abcd} + \delta_{acd} + \delta_{bcd}$

Labeling *a*, *b*, *c*, and *d* as *E*, *F*, *G*, and *H*, we have

$2\gamma_{M\ddot{N}} = \gamma_{EGH} + \gamma_{FGH} = 2\delta_{EFGH} + \delta_{EGH} + \delta_{FGH} = 2(0) + 0 + 0 = 0$

(6) $F_{\ddot{M}} = \theta_{EF} = 0$

(7) $F_{\ddot{N}} = \theta_{GH} = 0$

(8) $\theta_{MN} = \theta_{(EF)(GH)} = \frac{1}{4}\left(\theta_{EG} + \theta_{EH} + \theta_{FG} + \theta_{FH}\right) = \frac{1}{4}\left(0 + 0 + \frac{1}{4} + 0\right) = \frac{1}{16}$

In summary, for *M* and *N* we have

(1) $\delta_{\ddot{M}\ddot{N}} = 0$, (2) $\Delta_{\ddot{M}\cdot\ddot{N}} = 0$, (3) $\Delta_{\ddot{M}+\ddot{N}} = 0$, (4) $\gamma_{\ddot{M}N} = 0$, (5) $\gamma_{M\ddot{N}} = 0$, (6) $F_{\ddot{M}} = 0$, (7) $F_{\ddot{N}} = 0$, (8) $\theta_{MN} = \frac{1}{16}$

Next, we consider *Q* and *R*. In Example 4.10, pp. 4.108 to 4.109, we considered full-sib mating and obtained the required quantities for *X* and *Y* as functions of two-, three-, and four-gene probabilities for the previous generation. Since the same rules apply, we simply substitute *Q* and *R* for *X* and *Y*, respectively, and *M* and *N* for *S* and *T*, respectively, in the derivation presented in Example 4.10 to obtain the required quantities for *Q* and *R*, followed by substitution of the appropriate numerical values for the probabilities. Thus, we have

R9 R16

(1) $\delta_{\ddot{Q}\ddot{R}} = \delta_{(MN)(MN)} = \delta_{MNMN} = \frac{1}{4}\left(\theta_{MN} + \gamma_{\ddot{M}N} + \gamma_{M\ddot{N}} + \delta_{\ddot{M}\ddot{N}}\right) = \frac{1}{4}\left(\frac{1}{16} + 0 + 0 + 0\right) = \frac{1}{64}$

R18 R25

(2) $\Delta_{\ddot{Q}\cdot\ddot{R}} = \Delta_{(MN)\cdot(MN)} = \Delta_{MN\cdot MN} = \frac{1}{4}\left(\theta_{MN} + \gamma_{\ddot{M}N} + \gamma_{M\ddot{N}} + \Delta_{\ddot{M}+\ddot{N}}\right) = \frac{1}{4}\left(\frac{1}{16} + 0 + 0 + 0\right) = \frac{1}{64}$

R28 R35 R24 R25

(3) $\Delta_{\ddot{Q}+\ddot{R}} = \Delta_{(MN)+(MN)} = \Delta_{MN+MN} = \frac{1}{2}\left(\Delta_{MM\cdot NN} + \Delta_{MN\cdot MN}\right)$

$= \frac{1}{2}\left[\frac{1}{4}\left(1 + F_{\ddot{M}} + F_{\ddot{N}} + \Delta_{\ddot{M}\cdot\ddot{N}}\right) + \frac{1}{4}\left(\theta_{MN} + \gamma_{\ddot{M}N} + \gamma_{M\ddot{N}} + \Delta_{\ddot{M}+\ddot{N}}\right)\right]$

$= \frac{1}{2}\left[\frac{1}{4}(1 + 0 + 0 + 0) + \frac{1}{4}\left(\frac{1}{16} + 0 + 0 + 0\right)\right] = \frac{1}{2}\left(\frac{1}{4} + \frac{1}{64}\right) = \frac{17}{128}$

R3 R5 R8 R8

(4) $\gamma_{\ddot{Q}R} = \gamma_{(MN)R} = \gamma_{MNR} = \gamma_{MN(MN)} = \frac{1}{2}\left(\gamma_{MMN} + \gamma_{MNN}\right)$

$= \frac{1}{2}\left[\frac{1}{2}\left(\theta_{MN} + \gamma_{\ddot{M}N}\right) + \frac{1}{2}\left(\theta_{MN} + \gamma_{M\ddot{N}}\right)\right] = \frac{1}{2}\left[\frac{1}{2}\left(\frac{1}{16} + 0\right) + \frac{1}{2}\left(\frac{1}{16} + 0\right)\right] = \frac{1}{2}\left(\frac{1}{32} + \frac{1}{32}\right) = \frac{1}{32}$

R3 R5 R8 R8

(5) $\gamma_{Q\ddot{R}} = \gamma_{Q(MN)} = \gamma_{QMN} = \gamma_{(MN)MN} = \frac{1}{2}\left(\gamma_{MMN} + \gamma_{MNN}\right) = \frac{1}{32}$ (see $\gamma_{\ddot{Q}R}$ above for the same expression)

(6) $F_{\ddot{Q}} = \theta_{MN} = \frac{1}{16}$

(7) $F_{\ddot{R}} = \theta_{MN} = \frac{1}{16}$

R2, eq. (4.42) R1 R1

(8) $\theta_{QR} = \theta_{(MN)(MN)} = \frac{1}{4}\left(\theta_{MM} + 2\theta_{MN} + \theta_{NN}\right) = \frac{1}{4}\left[\frac{1 + F_M}{2} + 2 \cdot \frac{1}{16} + \frac{1 + F_N}{2}\right] = \frac{1}{4}\left[\frac{1}{2} + \frac{1}{8} + \frac{1}{2}\right] = \frac{1}{4}\left(\frac{9}{8}\right) = \frac{9}{32}$

Then substituting these quantities for *Q* and *R* in equation (4.82), we obtain the condensed coefficients of identity for *Q* and *R*:

$\Delta_1 = \delta_{\ddot{Q}\ddot{R}} = \frac{1}{64}$

$\Delta_2 = 2\left(\gamma_{\ddot{Q}R} - \delta_{\ddot{Q}\ddot{R}}\right) = 2\left(\frac{1}{32} - \frac{1}{64}\right) = \frac{1}{32}$

$\Delta_3 = 2\left(\gamma_{Q\ddot{R}} - \delta_{\ddot{Q}\ddot{R}}\right) = 2\left(\frac{1}{32} - \frac{1}{64}\right) = \frac{1}{32}$

$\Delta_4 = \Delta_{\ddot{Q}\cdot\ddot{R}} - \delta_{\ddot{Q}\ddot{R}} = \frac{1}{64} - \frac{1}{64} = 0$

$$\Delta_5 = 2\left(\Delta_{\ddot{Q}+\ddot{R}} - \delta_{\ddot{Q}\ddot{R}}\right) = 2\left(\tfrac{17}{128} - \tfrac{1}{64}\right) = \frac{30}{128} = \tfrac{15}{64}$$

$$\Delta_6 = F_{\ddot{Q}} - \Delta_{\ddot{Q}\cdot\ddot{R}} - 2\left(\gamma_{\ddot{Q}R} - \delta_{\ddot{Q}\ddot{R}}\right) = \tfrac{1}{16} - \tfrac{1}{64} - 2\left(\tfrac{1}{32} - \tfrac{1}{64}\right) = \tfrac{1}{16} - \tfrac{1}{64} - \tfrac{2}{64} = \tfrac{1}{64}$$

$$\Delta_7 = F_{\ddot{R}} - \Delta_{\ddot{Q}\cdot\ddot{R}} - 2\left(\gamma_{Q\ddot{R}} - \delta_{\ddot{Q}\ddot{R}}\right) = \tfrac{1}{16} - \tfrac{1}{64} - 2\left(\tfrac{1}{32} - \tfrac{1}{64}\right) = \tfrac{1}{16} - \tfrac{1}{64} - \tfrac{2}{64} = \tfrac{1}{64}$$

$$\Delta_8 = 4\left(\theta_{QR} - \Delta_{\ddot{Q}+\ddot{R}} - \gamma_{\ddot{Q}R} - \gamma_{Q\ddot{R}} + 2\delta_{\ddot{Q}\ddot{R}}\right) = 4\left[\tfrac{9}{32} - \tfrac{17}{128} - \tfrac{1}{32} - \tfrac{1}{32} + 2\left(\tfrac{1}{64}\right)\right] = 4\left(\tfrac{36-17-4-4+4}{128}\right) = \tfrac{15}{32}$$

$$\Delta_9 = 1 - F_{\ddot{Q}} - F_{\ddot{R}} - 4\theta_{QR} + \Delta_{\ddot{Q}\cdot\ddot{R}} + 2\Delta_{\ddot{Q}+\ddot{R}} + 4\gamma_{\ddot{Q}R} + 4\gamma_{Q\ddot{R}} - 6\delta_{\ddot{Q}\ddot{R}}$$

$$= 1 - \tfrac{1}{16} - \tfrac{1}{16} - 4\cdot\tfrac{9}{32} + \tfrac{1}{64} + 2\cdot\tfrac{17}{128} + 4\cdot\tfrac{1}{32} + 4\cdot\tfrac{1}{32} - 6\left(\tfrac{1}{64}\right)$$

$$= 1 - \tfrac{2}{16} - \tfrac{9}{8} + \tfrac{1}{64} + \tfrac{17}{64} + \tfrac{1}{8} + \tfrac{1}{8} - \tfrac{3}{32} = 1 + \tfrac{1+17+8+8}{64} - \tfrac{8+72+6}{64} = 1 + \tfrac{34}{64} - \tfrac{86}{64} = 1 - \tfrac{52}{64} = \tfrac{12}{64} = \tfrac{3}{16}$$

Check:

$$\Delta_1 + \Delta_2 + \Delta_3 + \Delta_4 + \Delta_5 + \Delta_6 + \Delta_7 + \Delta_8 + \Delta_9 = \tfrac{1}{64} + \tfrac{1}{32} + \tfrac{1}{32} + 0 + \tfrac{15}{64} + \tfrac{1}{64} + \tfrac{1}{64} + \tfrac{15}{32} + \tfrac{3}{16} = 1$$

Exercise 4.21.

