

SYSTEMS OF MATING. II. THE EFFECTS OF INBREEDING ON THE GENETIC COMPOSITION OF A POPULATION

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INTRODUCTION

The problem before us in the present paper is to discover the changes which are brought about by following a given system of consanguine mating in a population which has previously been breeding at random and has reached equilibrium as regards the distribution of Mendelian factors. Formulae were derived in the first paper of this series (WRIGHT 1921) by which the essential data for any generation can be expressed in terms of those for the preceding generation, provided that the system of mating is such that the correlation between mated animals can be so expressed. These formulae are repeated here for convenience. The correlations and path coefficients are represented by small letters. Primes are used to indicate the preceding generation.

FORMULAE

Correlation between zygotic formulae of mates,	$m = \varphi (a'b'm')$
Correlation between gametes from one gametocyte,	$g = f'$
Squared path coefficient, zygote to gamete,	$b^2 = \frac{1}{2} (1 + f')$
Correlation between uniting egg and sperm,	$= b^2 m$
Squared path coefficient, gamete to fertilized egg,	$a^2 = \frac{1}{2(1 + f)}$
Percentage of heterozygosis,	$p = \frac{1}{2} (1 - f)$
Determination by heredity,	$h^2 = \frac{2h_0^2(1 - p)}{h_0^2(1 - 2p) + 1}$

As in the previous paper, the percentage of heterozygosis is calculated for pairs of allelomorphs which are equally represented in the population. On this basis, 50 percent of the individuals are heterozygous in the original random-bred stock.

The correlations between the characteristics of individuals depend, of course, on the degree of determination by heredity (h^2) as well as on the correlation between the zygotic formulae. The formulae are given below both in the general form under which part of the variation may be due to tangible environmental factors (e^2) and part to chance in development (d^2), and also for the case in which variation is wholly genetic ($h^2 = 1$). The results in the present paper will be expressed on this latter basis, but may easily be converted into the more general form if h^2 , e^2 and d^2 are known. The results will also be given on the basis of no dominance. Allowance can be made for perfect dominance in the typical case in which dominant and recessive gametes are equally numerous, by multiplying each of these correlations by $\frac{1}{1 + p}$. The correlation between brothers (r_{oo}) as given below applies best to litter-mates in so far as it involves e^2 , common environmental influences.

General formulae ($h^2 + d^2 + e^2 = 1$). No dominance

Correlation between mates	$r_{pp} = m h'^2$
Correlation between parent and offspring	$r_{po} = abhh' (1 + m)$
Correlation between brothers	$r_{oo} = 2a^2b h^2 (1 + m) + e^2$

Complete determination by heredity ($h^2 = 1$). No dominance

Correlation between mates	$r_{pp} = m$
Correlation between parent and offspring	$r_{po} = ab (1 + m)$
Correlation between brothers	$r_{oo} = 2a^2b^2 (1 + m)$

BROTHER-SISTER MATINGS

As the reader may feel some doubt as to the validity of the method of analysis used here, it will be well to begin with a case in which the results have already been determined by direct methods. We will start with a population which has been mating at random and has reached Mendelian equilibrium. We will assume that after a certain date nothing but brother-sister matings are made. The population will become broken up into

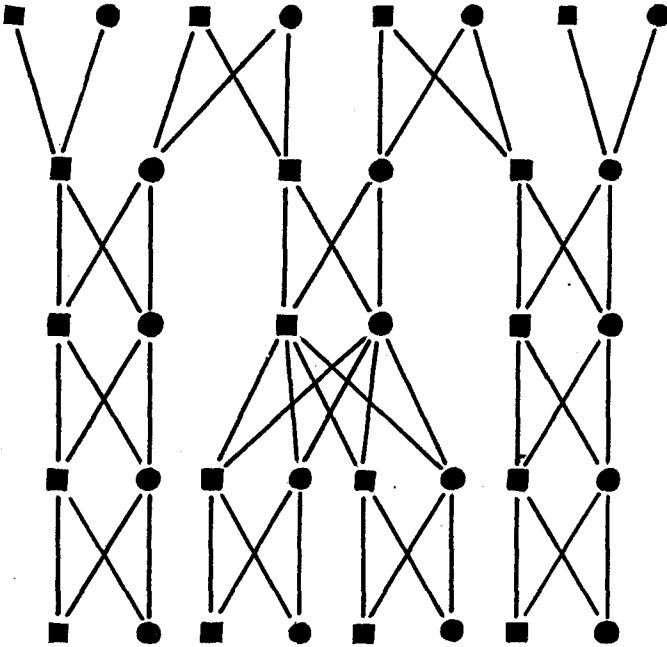


FIGURE 1.—Continued mating of brother with sister following random mating.

permanently separate, but branching lines of descent, as illustrated in the diagram (figure 1). In this case the correlation between mates is simply that between a brother and sister, produced by the preceding generation. The key formula is thus:

$$m = 2a'^2b'^2 (1 + m')$$

The work of finding the path coefficients, correlations, etc., in succeeding generations can be arranged as shown in table 1.

The percentage of heterozygosis as given by the present method is the same as that derived by FISH (1914), PEARL (1914) and JENNINGS (1914) by direct methods, starting from a population of $AA + 2Aa + aa$. On

starting from a cross of $Aa \times Aa$, the result is the same except for a lag of one generation, there being no correlation between the brothers and sisters of the first generation.

TABLE 1

GENERATION	m $= r'_{oo}$	g $= f'$	b^2 $= \frac{1}{2}(1+g)$	f $= mb^2$	a^2 $= \frac{1}{2}(1+f)$	a^2b^2	r_{oo} $= 2a^2b^2(1+m)$	r_{po} $= ab(1+m)$	ϕ $= \frac{1}{2}(1-f)$
0	0	0	$\frac{1}{2}$	0	$\frac{1}{2}$	$\frac{1}{4}$	$\frac{1}{2}$	$\frac{1}{2}$	$\frac{2}{4}$
1	$\frac{1}{2}$	0	$\frac{2}{4}$	$\frac{1}{4}$	$\frac{2}{5}$	$\frac{1}{5}$	$\frac{2}{5}$	$\frac{2}{5}$	$\frac{3}{5}$
2	$\frac{2}{3}$	$\frac{1}{4}$	$\frac{5}{8}$	$\frac{3}{8}$	$\frac{7}{11}$	$\frac{5}{22}$	$\frac{7}{11}$	$\frac{5}{8}$	$\frac{7}{15}$
3	$\frac{3}{4}$	$\frac{3}{8}$	$\frac{11}{16}$	$\frac{3}{8}$	$\frac{11}{24}$	$\frac{11}{48}$	$\frac{11}{24}$	$\frac{11}{16}$	$\frac{8}{32}$
4	$\frac{4}{5}$	$\frac{3}{8}$	$\frac{21}{32}$	$\frac{9}{32}$	$\frac{16}{32}$	$\frac{16}{102}$	$\frac{43}{51}$	$\frac{43}{24}$	$\frac{13}{24}$
5	$\frac{5}{6}$	$\frac{3}{8}$	$\frac{51}{64}$	$\frac{15}{64}$	$\frac{39}{107}$	$\frac{39}{214}$	$\frac{39}{107}$	$\frac{39}{51}$	$\frac{21}{128}$
6	$\frac{6}{7}$	$\frac{4}{8}$	$\frac{107}{128}$	$\frac{9}{128}$	$\frac{64}{222}$	$\frac{64}{444}$	$\frac{201}{222}$	$\frac{201}{107}$	$\frac{34}{256}$
7	$\frac{7}{8}$	$\frac{4}{8}$	$\frac{222}{128}$	$\frac{21}{256}$	$\frac{128}{256}$	$\frac{222}{467}$	$\frac{423}{467}$	$\frac{423}{51}$	$\frac{56}{512}$
8	$\frac{8}{9}$	$\frac{5}{8}$	$\frac{467}{512}$	$\frac{23}{512}$	$\frac{335}{335}$	$\frac{457}{1870}$	$\frac{335}{335}$	$\frac{335}{467}$	$\frac{88}{1024}$

The work of calculation is given in full above as an illustration of the general method. In the present case, the formula can easily be transformed in such a way that most of the series can be written from inspection for any number of generations. The key formula

$$m = 2a^2b^2(1+m')$$

can be written in the form

$$m = 2a^2(b^2 + f') = \frac{1 + 2f' + f''}{2(1 + f')}$$

Since

$$f = mb^2 \text{ and } b^2 = \frac{1}{2}(1 + f'),$$

we have

$$f = \frac{1}{4}(1 + 2f' + f'')$$

giving us a formula by which the series of values of the correlation between uniting gametes can easily be written for any number of generations without calculating the values of other variables. Since $g = f'$ this also gives us the series of correlations between gametes resulting from gametogenesis. From the equations

$$m = \frac{2f}{1 + f'}, \quad b^2 = \frac{1}{2}(1 + f'), \quad a^2 = \frac{1}{2(1 + f)}, \quad r_{po} = \frac{1 + 2f + f'}{2\sqrt{(1 + f)(1 + f')}}$$

$$\text{and } \phi = \frac{1}{2}(1 - f)$$

the corresponding series can be written as far as desired.

The various series can be expressed in terms of p , the percentage of heterozygosis, by substituting the value $f = 1 - 2p$ in the above equations.

$$\begin{aligned}
 m &= r'_{oo} = \frac{1 - 2p}{1 - p'} & a^2 &= \frac{1}{4(1 - p)} \\
 g &= 1 - 2p' & b^2 &= 1 - p' \\
 f &= 1 - 2p & p &= \frac{p'}{2} + \frac{p''}{4}
 \end{aligned}$$

The last equation by means of which the percentage of heterozygosis can be written for any number of generations is of special interest, as it gives a demonstration of JENNINGS'S (1914) empirical formula, according to which the percentages of heterozygosis in succeeding generations can be written as a series of common fractions $\frac{2}{4}, \frac{3}{8}, \frac{5}{16}, \frac{8}{32}$, etc., in which the numerators are the successive numbers of the Fibonacci series, each being

TABLE 2
Percentage of heterozygosis.

GENERATION	SELF-FERTILIZATION*	BROTHER-SISTER† (FIGURE 1)	DOUBLE FIRST COUSINS* (FIGURE 5)	QUADRUPLÉ SECOND COUSINS (FIGURE 6)	OCTUPLE THIRD COUSINS	HALF-BROTHER AND SISTER			SINGLE FIRST COUSINS (FIGURE 10)	SINGLE SECOND COUSINS‡ (FIGURE 12)
						Figure 7	Figure 8	Figure 9		
0	0.500	0.500	0.500	0.500	0.500	0.500	0.500	0.500	0.500	0.500
1	0.250	0.375	0.438	0.469	0.484	0.438	0.438	0.438	0.469	0.491
2	0.125	0.312	0.406	0.453	0.477	0.375	0.391	0.406	0.453	0.491
3	0.062	0.250	0.375	0.438	0.469	0.328	0.348	0.379	0.439	0.491
4	0.031	0.203	0.344	0.422	0.461	0.285	0.310	0.357	0.427	0.491
5	0.016	0.164	0.316	0.406	0.453	0.248	0.276	0.339	0.416	0.491
10	0.000	0.057	0.208	0.338	0.416	0.124	0.154	0.279	0.374	0.491
15	0.000	0.020	0.137	0.281	0.382	0.062	0.085	0.243	0.344	0.491
∞	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.491

* Repeated mating back to a homozygous sire (figure 3) results in the same rate of decrease in heterozygosis as self-fertilization.

† Mating of offspring with younger parent (figure 4) generation after generation results in same series as brother-sister mating.

‡ Continuous mating of half-first cousins (figure 11) rapidly reaches equilibrium at 0.481.

the sum of the two preceding, while the denominators double each generation. We will find that analogous rules can be applied to some of the more complex systems of breeding. The same relation can also be expressed in

the form, $p = p' - \frac{p'''}{8}$.