R5 P R5 R5 R5

$$\gamma_{KLM} = \gamma_{(DI)LM} = \tfrac{1}{2}\left(\gamma_{DLM} + \gamma_{ILM}\right) = \tfrac{1}{2}\gamma_{ILM} = \tfrac{1}{2}\gamma_{IL(EF)} = \tfrac{1}{2}\tfrac{1}{2}\left(\gamma_{ILE} + \gamma_{ILF}\right) = \tfrac{1}{4}\left(\gamma_{I(EF)E} + \gamma_{I(EF)F}\right)$$

R8 R5 R8 par-off R4 par-off R4

$$= \tfrac{1}{4}\left[\tfrac{1}{2}\left(\gamma_{IEE} + \gamma_{IFE}\right) + \tfrac{1}{2}\left(\gamma_{IEF} + \gamma_{IFF}\right)\right] = \tfrac{1}{8}\left[\tfrac{1}{2}\left(\theta_{IE} + \gamma_{\ddot{E}I}\right) + 2\gamma_{(EF)FE} + \tfrac{1}{2}\left(\theta_{IF} + \gamma_{\ddot{F}I}\right)\right]$$

R8 R8

$$= \tfrac{1}{16}\left[\tfrac{1}{4} + \gamma_{\ddot{E}(EF)} + 4\cdot\tfrac{1}{2}\left(\gamma_{EEF} + \gamma_{FFE}\right) + \tfrac{1}{4} + \gamma_{\ddot{F}(EF)}\right]$$

R6 P A P A P P R6

$$= \tfrac{1}{16}\left[\tfrac{1}{2} + \tfrac{1}{2}\left(\gamma_{\ddot{E}E} + \gamma_{\ddot{E}F}\right) + 2\left[\tfrac{1}{2}\left(\theta_{EF} + \gamma_{\ddot{E}F}\right) + \tfrac{1}{2}\left(\theta_{EF} + \gamma_{E\ddot{F}}\right)\right] + \tfrac{1}{2}\left(\gamma_{\ddot{F}E} + \gamma_{\ddot{F}F}\right)\right]$$

A A

$$= \tfrac{1}{32}\left\{1 + F_E + 0 + 2\left[0 + 0 + 0 + 0\right] + 0 + F_F\right\} = \tfrac{1}{32}$$

R10 P R10 R10 P

$$\delta_{KLMN} = \delta_{(DE)LMN} = \tfrac{1}{2}\left(\delta_{DLMN} + \delta_{ILMN}\right) = \tfrac{1}{2}\delta_{ILM(GH)} = \tfrac{1}{2}\left[\tfrac{1}{2}\left(\delta_{ILMG} + \delta_{ILMH}\right)\right] = \tfrac{1}{4}\left(\delta_{IL(EF)G}\right)$$

R10 R10 P P P R17

$$= \tfrac{1}{4}\left[\tfrac{1}{2}\left(\delta_{ILEG} + \delta_{ILFG}\right)\right] = \tfrac{1}{8}\left(\delta_{I(EF)EG} + \delta_{I(EF)FG}\right) = \tfrac{1}{8}\left[\tfrac{1}{2}\left(\delta_{IEEG} + \delta_{IFEG}\right) + \tfrac{1}{2}\left(\delta_{IEFG} + \delta_{IFFG}\right)\right]$$

R5 R10 P R8 P R13

$$= \tfrac{1}{16}\left[\tfrac{1}{2}\left(\gamma_{IFG} + \delta_{I\ddot{F}G}\right)\right] = \tfrac{1}{32}\left[\gamma_{(EF)FG} + \delta_{(EF)\ddot{F}G}\right] = \tfrac{1}{32}\left[\tfrac{1}{2}\left(\gamma_{EFG} + \delta_{FFG}\right) + \tfrac{1}{2}\left(\delta_{E\ddot{F}G} + \delta_{F\ddot{F}G}\right)\right]$$

R2 R4 R4

$$= \tfrac{1}{64}\left[\tfrac{1}{2}\left(\theta_{FG} + \gamma_{\ddot{F}G}\right) + \gamma_{\ddot{F}G}\right] = \tfrac{1}{64}\left[\tfrac{1}{2}\left(\theta_{F(AB)} + \gamma_{\ddot{F}(AB)}\right) + \gamma_{\ddot{F}(AB)}\right]$$

$$=\frac{1}{128}\left[\frac{1}{2}\left(\overset{R2}{\theta_{FA}}+\overset{R2}{\gamma_{FB}}\right)+\frac{1}{2}\left(\overset{R3}{\gamma_{\ddot{F}A}}+\overset{R3}{\gamma_{\ddot{F}B}}\right)+2\cdot\frac{1}{2}\left(\gamma_{\ddot{F}A}+\gamma_{\ddot{F}B}\right)\right]$$

$$=\frac{1}{256}\left[\theta_{(AB)A}+\theta_{(AB)B}+\overset{P}{\gamma_{(AB)A}}+\overset{P}{\gamma_{(AB)B}}+2\left(\overset{P}{\gamma_{(AB)A}}+\overset{P}{\gamma_{(AB)B}}\right)\right]$$

$$=\frac{1}{256}\left[\frac{1}{2}\left(\theta_{AA}+\overset{P}{\theta_{AB}}\right)+\frac{1}{2}\left(\overset{P}{\theta_{AB}}+\theta_{BB}\right)\right]=\frac{1}{512}\left[\frac{1+F_A}{2}+\frac{1+F_B}{2}\right]=\frac{1}{512}$$

An alternative method of evaluating γ_{KLM} is to calculate directly the probability of a random gene drawn from each of the individuals *K*, *L*, and *M* being identical by descent. This method is satisfactory only for simple pedigrees. First we identify all of the common ancestral individuals, *E* and *F*, and for each common ancestor we evaluate the probability that the random genes drawn from *K*, *L*, and *M* are the same gene. For common ancestor *E* we symbolize the two genes in *E* as genes a_1 and a_2. From inspection of the pedigree the probability that a random gene drawn from each individual, *K*, *L*, and *M*, equals the event of all three genes being the gene a_1 is $\left(\frac{1}{2}\right)^3\left(\frac{1}{2}\right)^2\left(\frac{1}{2}\right)^2=\left(\frac{1}{2}\right)^7=\frac{1}{128}$ (see Section 4.5). That is, the probability of drawing a_1 from *K* is $\left(\frac{1}{2}\right)^3$, of drawing a_1 from *L* is $\left(\frac{1}{2}\right)^2$, and of drawing a_1 from *M* is $\left(\frac{1}{2}\right)^2$. The combined probability is the product $\left(\frac{1}{2}\right)^7=\frac{1}{128}$. Similarly the probability that the three random genes drawn from *K*, *L*, and *M* are the same gene a_2 is the same probability 1/128. The sum of the two mutually exclusive events is 1/64. In like manner for the other common ancestor *F* which bears the same pedigree relation to *K*, *L*, and *M* as *E* does, we obtain another 1/64. The sum of the two events gives $\gamma_{KLM}=\frac{1}{64}+\frac{1}{64}=\frac{1}{32}$ which is the answer obtained above.

This direct method of calculating the probability for δ_{KLMN} in terms of genes from the common ancestors *E*, *A*, and *B* is not suitable because individual *F* is common in the descent paths, so the events are not independent.

Exercise 4.22.

$$\overset{R5}{\gamma_{KLN}}=\gamma_{(DI)LN}=\frac{1}{2}\left(\overset{P}{\gamma_{DLN}}+\gamma_{ILN}\right)=\frac{1}{2}\overset{R5}{\gamma_{ILN}}=\frac{1}{2}\gamma_{IL(GH)}=\frac{1}{2}\left[\frac{1}{2}\left(\gamma_{ILG}\overset{P}{+}\gamma_{ILH}\right)\right]$$

$$=\frac{1}{4}\overset{R5}{\gamma_{ILG}}=\frac{1}{4}\gamma_{I(EF)G}=\frac{1}{4}\left[\frac{1}{2}\left(\gamma_{IEG}+\gamma_{IFG}\right)\right]=\frac{1}{8}\left(\overset{R5}{\gamma_{IEG}}+\overset{R5}{\gamma_{IFG}}\right)=\frac{1}{8}\left(\gamma_{(EF)EG}+\gamma_{(EF)FG}\right)$$

$$=\frac{1}{8}\left[\frac{1}{2}\left(\gamma_{EEG}+\gamma_{EFG}\right)+\frac{1}{2}\left(\gamma_{EFG}+\gamma_{FFG}\right)\right]=\frac{1}{16}\left[\overset{R8}{\gamma_{EEG}}+\overset{P}{2\gamma_{EFG}}+\overset{R8}{\gamma_{FFG}}\right]$$

$$=\frac{1}{16}\left[\frac{1}{2}\left(\overset{P}{\theta_{EG}}+\overset{P}{\gamma_{\ddot{E}G}}\right)+0+\frac{1}{2}\left(\overset{\text{Exam. 4.10}}{\theta_{FG}}+\gamma_{\ddot{F}G}\right)\right]=\frac{1}{32}\left[0+0+\frac{1}{4}+0\right]=\frac{1}{128}$$

$$\overset{R5}{\gamma_{KMN}}=\gamma_{(DI)MN}=\frac{1}{2}\left(\overset{P}{\gamma_{DMN}}+\gamma_{IMN}\right)=\frac{1}{2}\overset{R5}{\gamma_{IMN}}=\frac{1}{2}\gamma_{IM(GH)}=\frac{1}{2}\left[\frac{1}{2}\left(\gamma_{IMG}\overset{P}{+}\gamma_{IMH}\right)\right]$$

R5 P R5

$$=\tfrac{1}{4}\gamma_{IMG}=\tfrac{1}{4}\gamma_{I(EF)G}=\tfrac{1}{4}\left[\tfrac{1}{2}\left(\gamma_{IEG}+\gamma_{IFG}\right)\right]=\tfrac{1}{8}\left[\gamma_{(EF)FG}\right]$$