In interpreting the correlations r_{oo} and r_{po} in this and other cases, it is of course to be understood that we are dealing with a population representing all lines of descent from the original random-bred population. The

correlation between parent and offspring (r_{po}) brings out the rapidly increasing control over heredity due to the inbreeding. The correlation between brothers (r_{oo}) brings out the increasing uniformity among the progeny of a single pair. The percentage of homozygosis ($1 - p$) measures the degree of fixation of heredity, and as far as possible, the pre-

TABLE 3
Correlation between mated individuals.

GENERATION	SELF-FERTILIZATION	BROTHER-SISTER (FIGURE 1)	DOUBLE FIRST COUSINS (FIGURE 5)	QUADRUUPLE SECOND COUSINS (FIGURE 6)	OCTUPLE THIRD COUSINS	HALF-BROTHER AND SISTER			SINGLE FIRST COUSINS (FIGURE 10)	SINGLE* SECOND COUSINS (FIGURE 12)
						Figure 7	Figure 8	Figure 9		
0	1.000	0	0	0	0	0	0	0	0	0
1	1.000	0.500	0.250	0.125	0.062	0.250	0.250	0.250	0.125	0.037
2	1.000	0.600	0.333	0.176	0.091	0.444	0.389	0.333	0.176	0.037
3	1.000	0.727	0.421	0.229	0.119	0.550	0.500	0.408	0.221	0.037
4	1.000	0.792	0.500	0.278	0.147	0.640	0.584	0.459	0.261	0.037
5	1.000	0.843	0.560	0.324	0.174	0.705	0.650	0.500	0.294	0.037
10	1.000	0.953	0.754	0.499	0.292	0.877	0.836	0.621	0.407	0.037
15	1.000	0.985	0.853	0.618	0.387	0.944	0.916	0.684	0.477	0.037
∞	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.037

* Half-first cousins $m = 0.071$.

TABLE 4
Correlation between parent and offspring.

GENERATION	SELF-FERTILIZATION	BROTHER-SISTER (FIGURE 1)	DOUBLE FIRST COUSINS (FIGURE 5)	QUADRUUPLE SECOND COUSINS (FIGURE 6)	OCTUPLE THIRD COUSINS	HALF-BROTHER AND SISTER			SINGLE FIRST COUSINS (FIGURE 10)	SINGLE* SECOND COUSINS (FIGURE 12)
						Figure 7	Figure 8	Figure 9		
0	0.500	0.500	0.500	0.500	0.500	0.500	0.500	0.500	0.500	0.500
1	0.817	0.671	0.589	0.546	0.523	0.589	0.589	0.589	0.546	
2	0.926	0.763	0.649	0.580	0.541	0.685	0.667	0.649	0.580	
3	0.966	0.827	0.693	0.606	0.556	0.747	0.725	0.688	0.603	
4	0.984	0.869	0.732	0.630	0.569	0.795	0.770	0.717	0.624	
5	0.992	0.900	0.764	0.653	0.583	0.831	0.805	0.740	0.641	
10	1.000	0.970	0.867	0.742	0.642	0.929	0.908	0.805	0.700	
15	1.000	0.990	0.920	0.803	0.690	0.967	0.952	0.839	0.737	
∞	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.519

* Half-first cousins $r_{po} = 0.536$.

potency to be expected in outside crosses. This is on the assumption that prepotency is due to homozygosis in dominant factors.

It is easy to see that in the present case r_{po} and r_{oo} approach unity, while the percentage of heterozygosis approaches 0. The values for generations 1 to 5 and 10, 15 and ∞ are given in tables 2, 3, 4 and 5.

TABLE 5
Correlation between offspring of a mating.

GENERATION	SELF-FERTILIZATION	BROTHER-SISTER (FIGURE 1)	DOUBLE FIRST COUSINS (FIGURE 5)	QUADRUUPLE SECOND COUSINS (FIGURE 6)	OCTUPLE THIRD COUSINS	HALF-BROTHER AND SISTER			SINGLE FIRST COUSINS (FIGURE 10)	SINGLE* SECOND COUSINS (FIGURE 12)
						Figure 7	Figure 8	Figure 9		
0	0.500	0.500	0.500	0.500	0.500	0.500	0.500	0.500	0.500	0.500
1	0.667	0.600	0.556	0.529	0.515	0.556	0.556	0.556	0.529	
2	0.857	0.727	0.632	0.571	0.537	0.650	0.641	0.632	0.571	
3	0.933	0.792	0.675	0.597	0.552	0.721	0.701	0.673	0.596	
4	0.968	0.843	0.714	0.622	0.565	0.770	0.748	0.705	0.617	
5	0.992	0.879	0.749	0.645	0.579	0.810	0.786	0.730	0.635	
10	1.000	0.963	0.857	0.735	0.638	0.919	0.898	0.800	0.696	
15	1.000	0.989	0.914	0.797	0.686	0.962	0.947	0.835	0.733	
∞	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.519

* Half-first cousins $r_{00} = 0.536$.

SELF-FERTILIZATION

It may be interesting to consider the case of self-fertilization as another check on the method of analysis. Self-fertilization gives the same results as a system in which individuals are mated which are identical in genetic constitution with respect to each factor. This means that m equals 1. We have

$$f = b^2 = \frac{1}{2} (1 + g) = \frac{1}{2} (1 + f')$$

$$p = \frac{1}{2} (1 - f) = \frac{1}{4} (1 - f') = \frac{1}{2} p'$$

Thus the percentage of heterozygosis is simply divided by two in each succeeding generation, giving JENNINGS'S well-known series $\frac{1}{2}$, $\frac{1}{4}$, $\frac{1}{8}$, $\frac{1}{16}$ (JENNINGS 1912).

PARENT-OFFSPRING MATING

The general formulae which have been given, were calculated on the basis that the two parents were derived symmetrically from the original stock. Modifications may become necessary if the parents belong to different generations. The analysis of parent-offspring matings is of interest as an illustration of the flexibility of the method, besides giving additional checks.

JENNINGS (1916) gives formulae for a number of systems of mating parent with offspring. One of these is the mating of the daughters with the sire, generation after generation, as in figure 2.

We will start with a random lot of both sexes. The path coefficient, sire to germ-cells, will always be $\sqrt{\frac{1}{2}}$, the value in a random stock. The

path coefficients, sperm to fertilized egg, and ovum to fertilized egg, will be equal, because the chance of getting a certain factor from the group of sires is the same as from the dams.

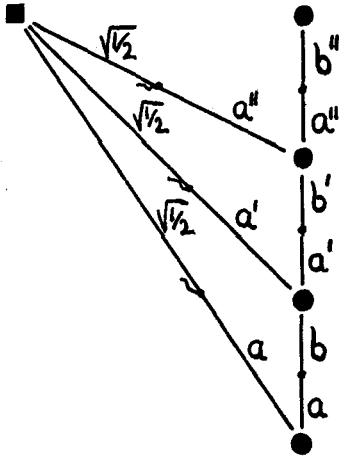


FIGURE 2

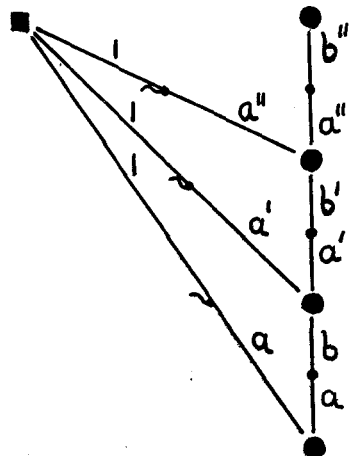


FIGURE 3

FIGURE 2.—Mating of sire of unknown genetic constitution with daughters, granddaughters, etc., generation after generation.

FIGURE 3.—Mating of homozygous sire with daughters, granddaughters, etc., generation after generation.

The key formula in the present case is clearly:

$$m = \sqrt{\frac{1}{2}} a' + a' b' m'$$

$$f = \sqrt{\frac{1}{2}} b m$$

$$m = \sqrt{\frac{1}{2}} a' (1 + 2 f')$$

$$a = \sqrt{\frac{1}{2(1+f)}}$$

$$b = \sqrt{\frac{1}{2}(1+f')}$$

$$m = \frac{1}{2} \frac{1 + 2 f'}{\sqrt{1 + f'}}$$

$$f = \frac{1}{4} (1 + 2 f')$$

$$p = \frac{1}{2} (1 - f) = \frac{1}{8} (1 + 4 p')$$

The last formula gives a means of writing the percentages of heterozygosis in successive generations by inspection. We obtain the series $\frac{3}{8}, \frac{5}{16}, \frac{9}{32}, \frac{7}{16},$ etc. By putting $p' = p$, we obtain $p = \frac{1}{4}$ as the limit when equilibrium is reached. These figures are the same as those given by JENNINGS (1916).

Figure 3 represents the same system of breeding as the last, except that the males are all homozygous (AA and aa).

The constitution of the male gametes is now completely determined, nothing being left to chance

$$\begin{aligned} m &= a' + a'b'm' \\ f &= bm \\ m &= a'(1 + f') = \sqrt{\frac{1 + f'}{2}} \\ f &= \frac{1}{2}(1 + f') \\ p &= \frac{p'}{2} \end{aligned}$$

Thus in this case, the percentage of heterozygosis is halved, each generation giving the series $\frac{1}{2}$, $\frac{1}{4}$, $\frac{1}{8}$, etc.

If all the original males had been of type AA and the original females of type aa , or *vice versa*, the results would obviously have been the same as that given above, which agrees with JENNINGS'S (1916) formulae 35 and 36.

This system of breeding is essentially that known among live-stock breeders as grading up. Males of the same pure breed, which is presumably homozygous in many factors, are used generation after generation on a scrub foundation.

Figure 4 represents another system of parent-offspring mating, in which each individual is bred successively with his younger parent and with his offspring. The path coefficient, parent to gamete, is of course the same in both cases.

$$\begin{aligned} m &= a'b' + a'b''m' \\ f &= bb'm \\ m &= a'b' + \frac{a'}{b'}f' \\ f &= a'b(b'^2 + f') \\ &= \frac{1}{4}(1 + 2f' + f'') \\ p &= \frac{1}{2}(1 - f) = \frac{p'}{2} + \frac{p''}{4} \end{aligned}$$

This gives us the same series for the percentages of heterozygosis as in brother-sister mating, $\frac{2}{4}$, $\frac{3}{8}$, $\frac{5}{16}$, $\frac{8}{32}$. . . 0, as given by JENNINGS (1916, formula 48).

In all of the preceding cases it will be seen that the present method of analysis gives the same results as the direct working out of the Mendelian formulae. We may now pass on to more complicated systems of breeding which would be cumbersome to deal with by direct methods.

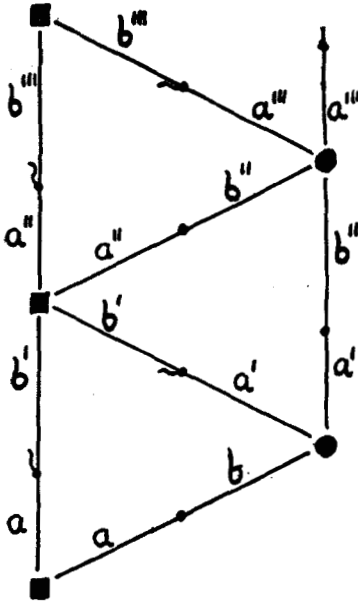


FIGURE 4

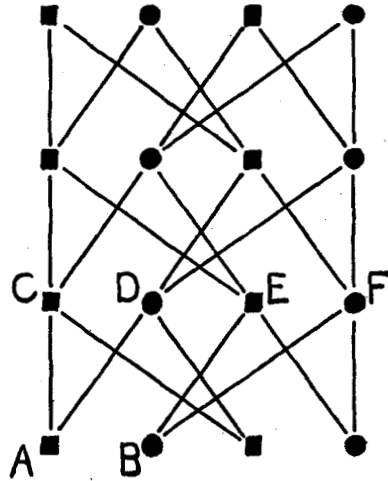


FIGURE 5

FIGURE 4.—Mating of offspring with younger parent, generation after generation.
 FIGURE 5.—Continued mating of double first cousins. The original random-bred population breaks up into lines containing 4 individuals in each generation.