P R8

$$=\tfrac{1}{8}\left[\tfrac{1}{2}\left(\gamma_{EFG}+\gamma_{FFG}\right)\right]=\tfrac{1}{16}\gamma_{FFG}$$

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$$=\tfrac{1}{16}\left[\tfrac{1}{2}\left(\theta_{FG}+\gamma_{\ddot{F}G}\right)\right]=\tfrac{1}{32}\left[\tfrac{1}{4}+0\right]=\tfrac{1}{128}$$

R5 P R5 P R5

$$\gamma_{LMN}=\gamma_{LM(GH)}=\tfrac{1}{2}\left(\gamma_{LMG}+\gamma_{LMH}\right)=\tfrac{1}{2}\gamma_{LMG}=\tfrac{1}{2}\gamma_{L(EF)G}=\tfrac{1}{2}\left[\tfrac{1}{2}\left(\gamma_{LEG}+\gamma_{LFG}\right)\right]$$

P

$$=\tfrac{1}{4}\left(0+\gamma_{(EF)FG}\right)=\tfrac{1}{4}\left[\tfrac{1}{2}\left(\gamma_{EFG}+\gamma_{FFG}\right)\right]$$

R8 Exam. 4.10

$$=\tfrac{1}{8}\left(0+\gamma_{FFG}\right)=\tfrac{1}{8}\left[\tfrac{1}{2}\left(\theta_{FG}+\gamma_{\ddot{F}G}\right)\right]=\tfrac{1}{16}\left(\tfrac{1}{4}+0\right)=\tfrac{1}{64}$$

R10 P R10

$$\delta_{JKLM}=\delta_{(CI)KLM}=\tfrac{1}{2}\left(\delta_{CKLM}+\delta_{IKLM}\right)=\tfrac{1}{2}\delta_{IKLM}=\tfrac{1}{2}\delta_{I(DI)LM}$$

P R17 R5 R9b

$$=\tfrac{1}{2}\left[\tfrac{1}{2}\left(\delta_{IDLM}+\delta_{IILM}\right)\right]=\tfrac{1}{4}\left[\tfrac{1}{2}\left(\gamma_{ILM}+\delta_{\ddot{I}LM}\right)\right]=\tfrac{1}{8}\left[\gamma_{IL(EF)}+\delta_{(EF)LM}\right]$$

R5 R5 R10b

$$=\tfrac{1}{8}\left[\tfrac{1}{2}\left(\gamma_{ILE}+\gamma_{ILF}\right)+\delta_{EFLM}\right]=\tfrac{1}{8}\left[\tfrac{1}{2}\left(\gamma_{(EF)LE}+\gamma_{(EF)LF}\right)+\tfrac{2}{2}\delta_{EFL(EF)}\right]$$

R8 P P R8 P P

$$=\tfrac{1}{16}\left[\tfrac{1}{2}\left(\gamma_{EEL}+\gamma_{FLE}\right)+\tfrac{1}{2}\left(\gamma_{ELF}+\gamma_{FFL}\right)+2\tfrac{1}{2}\left(\delta_{EEFL}+\delta_{EFFL}\right)\right]$$

R2 R4 R2 R4

$$=\tfrac{1}{32}\left[\tfrac{1}{2}\left(\theta_{EL}+\gamma_{\ddot{E}L}\right)+\tfrac{1}{2}\left(\theta_{FL}+\gamma_{\ddot{F}L}\right)\right]=\tfrac{1}{64}\left[\theta_{E(EF)}+\gamma_{\ddot{E}(EF)}+\theta_{F(EF)}+\gamma_{\ddot{F}(EF)}\right]$$

P P P

$$=\tfrac{1}{64}\left[\tfrac{1}{2}\left(\theta_{EE}+\theta_{EF}\right)+\tfrac{1}{2}\left(\gamma_{\ddot{E}E}+\gamma_{\ddot{E}F}\right)+\tfrac{1}{2}\left(\theta_{EF}+\theta_{FF}\right)+\tfrac{1}{2}\left(\gamma_{\ddot{F}E}+\gamma_{\ddot{F}F}\right)\right]$$

$$=\tfrac{1}{128}\left[\frac{1+F_E}{2}+0+F_{\ddot{E}}+\frac{1+F_F}{2}+F_{\ddot{F}}\right]=\tfrac{1}{128}[1]=\tfrac{1}{128}$$

R10 P R10

$$\delta_{JKLN}=\delta_{(CI)KLN}=\tfrac{1}{2}\left(\delta_{CKLN}+\delta_{IKLN}\right)=\tfrac{1}{2}\delta_{IKLN}=\tfrac{1}{2}\delta_{IKL(GH)}$$

P P P

$$=\tfrac{1}{2}\left[\tfrac{1}{2}\left(\delta_{IKLG}+\delta_{IKLH}\right)\right]=\tfrac{1}{4}\left(\delta_{I(DI)LG}+\delta_{I(DI)LH}\right)=\tfrac{1}{4}\left[\tfrac{1}{2}\left(\delta_{IDLG}+\delta_{IILG}\right)+\tfrac{1}{2}\left(\delta_{IDLH}+\delta_{IILH}\right)\right]$$

R17 R5 R10a

$$\tfrac{1}{8}\delta_{IILG}=\tfrac{1}{8}\left[\tfrac{1}{2}\left(\gamma_{ILG}+\delta_{\ddot{I}LG}\right)\right]=\tfrac{1}{16}\left[\gamma_{I(EF)G}+\delta_{\ddot{I}(EF)G}\right]$$

P P R5 R9b

$$=\tfrac{1}{16}\left[\tfrac{1}{2}\left(\gamma_{IEG}+\gamma_{IFG}\right)+\tfrac{1}{2}\left(\delta_{\ddot{I}EG}+\delta_{\ddot{I}FG}\right)\right]=\tfrac{1}{32}\left(\gamma_{IFG}+\delta_{\ddot{I}FG}\right)=\tfrac{1}{32}\left(\gamma_{(EF)FG}+\delta_{(EF)FG}\right)$$

P P Exam. 4.10

$$=\frac{1}{32}\left[\frac{1}{2}\left(\gamma_{EFG}+\gamma_{FFG}\right)+\delta_{EFFG}\right]=\frac{1}{64}\left[\frac{1}{2}\left(\theta_{FG}+\gamma_{\ddot{F}G}\right)\right]=\frac{1}{128}\left[\frac{1}{4}+0\right]=\frac{1}{512}$$

Exercise 4.23.

	A	B	E	F	G	I	J	K	L	M	N	O	P	Q	R
	- -	- -	- -	A B	A B	E F	- I	- I	E F	E F	G -	J L	K L	M N	M N
A	$\frac{1}{2}$	0	0	$\frac{1}{4}$	$\frac{1}{4}$	$\frac{1}{8}$	$\frac{1}{16}$	$\frac{1}{16}$	$\frac{1}{8}$	$\frac{1}{8}$	$\frac{1}{8}$	$\frac{3}{32}$	$\frac{3}{32}$	$\frac{1}{8}$	$\frac{1}{8}$
B		$\frac{1}{2}$	0	$\frac{1}{4}$	$\frac{1}{4}$	$\frac{1}{8}$	$\frac{1}{16}$	$\frac{1}{16}$	$\frac{1}{8}$	$\frac{1}{8}$	$\frac{1}{8}$	$\frac{3}{32}$	$\frac{3}{32}$	$\frac{1}{8}$	$\frac{1}{8}$
E			$\frac{1}{2}$	0	0	$\frac{1}{4}$	$\frac{1}{8}$	$\frac{1}{8}$	$\frac{1}{4}$	$\frac{1}{4}$	0	$\frac{3}{16}$	$\frac{3}{16}$	$\frac{1}{8}$	$\frac{1}{8}$
F				$\frac{1}{2}$	$\frac{1}{4}$	$\frac{1}{4}$	$\frac{1}{8}$	$\frac{1}{8}$	$\frac{1}{4}$	$\frac{1}{4}$	$\frac{1}{8}$	$\frac{3}{16}$	$\frac{3}{16}$	$\frac{3}{16}$	$\frac{3}{16}$
G					$\frac{1}{2}$	$\frac{1}{8}$	$\frac{1}{16}$	$\frac{1}{16}$	$\frac{1}{8}$	$\frac{1}{8}$	$\frac{1}{4}$	$\frac{3}{32}$	$\frac{3}{32}$	$\frac{3}{16}$	$\frac{3}{16}$
I						$\frac{1}{2}$	$\frac{1}{4}$	$\frac{1}{4}$	$\frac{1}{4}$	$\frac{1}{4}$	$\frac{1}{16}$	$\frac{1}{4}$	$\frac{1}{4}$	$\frac{5}{32}$	$\frac{5}{32}$
J							$\frac{1}{2}$	$\frac{1}{8}$	$\frac{1}{8}$	$\frac{1}{8}$	$\frac{1}{32}$	$\frac{5}{16}$	$\frac{1}{8}$	$\frac{5}{64}$	$\frac{5}{64}$
K								$\frac{1}{2}$	$\frac{1}{8}$	$\frac{1}{8}$	$\frac{1}{32}$	$\frac{1}{8}$	$\frac{5}{16}$	$\frac{5}{64}$	$\frac{5}{64}$
L									$\frac{1}{2}$	$\frac{1}{4}$	$\frac{1}{16}$	$\frac{5}{16}$	$\frac{5}{16}$	$\frac{5}{32}$	$\frac{5}{32}$
M										$\frac{1}{2}$	$\frac{1}{16}$	$\frac{3}{16}$	$\frac{3}{16}$	$\frac{9}{32}$	$\frac{9}{32}$
N											$\frac{1}{2}$	$\frac{3}{64}$	$\frac{3}{64}$	$\frac{9}{32}$	$\frac{9}{32}$
O												$\frac{9}{16}$	$\frac{7}{32}$	$\frac{15}{128}$	$\frac{15}{128}$
P													$\frac{9}{16}$	$\frac{15}{128}$	$\frac{15}{128}$
Q														$\frac{17}{32}$	$\frac{9}{32}$
R															$\frac{17}{32}$

The coefficients of inbreeding of O, P, Q, and R are:

$F_O=\theta_{JL}=\frac{1}{8}, F_P=\theta_{KL}=\frac{1}{8}, F_Q=\theta_{MN}=\frac{1}{16}, F_R=\theta_{MN}=\frac{1}{16}$.