DOUBLE FIRST COUSINS

If mating of double first cousins is begun in a random-bred population, the latter becomes broken up into distinct lines of descent, each involving four individuals in each generation. These lines of descent may, of course, bifurcate at any time as in the case of brother-sister matings. The relationships within a single line of descent are brought out in figure 5. Our problem is to express the correlation between mated individuals such as A and B in terms of path coefficients and correlations applying to the previous generation.

The path coefficient to A from either of his parents C or D and to B from E or F is $a'b'$. C and E are brothers (or brother and sister). The correlation between them is thus $2a''^2b''^2(1 + m'')$. The same is true of D and F. The correlation between C and F is not so obvious, but noting that F is a full brother of D, we see that the relationship between C and F

must be the same as between C and D, which are mated individuals with a correlation of m' . The same is true of the relation between D and E.

Summing up the four chains of path coefficients and correlations by which A and B are connected, we obtain:

$$m = a'^2 b'^2 (2 m' + 4 a''^2 b''^2 (m'' + 1))$$

This can be simplified considerably by noting that $a'^2 b'^2$, $a''^2 b''^2$, etc., always equals $\frac{1}{4}$, that $b^2 m = f$ and that $b^2 = \frac{1}{2} (1 + f')$

$$m = \frac{a'^2}{2} (4f' + 2f'' + f''' + 1)$$

From this formula we obtain at once a formula by which the series of values of f can be written by inspection.

$$f = \frac{1}{8} (4f' + 2f'' + f''' + 1)$$

The formula for the percentages of heterozygosis can be written by making the substitution $f = 1 - 2p$.

$$\begin{aligned} p &= \frac{1}{8} (4p' + 2p'' + p''') \\ &= p' - \frac{p''''}{16} \end{aligned}$$

The series of values of p is thus

$$\left(\frac{1}{2}, \frac{2}{4}\right), \frac{4}{8}, \frac{7}{16}, \frac{13}{32}, \frac{24}{64}, \frac{44}{128} \dots .0.$$

Each numerator is the sum of the preceding three numerators if the denominators are doubled each generation.

That there is no equilibrium point until $p = 0$ may be seen by substituting $p''' = p'' = p' = p$.

QUADRUPLE SECOND COUSINS

Theoretically a population can be broken up into groups of eight which perpetuate themselves indefinitely without making matings closer than between second cousins. This will be clear from a study of the accompanying diagram (figure 6).

Letting r_{00} , r_{11} and m be the correlations between brothers, first cousins and second cousins, respectively, we find by inspection of this diagram:

$$\begin{aligned} m &= a'^2 b'^2 (2 m' + 2 r'_{11}) \\ r'_{11} &= a''^2 b''^2 (2 m'' + 2 r''_{00}) \\ r''_{00} &= a'''^2 b'''^2 (2 m''' + 2) \end{aligned}$$

Simplifying in the same way as in the case of double first cousins, we obtain:

$$\begin{aligned}
 m &= \frac{a'^2}{4} (8f' + 4f'' + 2f''' + f'''' + 1) \\
 f &= \frac{1}{16} (8f' + 4f'' + 2f''' + f'''' + 1) \\
 p &= \frac{1}{16} (8p' + 4p'' + 2p''' + p'''') \\
 &= p' - \frac{1}{32} p'''''.
 \end{aligned}$$

This gives a series of percentages of heterozygosis which can be expressed in fractions, such that each numerator is the sum of the preceding four numerators and the denominators double:

$$\left(\frac{1}{2}, \frac{2}{4}, \frac{4}{8}\right), \frac{8}{16}, \frac{15}{32}, \frac{29}{64}, \frac{56}{128}, \frac{108}{256} \dots 0.$$

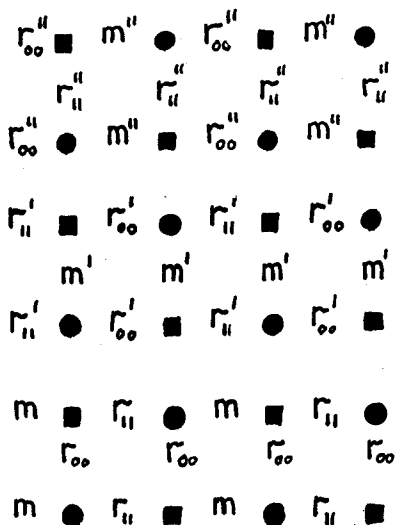


FIGURE 6.—Continued mating of quadruple second cousins, the population breaking up into lines of 8 individuals.

OCTUPLE THIRD COUSINS

The analogy between the results for self-fertilization, brother-sister matings, double first cousins and quadruple second cousins, is now obvious. The situation in groups of 16 in which matings are between octuple third cousins, can be analyzed in the same way and also gives analogous results:

MATING	SIZE OF GROUP	PERCENTAGE OF HETEROZYGOISIS
Self-fertilization.....	1	$p = p' / 2$
Brother-sister.....	2	$p = p' / 2 + p'' / 4$
Double first cousins.....	4	$p = p' / 2 + p'' / 4 + p''' / 8$
Quadruple second cousins.....	8	$p = p' / 2 + p'' / 4 + p''' / 8 + p'''' / 16$
Octuple third cousins.....	16	$p = p' / 2 + p'' / 4 + p''' / 8 + p'''' / 16 + p''''' / 32$

The decrease in heterozygosity is very slow in the case of octuple third cousins. After 15 generations (table 2) there is still 38 percent heterozygosity. Nevertheless it is obvious that no equilibrium point is reached until genetic variation is entirely eliminated.

The systems of mating given above represent the least possible inbreeding within closed populations of the given size in each generation. It follows that constant breeding within any population of limited size, even where consanguinity is avoided as far as possible, leads slowly to perfect homozygosity, provided that there are no disturbances from differential fecundity, etc. The population $x^2 AA + 2xy Aa + y^2 aa$ is in equilibrium

only in a population of indefinitely large size. This increase in homozygosity is, however, at such a slow rate in populations larger than 16 (where inbreeding is avoided) that it is practically negligible.

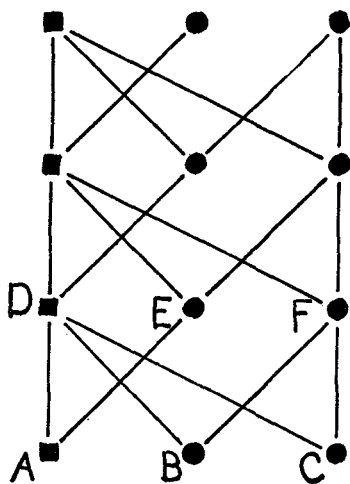


FIGURE 7.—Mating of one male in each line with two half-sisters, full sisters of each other.

MATINGS OF HALF-BROTHER AND SISTER

A number of systems of mating between half-brothers and sisters can be devised. The simplest, at first sight, is that represented in figure 7. The population becomes broken into distinct lines of descent in which three individuals are bred in each generation, one male and two of his half-sisters, which, however, are full sisters of each other. The correlation between mated individuals, such as A and B, depends not

only on their common sire D, but on the fact that the sire of A and the dam of B, and also the dam of A and sire of B, are half-brother and sister, and that the dams are full sisters. The correlation between half-brother and sister of the previous generation is m' . The correlation between full sisters is $2a''^2b''^2(1 + m')$. Thus the correlation between mated individuals A and B can be written

$$\begin{aligned}
 m &= a'^2 b'^2 [1 + 2m' + 2a''^2 b''^2 (1 + m')] \\
 &= \frac{1}{4} a'^2 (8f' + 4f'' + f''' + 3) \\
 f &= \frac{1}{16} (8f' + 4f'' + f''' + 3) \\
 p &= \frac{1}{16} (8p' + 4p'' + p''')
 \end{aligned}$$

This gives us the series of percentages of heterozygosis,

$$\left(\frac{2}{4}, \frac{4}{8}\right), \frac{8}{16}, \frac{13}{32}, \frac{23}{64}, \frac{40}{128}, \frac{139}{512} \dots 0.$$

On going back to the derivation of the key formula, it will be seen that we are assuming that inbreeding is preceded by a generation in which a male is mated with two females unrelated to him, but full sisters of each other. If the three individuals in the last generation of random mating back of each inbred line are all unrelated, the series runs, $\frac{4}{8}, \frac{7}{16}, \frac{13}{32}, \frac{21}{64}, \frac{73}{256} \dots 0$.

If one male is mated with an indefinite number of his half-sisters which are also merely half-sisters of each other (figure 8) the analysis is even simpler than in the last case. The slight departure from this system which would be necessary to keep up the numbers in each generation may be neglected.

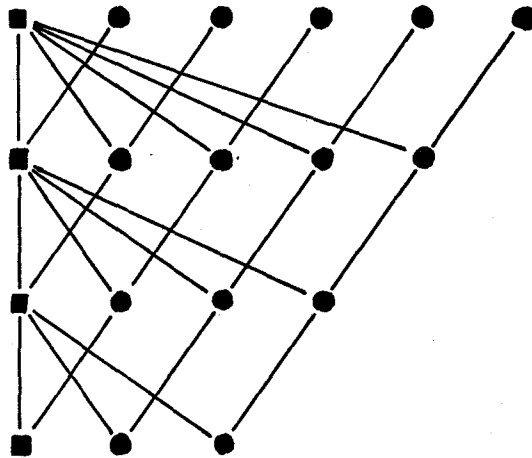


FIGURE 8.—Mating of one male in each line with an indefinitely large number of half-sisters, which are also half-sisters of each other.

The key formula is obviously:

$$\begin{aligned} m &= a'^2 b'^2 (1 + 3m') \\ &= \frac{1}{2} a'^2 (6f' + f'' + 1) \\ f &= \frac{1}{8} (6f' + f'' + 1) \\ p &= \frac{1}{8} (6p' + p'') = \frac{3}{4} p' + \frac{2}{16} p'' \end{aligned}$$

The series runs $\frac{2}{4}, \frac{7}{16}, \frac{25}{64}, \frac{89}{256}, \frac{317}{1024} \dots 0$. Each numerator is thrice the preceding, plus twice the one before that, while the denominators are multiplied by four.

The last system of mating is of special interest since it is perhaps the most rapid practical method of fixing characters in live stock. If a breeder consistently uses a single male of his own breeding to head his herd, the typical mating will be between half-brother and sister, the females being in general half-sisters of each other. There will, of course, be some more remote matings—half-uncle and niece, etc.,—but these will be balanced, in part at least, by matings of full brother and sister, and parent and offspring. The rate of increase in homozygosis is fairly rapid. In three generations, there is 65 percent homozygosis compared with 75 percent with brother-sister matings. In eight generations, the figures are 80

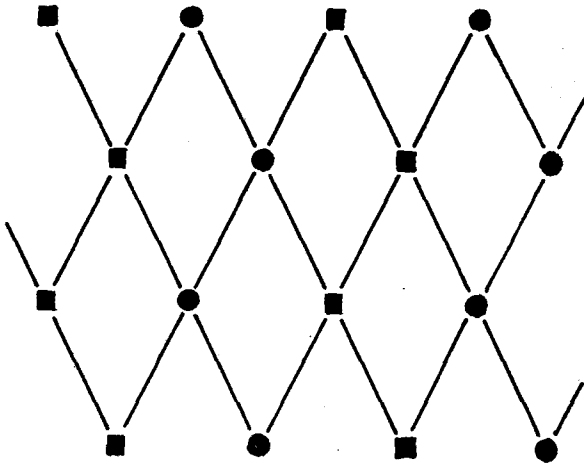


FIGURE 9.—Mating of each male with two half-sisters and each female with two half-brothers.

percent and 91 percent respectively. In fifteen generations 92 percent and 98 percent respectively. With brother-sister mating, the herd breaks up into distinct lines in each generation, which cannot be held together. With the system under discussion, the character of the whole herd can be fixed at once.