Exercise 4.24.

$$\text{(1)}\quad \gamma_{JKL}\overset{\text{R5}}{=}\gamma_{(CI)KL}\overset{\text{P}}{=}\frac{1}{2}(\gamma_{CKL}+\gamma_{IKL})\overset{\text{R5}}{=}\frac{1}{2}\gamma_{I(DI)L}\overset{\text{P}}{=}\frac{1}{2}\left[\frac{1}{2}(\gamma_{IDL}+\gamma_{IIL})\right]=\frac{1}{4}\gamma_{IIL}\overset{\text{R8}}{=}\frac{1}{4}\left[\frac{1}{2}\left(\theta_{IL}+\gamma_{\ddot{I}L}\right)\right]$$

$$=\frac{1}{8}\left(\frac{1}{4}+\gamma_{\ddot{I}L}\right)\overset{\text{R3}}{=}\frac{1}{8}\left(\frac{1}{4}+\gamma_{(EF)L}\right)=\frac{1}{8}\left(\frac{1}{4}+\gamma_{EFL}\right)\overset{\text{R5}}{=}\frac{1}{8}\left(\frac{1}{4}+\gamma_{EF(EF)}\right)=\frac{1}{8}\left[\frac{1}{4}+\frac{1}{2}(\gamma_{EEF}+\gamma_{EFF})\right]$$

$$=\frac{1}{16}\left[\frac{1}{2}+\overset{\text{R8}}{\gamma_{EEF}}+\overset{\text{R8}}{\gamma_{EFF}}\right]=\frac{1}{16}\left[\frac{1}{2}+\frac{1}{2}\left(\overset{\text{P}}{\theta_{EF}}+\overset{\text{P}}{\gamma_{\ddot{E}F}}\right)+\frac{1}{2}\left(\overset{\text{P}}{\theta_{EF}}+\overset{\text{P}}{\gamma_{E\ddot{F}}}\right)\right]=\frac{1}{32}$$

(2) $\gamma_{JKM}\overset{\text{R5}}{=}\gamma_{JK(EF)}$ which is equal to $\overset{\text{see (1) above}}{\gamma_{JKL}}=\gamma_{JK(EF)}=\frac{1}{32}$

$$\text{(3)}\quad \gamma_{JKN}\overset{\text{R5}}{=}\gamma_{JK(GH)}=\frac{1}{2}(\gamma_{JKG}+\gamma_{JKH})\overset{\text{P}}{=}\frac{1}{2}\gamma_{JKG}\overset{\text{R5}}{=}\frac{1}{2}\gamma_{J(DI)G}\overset{\text{P}}{=}\frac{1}{2}\left[\frac{1}{2}(\gamma_{JDG}+\gamma_{JIG})\right]\overset{\text{R5}}{=}\frac{1}{4}\gamma_{JIG}$$

$$=\frac{1}{4}\gamma_{(CI)IG}\overset{\text{P}}{=}\frac{1}{4}\left[\frac{1}{2}(\gamma_{CIG}+\gamma_{IIG})\right]=\frac{1}{8}\gamma_{IIG}\overset{\text{R8}}{=}\frac{1}{8}\left[\frac{1}{2}\left(\theta_{IG}+\gamma_{\ddot{I}G}\right)\right]\overset{\text{R3}}{=}\frac{1}{16}\left[\overset{\text{table}}{\frac{1}{8}}+\gamma_{(EF)G}\right]\overset{\text{P}}{=}\frac{1}{128}$$

$$\text{(4)}\quad \gamma_{JLM}\overset{\text{R5}}{=}\gamma_{(CI)LM}\overset{\text{P}}{=}\frac{1}{2}(\gamma_{CLM}+\gamma_{ILM})\overset{\text{given in Exer.}}{=}\frac{1}{2}\left(0+\frac{1}{16}\right)=\frac{1}{32}$$

$$\text{(5)}\quad \gamma_{JLN}\overset{\text{R5}}{=}\gamma_{(CI)LN}\overset{\text{P}}{=}\frac{1}{2}(\gamma_{CLN}+\gamma_{ILN})\overset{\text{given in Exer.}}{=}\frac{1}{2}\left(0+\frac{1}{64}\right)=\frac{1}{128}$$

$$\text{(6)}\quad \gamma_{JMN}\overset{\text{R5}}{=}\gamma_{(CI)MN}\overset{\text{P}}{=}\frac{1}{2}(\gamma_{CMN}+\gamma_{IMN})\overset{\text{given in Exer.}}{=}\frac{1}{2}\left(0+\frac{1}{64}\right)=\frac{1}{128}$$

$$\text{(1)}\quad \delta_{JKMN}\overset{\text{R10b}}{=}\delta_{(CI)KMN}\overset{\text{P}}{=}\frac{1}{2}(\delta_{CKMN}+\delta_{IKMN})\overset{\text{R10b}}{=}\frac{1}{2}\delta_{I(DI)MN}\overset{\text{P}}{=}\frac{1}{2}\left[\frac{1}{2}\left(\delta_{IDMN}+\frac{1}{2}\delta_{IIMN}\right)\right]\overset{\text{R17}}{=}\frac{1}{4}\delta_{IIMN}$$

$$=\frac{1}{4}\left[\frac{1}{2}\left(\overset{\text{given in Exer.}}{\gamma_{IMN}}+\delta_{\ddot{I}MN}\right)\right]\overset{\text{R10a}}{=}\frac{1}{8}\left[\frac{1}{64}+\delta_{(EF)MN}\right]=\frac{1}{8}\left[\frac{1}{64}+\delta_{EFMN}\right]\overset{\text{P}}{=}\frac{1}{512}$$

$$\text{(2)}\quad \delta_{JLMN}\overset{\text{R10b}}{=}\delta_{(CI)LMN}\overset{\text{P}}{=}\frac{1}{2}(\delta_{CLMN}+\delta_{ILMN})\overset{\text{given in Exer.}}{=}\frac{1}{2}\left(0+\frac{1}{256}\right)=\frac{1}{512}$$

Exercise 4.25.

A table of coancestries is:

	O	P	Q	R	S	T	U	V
	- -	- -	- -	- -	O Q	P R	S T	S T
O	$\frac{9}{16}$	$\frac{7}{32}$	$\frac{15}{128}$	$\frac{15}{128}$	$\frac{87}{256}$	$\frac{43}{256}$	$\frac{65}{256}$	$\frac{65}{256}$
P		$\frac{9}{16}$	$\frac{15}{128}$	$\frac{15}{128}$	$\frac{43}{256}$	$\frac{87}{256}$	$\frac{65}{256}$	$\frac{65}{256}$
Q			$\frac{17}{32}$	$\frac{9}{32}$	$\frac{83}{256}$	$\frac{51}{256}$	$\frac{67}{256}$	$\frac{67}{256}$
R				$\frac{17}{32}$	$\frac{51}{256}$	$\frac{83}{256}$	$\frac{67}{256}$	$\frac{67}{256}$
S					$\frac{143}{256}$	$\frac{47}{256}$	$\frac{95}{256}$	$\frac{95}{256}$
T						$\frac{143}{256}$	$\frac{95}{256}$	$\frac{95}{256}$
U							$\frac{303}{512}$	$\frac{95}{256}$
V								$\frac{303}{512}$

The inbreeding coefficient of U and V is $F_U = F_V = \theta_{ST} = \frac{47}{256}$ and the inbreeding coefficient of the offspring between U and V is $F_{(U\times V)} = \frac{95}{256}$.

Exercise 4.26.

a.

R17 given = 0 P

$$\delta_{\ddot{O}\ddot{P}} = \delta_{(JL)(KL)} = \delta_{JKLL} = \tfrac{1}{2}\left(\gamma_{JKL} + \delta_{JK\ddot{L}}\right) = \tfrac{1}{2}\left(\tfrac{1}{32}\right) = \tfrac{1}{64}$$

R18a R27 given R29a

$$\Delta_{\ddot{O}\cdot\ddot{P}} = \Delta_{(JL)\cdot(KL)} = \Delta_{JL\cdot KL} = \tfrac{1}{2}\left(\gamma_{JKL} + \Delta_{JK+\ddot{L}}\right) = \tfrac{1}{2}\left(\tfrac{1}{32} + \Delta_{J(DI)+\ddot{L}}\right) = \tfrac{1}{64} + \tfrac{1}{2}\tfrac{1}{2}\left(\Delta_{JD+\ddot{L}} + \Delta_{JI+\ddot{L}}\right)$$

R29a R29a = 0 P = 0 P = 0 P R21a

$$= \tfrac{1}{64} + \tfrac{1}{4}\left(\Delta_{(CI)D+\ddot{L}} + \Delta_{(CI)I+\ddot{L}}\right) = \tfrac{1}{64} + \tfrac{1}{4}\left[\tfrac{1}{2}\left(\Delta_{CD+\ddot{L}} + \Delta_{ID+\ddot{L}}\right) + \tfrac{1}{2}\left(\Delta_{CI+\ddot{L}} + \Delta_{II+\ddot{L}}\right)\right]$$

= 0 P = 0 P

$$= \tfrac{1}{64} + \tfrac{1}{8}\tfrac{1}{2}\left(F_{\ddot{L}} + \Delta_{\ddot{I}\cdot\ddot{L}}\right) = \tfrac{1}{64}$$

R18 R37 R26 R27 given R19a given R29a

$$\Delta_{\ddot{O}+\ddot{P}} = \Delta_{(JL)+(KL)} = \tfrac{1}{2}\left(\Delta_{JK\cdot LL} + \Delta_{JL\cdot KL}\right) = \tfrac{1}{2}\left[\tfrac{1}{2}\left(\theta_{JK} + \Delta_{JK\cdot\ddot{L}}\right) + \tfrac{1}{2}\left(\gamma_{JKL} + \Delta_{JK+\ddot{L}}\right)\right]$$

= 0 P =0 P = 0 P = 0 in $\Delta_{\ddot{O}\cdot\ddot{P}}$ above

$$= \tfrac{1}{4}\left[\tfrac{1}{8} + \Delta_{J(DI)\cdot\ddot{L}} + \tfrac{1}{32} + \Delta_{J(DI)+\ddot{L}}\right] = \tfrac{1}{4}\left[\tfrac{1}{8} + \tfrac{1}{2}\left(\Delta_{JD\cdot\ddot{L}} + \Delta_{JI\cdot\ddot{L}}\right) + \tfrac{1}{32} + \tfrac{1}{2}\left(\Delta_{JD+\ddot{L}} + \Delta_{JI+\ddot{L}}\right)\right]$$

$$= \tfrac{1}{4}\left[\tfrac{1}{8} + \tfrac{1}{32}\right] = \tfrac{1}{4}\left[\tfrac{4+1}{32}\right] = \tfrac{1}{4}\tfrac{5}{32} = \tfrac{5}{128}$$

R3 R5 A R8 given = 0 P

$$\gamma_{\ddot{O}P} = \gamma_{JLP} = \gamma_{JL(KL)} = \tfrac{1}{2}\left(\gamma_{JKL} + \gamma_{JLL}\right) = \tfrac{1}{2}\left[\tfrac{1}{32} + \tfrac{1}{2}\left(\theta_{JL} + \gamma_{J\ddot{L}}\right)\right] = \tfrac{1}{64} + \tfrac{1}{4}\left(\tfrac{1}{8}\right) = \tfrac{1}{64} + \tfrac{1}{32} = \tfrac{3}{64}$$

R4 R3 R3 given R8 given = 0 P

$$\gamma_{O\ddot{P}} = \gamma_{(JL)\ddot{P}} = \tfrac{1}{2}\left(\gamma_{J\ddot{P}} + \gamma_{L\ddot{P}}\right) = \tfrac{1}{2}\left(\gamma_{JKL} + \gamma_{KLL}\right) = \tfrac{1}{2}\left[\tfrac{1}{32} + \tfrac{1}{2}\left(\theta_{KL} + \gamma_{K\ddot{L}}\right)\right] = \tfrac{1}{64} + \tfrac{1}{4}\left(\tfrac{1}{8}\right) = \tfrac{1}{64} + \tfrac{1}{32} = \tfrac{3}{64}$$

$F_{\ddot{O}} = \theta_{JL} = \tfrac{1}{8}$ given

$F_{\ddot{P}} = \theta_{KL} = \tfrac{1}{8}$ given

given given given given

$$\theta_{OP} = \theta_{(JL)(KL)} = \tfrac{1}{4}\left(\theta_{JK} + \theta_{JL} + \theta_{LK} + \theta_{LL}\right) = \tfrac{1}{4}\left(\tfrac{1}{8} + \tfrac{1}{8} + \tfrac{1}{8} + \tfrac{1}{2}\right) = \tfrac{1}{4}\left(\tfrac{3+4}{8}\right) = \tfrac{1}{4}\tfrac{7}{8} = \tfrac{7}{32}$$

b. [see equation (4.82)]

$$\Delta_1 = \delta_{\ddot{O}\ddot{P}} = \tfrac{1}{64}$$

$$\Delta_2 = 2\left(\delta_{\ddot{O}P} - \delta_{\ddot{O}\ddot{P}}\right) = 2\left(\tfrac{3}{64} - \tfrac{1}{64}\right) = \tfrac{4}{64} = \tfrac{1}{16}$$

$$\Delta_3 = 2\left(\delta_{O\ddot{P}} - \delta_{\ddot{O}\ddot{P}}\right) = 2\left(\tfrac{3}{64} - \tfrac{1}{64}\right) = \tfrac{4}{64} = \tfrac{1}{16}$$

$$\Delta_4 = 2\left(\Delta_{\ddot{O}\cdot\ddot{P}} - \delta_{\ddot{O}\ddot{P}}\right) = \tfrac{1}{64} - \tfrac{1}{64} = 0$$

$$\Delta_5 = 2\left(\delta_{\ddot{O}+\ddot{P}} - \delta_{\ddot{O}\ddot{P}}\right) = 2\left(\tfrac{5}{128} - \tfrac{1}{64}\right) = 2\left(\tfrac{5-2}{128}\right) = \tfrac{6}{128} = \tfrac{3}{64}$$

$$\Delta_6 = F_{\ddot{O}} - \Delta_{\ddot{O}\cdot\ddot{P}} - 2\left(\gamma_{\ddot{O}P} - \delta_{\ddot{O}\ddot{P}}\right) = \tfrac{1}{8} - \tfrac{1}{64} - 2\left(\tfrac{3}{64} - \tfrac{1}{64}\right) = \tfrac{1}{8} - \tfrac{1}{64} - 2\left(\tfrac{2}{64}\right) = \tfrac{8-1-4}{64} = \tfrac{3}{64}$$

$$\Delta_7 = F_{\ddot{P}} - \Delta_{\ddot{O}\cdot\ddot{P}} - 2\left(\gamma_{O\ddot{P}} - \delta_{\ddot{O}\ddot{P}}\right) = \tfrac{1}{8} - \tfrac{1}{64} - 2\left(\tfrac{3}{64} - \tfrac{1}{64}\right) = \tfrac{1}{8} - \tfrac{1}{64} - 2\left(\tfrac{2}{64}\right) = \tfrac{8-1-4}{64} = \tfrac{3}{64}$$

$$\Delta_8 = 4\left(\theta_{OP} - \Delta_{\ddot{O}+\ddot{P}} - \gamma_{\ddot{O}P} - \gamma_{O\ddot{P}} + 2\delta_{\ddot{O}\ddot{P}}\right) = 4\left[\tfrac{7}{32} - \tfrac{5}{128} - \tfrac{3}{64} - \tfrac{3}{64} + 2\left(\tfrac{1}{64}\right)\right] = 4\left(\tfrac{28-5-6-6+4}{128}\right) = \tfrac{4(15)}{128} = \tfrac{15}{32}$$

$$\Delta_9 = 1 - F_{\ddot{O}} - F_{\ddot{P}} - 4\theta_{OP} + \Delta_{\ddot{O}\cdot\ddot{P}} + 2\Delta_{\ddot{O}+\ddot{P}} + 4\gamma_{\ddot{O}P} + 4\gamma_{O\ddot{P}} - 6\delta_{\ddot{O}\ddot{P}}$$

$$= 1 - \tfrac{1}{8} - \tfrac{1}{8} - 4\left(\tfrac{7}{32}\right) + \tfrac{1}{64} + 2\left(\tfrac{5}{128}\right) + 4\left(\tfrac{3}{64}\right) + 4\left(\tfrac{3}{64}\right) - 6\left(\tfrac{1}{64}\right) = \tfrac{64-8-8-56+1+5+12+12-6}{64} = \tfrac{94-78}{64} = \tfrac{1}{4}$$

Check: $\Delta_1 + \Delta_2 + \Delta_3 + \Delta_4 + \Delta_5 + \Delta_6 + \Delta_7 + \Delta_8 + \Delta_9 = \tfrac{1}{64} + \tfrac{1}{16} + \tfrac{1}{16} + 0 + \tfrac{3}{64} + \tfrac{3}{64} + \tfrac{3}{64} + \tfrac{15}{32} + \tfrac{1}{4}$

$$= \tfrac{1+4+4+0+3+3+3+30+16}{64} = \tfrac{64}{64} = 1$$

Exercise 4.27.

R5 R5 R5

1) $\gamma_{OPQ} = \gamma_{OP(MN)} = \tfrac{1}{2}\left(\gamma_{OPM} + \gamma_{OPN}\right) = \tfrac{1}{2}\left(\gamma_{O(KL)M} + \gamma_{O(KL)N}\right) = \tfrac{1}{2}\left[\tfrac{1}{2}\left(\gamma_{OKM} + \gamma_{OLM}\right) + \tfrac{1}{2}\left(\gamma_{OKN} + \gamma_{OLN}\right)\right]$

R5 R5 R5 R5

$$= \tfrac{1}{4}\left[\gamma_{OKM} + \gamma_{OLM} + \gamma_{OKN} + \gamma_{OLN}\right] = \tfrac{1}{4}\left[\gamma_{(JL)KM} + \gamma_{(JL)LM} + \gamma_{(JL)KN} + \gamma_{(JL)LN}\right]$$

given given given R8 given given given

$$= \tfrac{1}{4}\left[\tfrac{1}{2}\left(\gamma_{JKM} + \gamma_{LKM}\right) + \tfrac{1}{2}\left(\gamma_{JLM} + \gamma_{LLM}\right) + \tfrac{1}{2}\left(\gamma_{JKN} + \gamma_{LKN}\right) + \tfrac{1}{2}\left(\gamma_{JLN} + \gamma_{LLN}\right)\right]$$

given P = 0 given P = 0

$$= \tfrac{1}{8}\left[\left(\tfrac{1}{32} + \tfrac{1}{32}\right) + \left(\tfrac{1}{32} + \tfrac{1}{2}\left(\theta_{LM} + \gamma_{\ddot{L}M}\right)\right) + \left(\tfrac{1}{128} + \tfrac{1}{128}\right) + \left(\tfrac{1}{128} + \tfrac{1}{2}\left(\theta_{LN} + \gamma_{\ddot{L}N}\right)\right)\right]$$

$$= \tfrac{1}{8}\left[\tfrac{1}{32} + \tfrac{1}{32} + \tfrac{1}{32} + \tfrac{1}{8} + \tfrac{1}{128} + \tfrac{1}{128} + \tfrac{1}{128} + \tfrac{1}{32}\right] = \tfrac{1}{8}\left[\tfrac{4+4+4+16+1+1+1+4}{128}\right] = \tfrac{1}{8}\left[\tfrac{35}{128}\right] = \tfrac{35}{1024}$$

R5 same as for γ_{OPQ}

2) $\gamma_{OPR} = \gamma_{OP(MN)} = \tfrac{1}{2}\left(\gamma_{OPM} + \gamma_{OPN}\right) = \tfrac{35}{1024}$