Another system of mating half-brothers and sisters, of more theoretical than practical interest, is illustrated in figure 9. Each male and female is mated with two half-sisters or half-brothers. While the original population will tend to break up into distinct groups, there is no limit to the size of each group. The key formula is evidently:

$$m = a'^2 b'^2 (1 + 2m' + r'_{11})$$

where r'_{11} is the correlation between half-first cousins of the preceding generation. The value of r'_{11} can be expressed in terms of auxiliary formulae:

$$r'_{11} = a'^2 b'^2 (m'' + 2 r'_{11} + r'_{22})$$

$$r''_{22} = a''^2 b''^2 (r'_{11} + 2 r''_{22} + r'''_{33}), \text{ etc.}$$

The writer has found no other method of solving the value of m than of carrying these auxiliary formulae back to the point at which there is random mating. To find the percentage of heterozygosis and the correlations between relatives for fifteen generations, it is necessary to find values of r_{77} in one case.

In fifteen generations, the percentage of heterozygosis falls from 50 percent to 24 percent. This is a much slower decline than in the other kinds of half-brother and sister matings considered. It is, however, easy to see that there is no equilibrium point short of complete homozygosis. Under equilibrium

$$a^2 b^2 = \frac{1}{4} = a'^2 b'^2, \text{ etc.}, \quad m = m', \quad r_{11} = r'_{11}, \text{ etc.}$$

$$m = \frac{1}{4} (1 + 2 m + r_{11}) = \frac{1}{2} (1 + r_{11})$$

$$r_{11} = \frac{1}{4} (m + 2 r_{11} + r_{22}) = \frac{1}{2} (m + r_{22})$$

$$r_{22} = \frac{1}{4} (r_{11} + 2 r_{22} + r_{33}) = \frac{1}{2} (r_{11} + r_{33}), \text{ etc.}$$

Thus under equilibrium 1, $m, r_{11}, r_{22}, r_{33} \dots$, forms an arithmetic series. Therefore, by going a sufficient number of generations m can be made to approach 1 as closely as desired. This causes b^2 to approach 1, as is also true of f and g , while the percentage of heterozygosis, $p = \frac{1}{2} (1 - f)$, approaches 0.

MATING OF FIRST COUSINS

The continued mating of first cousins as in figure 10 is a system which is similar to the mating of half-brother and sister in figure 9, in that the number of ancestors of both sexes, of a given individual, increases in arithmetic progression with the generations. The method of analysis is also similar. Inspection of the figure gives the following key equation and auxiliary equations:

$$m = a'^2 b'^2 (r'_{00} + 2 m' + r'_{22})$$

$$r'_{22} = a''^2 b''^2 (m'' + 2 r'_{22} + r'''_{33})$$

$$r''_{33} = a'''^2 b'''^2 (r'_{22} + 2 r''_{33} + r''''_{44})$$

The percentage of heterozygosis decreases rather slowly, only falling from 50 percent to 34 percent in fifteen generations. Nevertheless, the limit is not reached until all heterozygosis is eliminated. This can be demonstrated by the same reasoning as in the case of half-brothers and sisters.

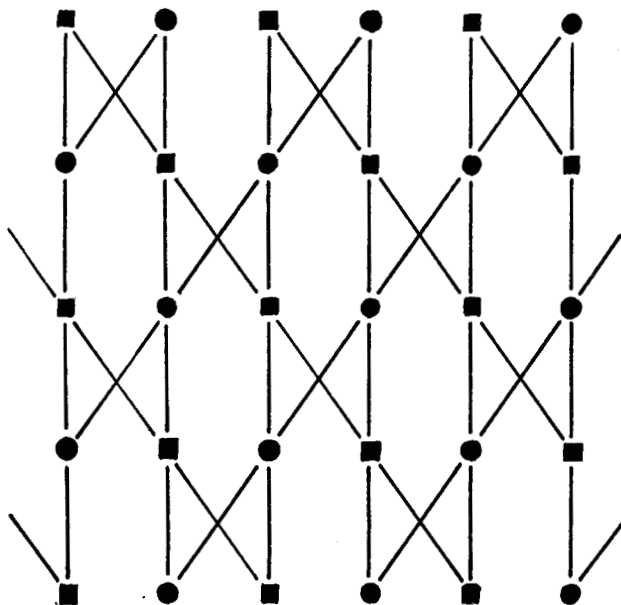


FIGURE 10.—Mating of single first cousins, generation after generation.

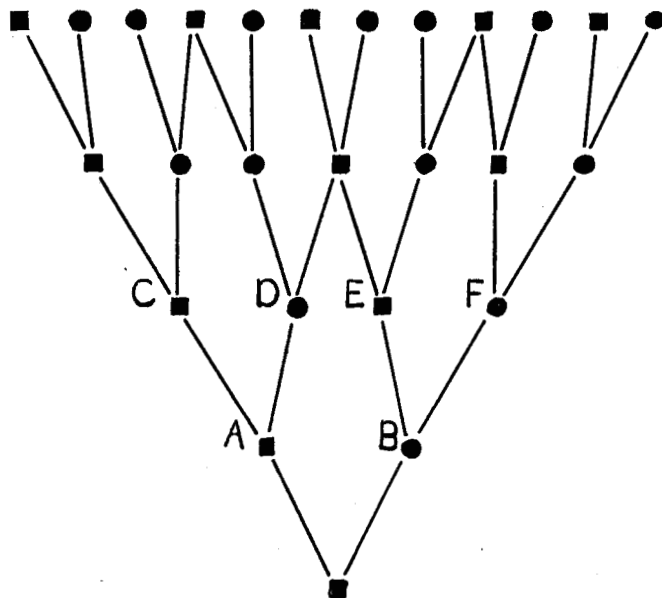


FIGURE 11.—A pedigree in which all matings are between half-first cousins.

HALF-FIRST COUSINS

It might be thought from the preceding cases that there can be no equilibrium short of perfect homozygosis with any consistent system of inbreeding. This, however, is not the case, as may be seen from a consideration of various systems in which the consanguinity is more remote than between first cousins. In the case of half-first cousins (figure 11) there is no necessary relationship between A and B except through one parent of each, E and D.