3)

$$\overset{\text{R5}}{\gamma_{OQR}}=\gamma_{OQ(MN)}=\frac{1}{2}\left(\overset{\text{R5}}{\gamma_{OQM}}+\overset{\text{R5}}{\gamma_{OQN}}\right)=\frac{1}{2}\left(\gamma_{O(MN)M}+\gamma_{O(MN)N}\right)=\frac{1}{2}\left[\frac{1}{2}\left(\overset{\text{R8}}{\gamma_{OMM}}+\overset{\text{R5}}{\gamma_{ONM}}\right)+\frac{1}{2}\left(\overset{\text{R5}}{\gamma_{OMN}}+\overset{\text{R8}}{\gamma_{ONN}}\right)\right]$$

$$=\frac{1}{4}\left[\frac{1}{2}\left(\overset{\text{R2}}{\theta_{OM}}+\overset{P\ =0}{\gamma_{\ddot{M}O}}\right)+\gamma_{(JL)NM}+\gamma_{(JL)MN}+\frac{1}{2}\left(\overset{\text{R2}}{\theta_{NO}}+\overset{P\ =0}{\gamma_{\ddot{N}O}}\right)\right]$$

$$=\frac{1}{4}\left[\frac{1}{2}\left(\theta_{(JL)M}+0\right)+\frac{1}{2}\left(\overset{\text{given}}{\gamma_{JMN}}+\overset{\text{given}}{\gamma_{LMN}}\right)+\frac{1}{2}\left(\overset{\text{given}}{\gamma_{JMN}}+\overset{\text{given}}{\gamma_{LMN}}\right)+\frac{1}{2}\left(\theta_{N(JL)}+0\right)\right]$$

$$=\frac{1}{8}\left[\frac{1}{2}\left(\overset{\text{given}}{\theta_{JM}}+\overset{\text{given}}{\theta_{LM}}\right)+\left(\frac{1}{128}+\frac{1}{64}\right)+\left(\frac{1}{128}+\frac{1}{64}\right)+\frac{1}{2}\left(\overset{\text{given}}{\theta_{JN}}+\overset{\text{given}}{\theta_{LN}}\right)\right]$$

$$=\frac{1}{8}\left[\frac{1}{2}\left(\frac{1}{8}+\frac{1}{4}\right)+\frac{1}{128}+\frac{1}{64}+\frac{1}{128}+\frac{1}{64}+\frac{1}{2}\left(\frac{1}{32}+\frac{1}{16}\right)\right]=\frac{1}{8}\left[\frac{1}{16}+\frac{1}{8}+\frac{1}{128}+\frac{1}{64}+\frac{1}{128}+\frac{1}{64}+\frac{1}{64}+\frac{1}{32}\right]$$

$$=\frac{1}{8}\left[\frac{8+16+1+2+1+2+2+4}{128}\right]=\frac{36}{1024}=\frac{18}{512}=\frac{9}{256}$$

4)

$$\overset{\text{R5}}{\gamma_{PQR}}=\gamma_{PQ(MN)}=\frac{1}{2}\left(\overset{\text{R5}}{\gamma_{PQM}}+\overset{\text{R5}}{\gamma_{PQN}}\right)=\frac{1}{2}\left(\gamma_{P(MN)M}+\gamma_{P(MN)N}\right)=\frac{1}{2}\left[\frac{1}{2}\left(\gamma_{PMM}+\overset{\text{R5}}{\gamma_{PNM}}\right)+\frac{1}{2}\left(\overset{\text{R5}}{\gamma_{PMN}}+\gamma_{PNN}\right)\right]$$

$$=\frac{1}{2}\left[\frac{1}{2}\left(\overset{\text{R8}}{\gamma_{PMM}}+\gamma_{(KL)NM}\right)+\frac{1}{2}\left(\gamma_{(KL)MN}+\overset{\text{R8}}{\gamma_{PNN}}\right)\right]$$

$$=\frac{1}{4}\left[\frac{1}{2}\left(\overset{\text{R2}}{\theta_{PM}}+\overset{\text{R4}}{\gamma_{P\ddot{M}}}\right)+\frac{1}{2}\left(\gamma_{KNM}+\gamma_{LNM}\right)+\frac{1}{2}\left(\gamma_{KMN}+\gamma_{LMN}\right)+\frac{1}{2}\left(\overset{\text{R2}}{\theta_{PN}}+\overset{\text{R4}}{\gamma_{P\ddot{N}}}\right)\right]$$

$$=\frac{1}{4}\left[\frac{1}{2}\left(\theta_{(KL)M}+\gamma_{(KL)\ddot{M}}\right)+\frac{1}{2}\left(\gamma_{KNM}+\gamma_{LNM}\right)+\frac{1}{2}\left(\gamma_{KMN}+\gamma_{LMN}\right)+\frac{1}{2}\left(\theta_{(KL)N}+\gamma_{(KL)\ddot{N}}\right)\right]$$

$$=\frac{1}{8}\left[\frac{1}{2}\left(\overset{\text{given}}{\theta_{KM}}+\overset{\text{given}}{\theta_{LM}}\right)+\frac{1}{2}\left(\gamma_{K\ddot{M}}+\gamma_{L\ddot{M}}\right)+\gamma_{KNM}+\gamma_{LNM}+\gamma_{KMN}+\gamma_{LMN}+\frac{1}{2}\left(\overset{\text{given}}{\theta_{KN}}+\overset{\text{given}}{\theta_{LN}}\right)+\frac{1}{2}\left(\overset{\text{R3}}{\gamma_{K\ddot{N}}}+\overset{\text{R3}}{\gamma_{L\ddot{N}}}\right)\right]$$

$$=\frac{1}{8}\left[\frac{1}{2}\left(\frac{1}{8}+\frac{1}{4}\right)+\frac{1}{2}\left(\overset{P\ =0}{\gamma_{K(EF)}}+\overset{P\ =0}{\gamma_{L(EF)}}\right)+\overset{\text{given}}{\gamma_{KNM}}+\overset{\text{given}}{\gamma_{LNM}}+\overset{\text{given}}{\gamma_{KMN}}+\overset{\text{given}}{\gamma_{LMN}}+\frac{1}{2}\left(\frac{1}{32}+\frac{1}{16}\right)+\frac{1}{2}\left(\overset{P\ =0}{\gamma_{K(GH)}}+\overset{P\ =0}{\gamma_{L(GH)}}\right)\right]$$

$$=\frac{1}{8}\left[\frac{1}{2}\left(\frac{1}{8}+\frac{1}{4}\right)+\frac{1}{2}\left(0+0\right)+\frac{1}{128}+\frac{1}{64}+\frac{1}{128}+\frac{1}{64}+\frac{1}{2}\left(\frac{1}{32}+\frac{1}{16}\right)+\frac{1}{2}\left(0+0\right)\right]$$

$$=\frac{1}{8}\left[\frac{3}{16}+0+\frac{1}{128}+\frac{1}{64}+\frac{1}{128}+\frac{1}{64}+\frac{3}{64}+0\right]=\frac{1}{8}\left[\frac{24+1+2+1+2+6}{128}\right]=\frac{36}{1024}=\frac{9}{256}$$

1) R10b

$$\delta_{OPQR}=\delta_{OPQ(MN)}=\frac{1}{2}\left(\delta_{OPQM}+\delta_{OPQN}\right)=\frac{1}{2}\left(\delta_{OP(MN)M}+\delta_{OP(MN)N}\right)$$

$$=\frac{1}{2}\left[\frac{1}{2}\left(\overset{\text{R17}}{\delta_{OPMM}}+\overset{\text{R10b}}{\delta_{OPNM}}\right)+\frac{1}{2}\left(\overset{\text{R10b}}{\delta_{OPMN}}+\overset{\text{R17}}{\delta_{OPNN}}\right)\right]$$

$$=\frac{1}{4}\left[\frac{1}{2}\left(\overset{\text{R5}}{\gamma_{OPM}}+\delta_{\ddot{M}OP}\right)+\delta_{O(KL)NM}+\delta_{O(KL)MN}+\frac{1}{2}\left(\overset{\text{R5}}{\gamma_{OPN}}+\delta_{\ddot{N}OP}\right)\right]$$

$$=\tfrac{1}{4}\Big[\tfrac{1}{2}\Big(\gamma_{O(KL)M}+\overset{\text{R10a}}{\delta_{\ddot{M}OP}}\Big)+\tfrac{1}{2}\big(\delta_{OKNM}+\delta_{OLNM}\big)+\tfrac{1}{2}\big(\delta_{OKMN}+\delta_{OLMN}\big)+\tfrac{1}{2}\Big(\gamma_{O(KL)N}+\overset{\text{R10a}}{\delta_{\ddot{N}OP}}\Big)\Big]$$

$$=\tfrac{1}{8}\Big[\tfrac{1}{2}\big(\overset{\text{R5}}{\gamma_{OKM}}+\overset{\text{R5}}{\gamma_{OLM}}\big)+\delta_{\ddot{M}O(KL)}+\overset{\text{R10b}}{2\delta_{OKMN}}+\overset{\text{R10b}}{2\delta_{OLMN}}+\tfrac{1}{2}\big(\gamma_{OKN}+\gamma_{OLN}\big)+\delta_{\ddot{N}O(KL)}\Big]$$

$$=\tfrac{1}{8}\Big[\tfrac{1}{2}\Big(\gamma_{(JL)KM}+\gamma_{(JL)LM}\Big)+\tfrac{1}{2}\Big(\overset{\text{R10a}}{\delta_{\ddot{M}OK}}+\overset{\text{R10a}}{\delta_{\ddot{M}OL}}\Big)+\tfrac{4}{2}\delta_{(JL)KMN}+\tfrac{4}{2}\delta_{(JL)LMN}+\tfrac{1}{2}\Big(\gamma_{(JL)KN}+\gamma_{(JL)LN}\Big)\Big]$$

$$+\tfrac{1}{8}\Big[\tfrac{1}{2}\Big(\overset{\text{R10a}}{\delta_{\ddot{N}OK}}+\overset{\text{R10a}}{\delta_{\ddot{N}OL}}\Big)\Big]$$

$$=\tfrac{1}{16}\Big[\tfrac{1}{2}\big(\gamma_{JKM}+\gamma_{LKM}\big)+\tfrac{1}{2}\big(\gamma_{JLM}+\overset{\text{R8}}{\gamma_{LLM}}\big)+\tfrac{2}{2}\overset{\text{R10a}}{\delta_{\ddot{M}(JL)K}}+\tfrac{2}{2}\overset{\text{R10a}}{\delta_{\ddot{M}(JL)L}}+4\Big(\tfrac{1}{2}\Big)\big(\delta_{JKMN}+\delta_{LKMN}\big)\Big]$$

$$+\tfrac{1}{16}\Big[4\Big(\tfrac{1}{2}\Big)\big(\delta_{JLMN}+\overset{\text{R17}}{\delta_{LLMN}}\big)+\tfrac{1}{2}\big(\gamma_{JKN}+\gamma_{LKN}\big)+\tfrac{1}{2}\big(\gamma_{JLN}+\overset{\text{R8}}{\gamma_{LLN}}\big)+\tfrac{2}{2}\delta_{\ddot{N}(JL)K}+\tfrac{2}{2}\delta_{\ddot{N}(JL)L}\Big]$$

$$=\tfrac{1}{32}\Big[\overset{\text{given}}{\gamma_{JKM}}+\overset{\text{given}}{\gamma_{LKM}}+\overset{\text{given}}{\gamma_{JLM}}+\tfrac{1}{2}\Big(\overset{\text{given}}{\theta_{LM}}+\overset{\text{P}=0}{\gamma_{\ddot{L}M}}\Big)+2\Big(\tfrac{1}{2}\Big)\Big(\overset{\text{P}=0}{\delta_{\ddot{M}JK}}+\overset{\text{P}=0}{\delta_{\ddot{M}LK}}\Big)+2\Big(\tfrac{1}{2}\Big)\Big(\overset{\text{P}=0}{\delta_{\ddot{M}JL}}+\overset{\text{P}=0}{\delta_{\ddot{M}LL}}\Big)\Big]$$

$$+\tfrac{1}{32}\Big[4\big(\overset{\text{given}}{\delta_{JKMN}}+\overset{\text{given}}{\delta_{LKMN}}\big)+4\Big[\overset{\text{given}}{\delta_{JLMN}}+\tfrac{1}{2}\Big(\overset{\text{given}}{\gamma_{LMN}}+\overset{\text{P}=0}{\delta_{\ddot{L}MN}}\Big)\Big]+\overset{\text{given}}{\gamma_{JKN}}+\overset{\text{given}}{\gamma_{LKN}}+\overset{\text{given}}{\gamma_{JLN}}+\tfrac{1}{2}\Big(\overset{\text{given}}{\theta_{LN}}+\overset{\text{P}=0}{\gamma_{\ddot{L}N}}\Big)\Big]$$

$$+\tfrac{1}{32}\Big[2\Big(\tfrac{1}{2}\Big)\Big(\overset{\text{P}=0}{\delta_{\ddot{N}JK}}+\overset{\text{P}=0}{\delta_{\ddot{N}LK}}\Big)+2\Big(\tfrac{1}{2}\Big)\Big(\overset{\text{P}=0}{\delta_{\ddot{N}JL}}+\overset{\text{P}=0}{\delta_{\ddot{N}LL}}\Big)\Big]$$

$$=\tfrac{1}{32}\Big[\tfrac{1}{32}+\tfrac{1}{32}+\tfrac{1}{32}+\tfrac{1}{2}\Big(\tfrac{1}{4}+0\Big)+(1)(0+0)+(1)(0+0)+4\Big(\tfrac{1}{512}+\tfrac{1}{512}\Big)+4\Big[\tfrac{1}{512}+\tfrac{1}{2}\Big(\tfrac{1}{64}+0\Big)\Big]+\tfrac{1}{128}+\tfrac{1}{128}+\tfrac{1}{128}\Big]$$

$$+\tfrac{1}{32}\Big[\tfrac{1}{2}\Big(\tfrac{1}{16}+0\Big)+(1)(0+0)+(1)(0+0)\Big]$$

$$=\tfrac{1}{32}\Big[\tfrac{1}{32}+\tfrac{1}{32}+\tfrac{1}{32}+\tfrac{1}{8}+\tfrac{4}{512}+\tfrac{4}{512}+\tfrac{4}{512}+\tfrac{4}{128}+\tfrac{1}{128}+\tfrac{1}{128}+\tfrac{1}{128}+\tfrac{1}{32}\Big]$$

$$=\frac{1}{32}\Big[\frac{8+8+8+32+2+2+2+8+2+2+2+8}{256}\Big]=\frac{84}{32(256)}=\frac{21}{2048}$$

Exercise 4.28.

a. The two-locus inbreeding coefficient F_{11} is equal to the probability that the genes at two loci are simultaneously identical by descent (see p. 4.119). Formally it is defined as a four-gene function—two genes identical by descent at the *A* locus and two genes identical by descent at the *B* locus, i.e., $F_{11}=P_4\left(a=a',b=b'\right)$ (see equation (4.175Xb). It is an extension of the concept of the one-locus inbreeding coefficient extended to two loci. For self-fertilization the probability in terms of the linkage value is equal to the sum of the squares of the frequencies of all gametes or the sum of the diagonals in equation (2.118), namely,

$$F_{11}=\left(\frac{1+\lambda}{4}\right)^2+\left(\frac{1-\lambda}{4}\right)^2+\left(\frac{1-\lambda}{4}\right)^2+\left(\frac{1+\lambda}{4}\right)^2=2\left(\frac{1+2\lambda+\lambda^2}{16}\right)+2\left(\frac{1-2\lambda+\lambda^2}{16}\right)=\frac{2+2\lambda^2}{8}=\frac{1+\lambda^2}{4}$$

The probability of the multi-locus inbreeding coefficient can be extended to *n* loci in that it is equal to the sum of the squares of the frequencies of all possible gametes as shown in equation (2.72K).

b,. The two-locus, two-gamete parental descent coefficient F^{11} is equal to the joint probability that both parental gametes are copies of the same gamete $\left({}_{11}F_{11}^{11}\right)$ or two different gametes$\left({}_{00}F_{00}^{11}\right)$. Formally it is defined as a four-gene function—two genes equivalent in one gamete and two genes equivalent in the other gamete, i.e., $F^{11} = P_4\left(a = b, a' = b'\right)$ [see equation (4.175Xc)].

The two-gamete recombinant descent coefficient ${}_{11}F$ is the joint probability that both pairs of genes, ab' and $a'b$, are copies of the same $\left({}_{11}F_{11}^{11}\right)$ or two different $\left({}_{11}F_{00}^{00}\right)$ initial ancestral gametes. Formally it is defined as a four-gene function—one gene in the paternal gamete and the other gene in the maternal gamete descended from a single ancestral gamete, i.e., ${}_{11}F = P_4\left(a = b', a' = b\right)$ [see equation (4.175Xd)]. They are called recombinant descent measures because the members of the gene pair lie in different gametes in that recombination must have occurred some place in the descent.

These ideas can obviously be extended to three or more loci in that with three loci there would be six genes and 15 pairs, each pair being equivalent or not, so the notation would become much more complex. There would also be many more than 15 states of equivalence which one has with only four genes. I would first extend these concepts to three loci and possibly four loci before attempting to generalize for *n* loci.

Exercise 4.29.

Method 1, a tabular approach

	A^h	B	C^h	D	E	F	G^h	H	I^h	J	K
	-	A^h -	B	A^h -	C^h D	E -	E	F G^h	H	G^h H	I^h J
A^h	1	$\frac{1}{2}$	$\frac{1}{2}$	$\frac{1}{2}$	$\frac{1}{2}$	$\frac{1}{4}$	$\frac{1}{2}$	$\frac{3}{8}$	$\frac{3}{8}$	$\frac{7}{16}$	$\frac{13}{32}$
B		$\frac{1}{2}$	$\frac{1}{2}$	$\frac{1}{4}$	$\frac{3}{8}$	$\frac{3}{16}$	$\frac{3}{8}$	$\frac{9}{32}$	$\frac{9}{32}$	$\frac{21}{64}$	$\frac{39}{128}$
C^h			1	$\frac{1}{4}$	$\frac{5}{8}$	$\frac{5}{16}$	$\frac{5}{8}$	$\frac{15}{32}$	$\frac{15}{32}$	$\frac{35}{64}$	$\frac{65}{128}$
D				$\frac{1}{2}$	$\frac{3}{8}$	$\frac{3}{16}$	$\frac{3}{8}$	$\frac{9}{32}$	$\frac{9}{32}$	$\frac{21}{64}$	$\frac{39}{128}$
E					$\frac{5}{8}$	$\frac{5}{16}$	$\frac{5}{8}$	$\frac{15}{32}$	$\frac{15}{32}$	$\frac{35}{64}$	$\frac{65}{128}$
F						$\frac{1}{2}$	$\frac{5}{16}$	$\frac{13}{32}$	$\frac{13}{32}$	$\frac{23}{64}$	$\frac{49}{128}$
G^h							1	$\frac{21}{32}$	$\frac{21}{32}$	$\frac{53}{64}$	$\frac{95}{128}$
H								$\frac{21}{32}$	$\frac{21}{32}$	$\frac{21}{32}$	$\frac{21}{32}$
I^h									1	$\frac{21}{32}$	$\frac{53}{64}$
J										$\frac{53}{64}$	$\frac{95}{128}$
K											$\frac{53}{64}$

$F_K = \theta_{I^h J} = \frac{21}{32}$ or $F_K = 2\theta_{KK} - 1 = 2\left(\frac{53}{64}\right) - 1 = \frac{53}{32} - \frac{32}{32} = \frac{21}{32}$

Method 2, chain of coancestry method

In the where statement associated with equation (4.186) (p. 4.139), it is stated that F_i (p. 4.140) for the *i*th ancestorial individual should be set equal to zero if the *i*th ancestorial individual is heterogametic.