The key formula is:

$$\begin{aligned} m &= a'^2 b'^2 a''^2 b''^2 (1 + 2 m'') \\ &= \frac{a'^2}{8} (1 + 4 f'' + f''') \\ f &= \frac{1}{8} (1 + 4 f'' + f''') \\ p &= \frac{1}{8} (4 p'' + p''' + 13) \end{aligned}$$

When equilibrium is reached, we find by substituting $m'' = m$, $f''' = f'' = f$, $p''' = p'' = p$ that $m = \frac{1}{14}$, $f = \frac{1}{7}$ and $p = \frac{3}{7}$, $r_{oo} = r_{p0} = \frac{5}{8}$

Thus the percentage of heterozygosis falls only from 50 percent to 48 percent if the system is continued indefinitely.

SECOND COUSINS

The mating of second cousins according to the system in figure 12 is even less efficient than the mating of half-first cousins, as regards decrease in heterozygosis.

The key equation is:

$$\begin{aligned} m &= a'^2 b'^2 a''^2 b''^2 [2 a'''^2 b'''^2 (1 + m''') + 2 m''] \\ &= \frac{1}{16} a'^2 (1 + 8 f'' + 2 f''' + f''') \\ f &= \frac{1}{16} (1 + 8 f'' + 2 f''' + f''') \\ p &= \frac{1}{16} (26 + 8 p'' + 2 p''' + p''') \end{aligned}$$

When equilibrium is reached

$$m = \frac{1}{27}, f = \frac{1}{9}, p = \frac{6}{9}, r_{oo} = r_{p0} = \frac{4}{7}$$

Thus, the continued mating of second cousins causes the percentage of heterozygosis to fall merely from 50.0 percent to 49.1 percent.

The general effects of inbreeding, such as the increase in uniformity, the prepotency in outside crosses, the usual decline in vigor in various respects are in all probability merely consequences of the increase in

homozygosis. It appears that while the continued mating of first cousins leads to perfect homozygosis, though rather slowly, systems based on more remote consanguinity cause only an insignificant increase in homozygosis if kept up forever. As far as this class of effects is concerned, the mating of half-first cousins or second cousins need hardly be considered as inbreeding. It should be added, however, that there is a somewhat distinct kind of effect for which these degrees of inbreeding may have some

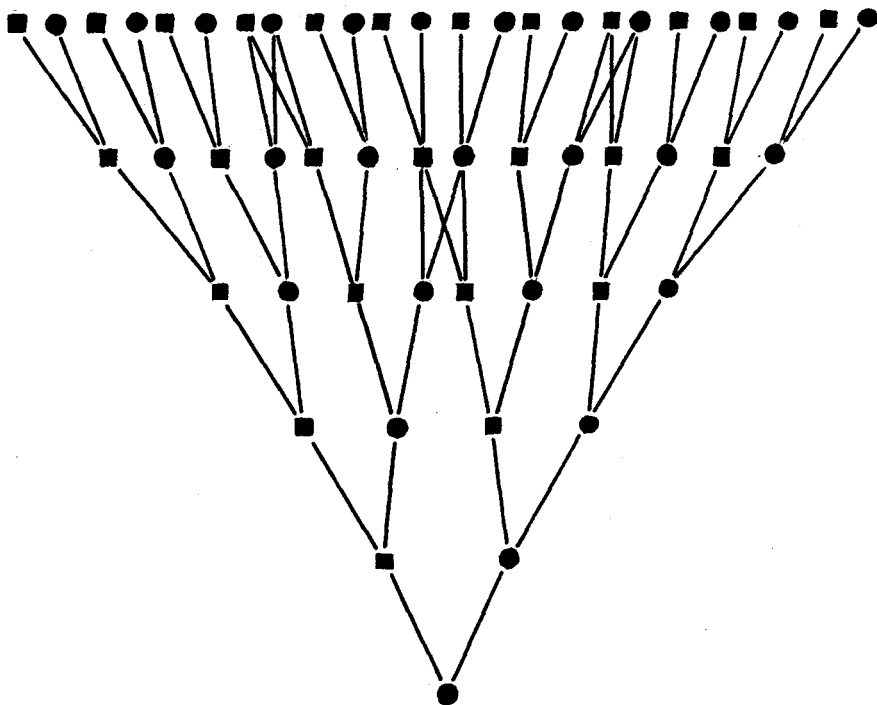


FIGURE 12.—A pedigree in which all matings are between second cousins.

significance. In the case of a characteristic which is due to a single recessive factor and is very rare in the general population, the chance of appearance following a mating which is not consanguineous is exceedingly slight, while the chance after a second- or even third-cousin mating in the affected family may be sufficiently great to be an important consideration. The chance of appearance in such a case could only be estimated by a study of the ancestry of the two individuals.

We have found that continued first-cousin mating leads ultimately to perfect assortative mating (1.00) while half-first cousin leads only to a coefficient of assortative mating of 0.07 and second-cousin mating a coeffi-

cient of 0.03. It may seem difficult to obtain a population in equilibrium with an intermediate degree of assortative mating based wholly on consanguinity (i.e., matings not made on the basis of physical resemblance). Suppose, however, that the population is separated into non-interbreeding classes, such that there is a correlation of m between members of the same class. The correlation between two individuals chosen at random from the next generation, will be $4a'^2b'^2m$. The value of $a'^2b'^2$ when equilibrium is reached is $\frac{1}{4}$. Thus, under random mating within the classes, the correlation of assortative mating for the whole population will remain m , indefinitely.

We will have

$$g = f = \frac{m}{2 - m}, \quad a^2 = \frac{1}{4}(2 - m), \quad b^2 = \frac{1}{2 - m}, \quad p = \frac{1 - m}{2 - m}$$

Thus with mating correlations of 0.25, 0.50 and 0.75, the percentages of heterozygosis will be 0.41, 0.33 and 0.20 respectively.

Such a system of non-interbreeding classes with a high correlation between members of each class can arise in various ways. For example, if any of the systems of consanguine mating which break the population into distinct classes are interrupted, being followed by random mating within each class, such a system as that just described would be formed.

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