Proof: On p. 4.47 [equation (4.51)] we show that for autosomal genes the probability of the random gene a_1 being identical by descent to a random gene a_2 is

$$P(a_1 \equiv a_2) = \theta_{AA} = \tfrac{1}{2}(1 + F_A) = \tfrac{1}{2}(1 + F_i)$$

For sex-linked genes, the corresponding probability [see equation (4.180)] is

$$P(a \equiv a) = \theta_{A^h A^h} = 1$$

Therefore we desire to equate the expression $\tfrac{1}{2}(1 + F_i)$ in (4.186) for sex-linked genes to one. For sex-linked genes we do not count the heterogametic individuals in the chain of coanecestry, so the power of $\tfrac{1}{2}$ becomes zero. Thus,

$$\begin{aligned} \left(\tfrac{1}{2}\right)^0 (1 + F_i) &= 1 \\ 1 + F_i &= 1 \\ F_i &= 1 - 1 \\ &= 0 \end{aligned}$$

Verifying the above result for the coefficient of inbreeding of *E*, we obtain $F_E = \left(\tfrac{1}{2}\right)^{4-2}(1 + F_i) = \tfrac{1}{4}$, which agrees with $F_E = \theta_{C^h D} = \tfrac{1}{4}$ in the table of coefficients of coancestry given above under Method 1.

Applying the chain of coancestry method to calculate the coefficient of inbreeding of individual *K*, we calculate the contribution of each chain for each common ancestor.

Chains of coancestry involving common ancestor *E*:

$$I^h HF\underline{E}G^h J \qquad 1\left(\tfrac{1}{2}\right)^4 \left(1 + \tfrac{1}{4}\right) = \tfrac{1}{16}\tfrac{5}{4} = \tfrac{5}{64}$$

$$I^h G^h \underline{E}FHJ \qquad 0\left(\tfrac{1}{2}\right)^4 \left(1 + \tfrac{1}{4}\right) = 0$$

Chains of coancestry involving common ancestor G^h:

$$I^h H\underline{G^h}J \qquad 1\left(\tfrac{1}{2}\right)^2 (1 + 0) = \tfrac{1}{4}$$

$$I^h \underline{G^h}HJ \qquad 0\left(\tfrac{1}{2}\right)^2 (1 + 0) = 0$$

$$I^h \underline{G^h}J \qquad 0\left(\tfrac{1}{2}\right)^1 (1 + 0) = 0$$

Chains of coancestry involving common ancestor *H*:

First, we calculate the coefficient of inbreeding of *H*:

$$F_H = \left(\tfrac{1}{2}\right)^2 (1 + F_E) = \tfrac{1}{4}\left(1 + \tfrac{1}{4}\right) = \tfrac{1}{4}\tfrac{5}{4} = \tfrac{5}{16}$$

Then the contribution of the chain is:

$$I^h \underline{H}J \quad 1\left(\tfrac{1}{2}\right)^2 \left(1 + \tfrac{5}{16}\right) = \tfrac{21}{4(16)} = \tfrac{21}{64}$$

Summing the mutually exclusive probabilities for all of the chains of coancestry, we obtain the coefficient of inbreeding of the homogametic individual *K*.

$$F_K = \tfrac{5}{64} + \tfrac{1}{4} + \tfrac{21}{64} = \tfrac{5+16+21}{64} = \tfrac{42}{64} = \tfrac{21}{32}$$

This value agrees with that obtained from Method 1, namely,

$$F_K = \theta_{I^h J} = \tfrac{21}{32}$$

Exercise 4.30.

a. For autosomal locus, using Method 1: a tabular coancestry approach

	A	B	C	D	E	F	G	H	I	J	K
	- -	- -	- A	- A	- A	B C	B D	- E	F G	B H	I J
A	$\frac{1}{2}$	0	$\frac{1}{4}$	$\frac{1}{4}$	$\frac{1}{4}$	$\frac{1}{8}$	$\frac{1}{8}$	$\frac{1}{8}$	$\frac{1}{8}$	$\frac{1}{16}$	$\frac{3}{32}$
B		$\frac{1}{2}$	0	0	0	$\frac{1}{4}$	$\frac{1}{4}$	0	$\frac{1}{4}$	$\frac{1}{4}$	$\frac{1}{4}$
C			$\frac{1}{2}$	$\frac{1}{8}$	$\frac{1}{8}$	$\frac{1}{4}$	$\frac{1}{16}$	$\frac{1}{16}$	$\frac{5}{32}$	$\frac{1}{32}$	$\frac{3}{32}$
D				$\frac{1}{2}$	$\frac{1}{8}$	$\frac{1}{16}$	$\frac{1}{4}$	$\frac{1}{16}$	$\frac{5}{32}$	$\frac{1}{32}$	$\frac{3}{32}$
E					$\frac{1}{2}$	$\frac{1}{16}$	$\frac{1}{16}$	$\frac{1}{4}$	$\frac{1}{16}$	$\frac{1}{8}$	$\frac{3}{32}$
F						$\frac{1}{2}$	$\frac{5}{32}$	$\frac{1}{32}$	$\frac{21}{64}$	$\frac{9}{64}$	$\frac{15}{64}$
G							$\frac{1}{2}$	$\frac{1}{32}$	$\frac{21}{64}$	$\frac{9}{64}$	$\frac{15}{64}$
H								$\frac{1}{2}$	$\frac{1}{32}$	$\frac{1}{4}$	$\frac{9}{64}$
I									$\frac{37}{64}$	$\frac{9}{64}$	$\frac{23}{64}$
J										$\frac{1}{2}$	$\frac{41}{128}$
K											$\frac{73}{128}$

$F_K = \theta_{IJ} = \frac{9}{64}$ or $F_K = 2\theta_{KK} - 1 = 2\left(\frac{73}{128}\right) - 1 = \frac{73}{64} - \frac{64}{64} = \frac{9}{64}$

For autosomal locus, Method 2: chain of coancestry method

i	*j*		
1	1	$IF\underline{B}J$	$\theta_{(IJ)_B} = \left(\frac{1}{2}\right)^4 (1 + F_B) = \frac{1}{16}$
	2	$IG\underline{B}J$	$\theta_{(IJ)_B} = \left(\frac{1}{2}\right)^4 (1 + F_B) = \frac{1}{16}$
2	1	$IFC\underline{A}EHJ$	$\theta_{(IJ)_A} = \left(\frac{1}{2}\right)^7 (1 + F_A) = \frac{1}{128}$
	2	$IGD\underline{A}EHJ$	$\theta_{(IJ)_A} = \left(\frac{1}{2}\right)^7 (1 + F_A) = \frac{1}{128}$
Total			$\frac{18}{128} = \frac{9}{64}$

b. For a sex-linked locus, using Method 1: a tabular coancestry approach

	A^h	B^h	C	D	E	F^h	G	H	I^h	J	K
	-	-	A^h -	A^h -	A^h -	C	B^h D	E -	G	B^h H	I^h J
A^h	1	0	$\frac{1}{2}$	$\frac{1}{2}$	$\frac{1}{2}$	$\frac{1}{2}$	$\frac{1}{4}$	$\frac{1}{4}$	$\frac{1}{4}$	$\frac{1}{8}$	$\frac{3}{16}$
B^h		1	0	0	0	0	$\frac{1}{2}$	0	$\frac{1}{2}$	$\frac{1}{2}$	$\frac{1}{2}$
C			$\frac{1}{2}$	$\frac{1}{4}$	$\frac{1}{4}$	$\frac{1}{2}$	$\frac{1}{8}$	$\frac{1}{8}$	$\frac{1}{8}$	$\frac{1}{16}$	$\frac{3}{32}$
D				$\frac{1}{2}$	$\frac{1}{4}$	$\frac{1}{4}$	$\frac{1}{4}$	$\frac{1}{8}$	$\frac{1}{4}$	$\frac{1}{16}$	$\frac{5}{32}$
E					$\frac{1}{2}$	$\frac{1}{4}$	$\frac{1}{8}$	$\frac{1}{4}$	$\frac{1}{8}$	$\frac{1}{8}$	$\frac{1}{8}$
F^h						1	$\frac{1}{8}$	$\frac{1}{8}$	$\frac{1}{8}$	$\frac{1}{16}$	$\frac{3}{32}$
G							$\frac{1}{2}$	$\frac{1}{16}$	$\frac{1}{2}$	$\frac{9}{32}$	$\frac{25}{64}$
H								$\frac{1}{2}$	$\frac{1}{16}$	$\frac{1}{4}$	$\frac{5}{32}$
I^h									1	$\frac{9}{32}$	$\frac{41}{64}$
J										$\frac{1}{2}$	$\frac{25}{64}$
K											$\frac{41}{64}$

$F_K = \theta_{I^h J} = \frac{9}{32}$ or $F_K = 2\theta_{KK} - 1 = 2\left(\frac{41}{64}\right) - 1 = \frac{41}{32} - \frac{32}{32} = \frac{9}{32}$

For sex-linked locus, Method 2: chain of coancestry method

i	j		λ	n_{ij}	
1	1	$I^hF^h\underline{B}^hJ$	0	1	$\theta_{(IJ)_B} = 0\left(\frac{1}{2}\right)^1(1+0) = 0$
	2	$I^hG\underline{B}^hJ$	1	2	$\theta_{(IJ)_B} = 1\left(\frac{1}{2}\right)^2(1+0) = \frac{1}{4}$
2	1	$I^hF^hC\underline{A}^hEHJ$	0	4	$\theta_{(IJ)_A} = 0\left(\frac{1}{2}\right)^4(1+0) = 0$
	2	$I^hGD\underline{A}^hEHJ$	1	5	$\theta_{(IJ)_A} = 1\left(\frac{1}{2}\right)^5(1+0) = \frac{1}{32}$
Total					$\frac{9}{32}$

c. The inbreeding coefficient for the sex-linked locus (9/32) is larger than that for the autsomal locus (9/64) in this case, because any contributing chain in the sex-linked case has the power of one-half reduced by the number of heterogametic ancestors, i.e., the factor of one-half becomes one for each heterogametic ancestor, and this gives a larger product or larger inbreeding. In this case, this force gives a larger inbreeding coefficient when summed over all contributing chains than the force of chain elimination due to two or more heterogametic individuals occurring together in sequence. This latter force tends to reduce the inbreeding coefficient.

This result of a larger inbreeding coefficient for a sex-linked locus can not be generalized, for it depends upon the particular pedigree. The inbreeding coefficient for a sex-linked locus could be zero if all chains have two consecutive heterogametic individuals in the chain.