

INBREEDING AND LINKAGE*

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When a heterozygous population is self-fertilized or inbred the ultimate result (apart from effects of mutation) is complete homozygosis. The final proportions of the various genotypes are usually independent of the system of inbreeding adopted, although, as JENNINGS (1916) and others have shown, the speed at which equilibrium is approached is greater in the case of self-fertilization than of brother-sister mating, and so on.

If however the population be heterozygous for linked genes, the final proportions depend on the system of mating, for crossing over can only occur in double heterozygotes, and the proportion of double heterozygotes falls off at a different rate in different mating systems. JENNINGS (1917) stated that he "would find it a relief if someone else would deal thoroughly with the laborious problem of the effects of inbreeding on two pairs of linked factors." This is the object of the present paper. ROBBINS (1918) solved the problem in the case of self-fertilization.

In what follows we employ a direct method to obtain the final proportions of the population. The rate of approach can be calculated, but this is a very laborious process, and always involves the irrational roots of quadratic, sometimes those of quartic or higher equations. In each case we shall suppose that the number of dominant and recessive genes of each type in the population is equal throughout the progress of the inbreeding. This enormously simplifies the mathematics. Thus a system of 55 equa-

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tions described by JENNINGS (1917) is at once reduced to 22. This restriction is later removed.

SELF-FERTILIZATION

This problem has been solved by ROBBINS, but the shorter solution here given serves to illustrate our method. Consider the results of crossing $AABB$ and $aabb$, where A and B are linked. The crossover values on the two sides of a hermaphrodite are taken as 100β percent and 100δ percent, so that the two gametic series given by $AB.ab$ are:

$$(1 - \beta)AB:\beta Ab:\beta aB:(1 - \beta)ab.$$

$$(1 - \delta)AB:\delta Ab:\delta aB:(1 - \delta)ab.$$

For the sake of symmetry we suppose the original population to be entirely $AB.ab$. Then in the n th generation which is self-fertilized, let the 10 zygotic types occur in the proportions:

$$C_n \text{ } AABB \text{ and } aabb.$$

$$D_n \text{ } AAbb \text{ and } aaBB.$$

$$E_n \text{ } AABb, AaBB, Aabb, \text{ and } aaBb.$$

$$F_n \text{ } AB.ab.$$

$$G_n \text{ } Ab.aB.$$

We assume $2C_n + 2D_n + 4E_n + F_n + G_n = 2$, so that $C_1 = D_1 = E_1 = G_1 = 0$, and $F_1 = 2$. Clearly $E_\infty = F_\infty = G_\infty = 0$, and D_∞ is the final proportion of crossover zygotes. Then considering the results of selfing each generation, we have:

$$\left. \begin{aligned} C_{n+1} &= C_n + \frac{1}{2}E_n + \frac{1}{4}(1 - \beta - \delta + \beta\delta)F_n + \frac{1}{4}\beta\delta G_n \\ D_{n+1} &= D_n + \frac{1}{2}E_n + \frac{1}{4}\beta\delta F_n + \frac{1}{4}(1 - \beta - \delta + \beta\delta)G_n \\ E_{n+1} &= \frac{1}{2}E_n + \frac{1}{4}(\beta + \delta - 2\beta\delta)(F_n + G_n) \\ F_{n+1} &= \frac{1}{2}(1 - \beta - \delta + \beta\delta)F_n + \frac{1}{2}\beta\delta G_n \\ G_{n+1} &= \frac{1}{2}\beta\delta F_n + \frac{1}{2}(1 - \beta - \delta + \beta\delta)G_n \end{aligned} \right\} \quad (1.1)$$

These equations are derived as follows. The homozygous types when selfed reproduce themselves only, so C_n and D_n contribute only to C_{n+1} and D_{n+1} . $AABb$ selfed gives $\frac{1}{4}AABB$, $\frac{1}{4}AAbb$, $\frac{1}{2}AABb$. Hence the contribution of E_n to E_{n+1} is $\frac{1}{2}E_n$. Since there are twice as many classes in the proportion E_n as C_{n+1} , the coefficient of its contribution to C_{n+1} must be doubled, and similarly for its contribution to D_{n+1} . The contributions of F_n and G_n are similarly calculated.

Now put $C_n - D_n = c_n$, $F_n - G_n = d_n$, and the average crossover value,

$\frac{1}{2}(\beta + \delta) = x$. Then subtracting the equations for C_{n+1} , D_{n+1} , and F_{n+1} , G_{n+1} , we have:

$$\left. \begin{aligned} c_{n+1} &= c_n + \frac{1}{4}(1 - 2x)d_n \\ d_{n+1} &= \frac{1}{2}(1 - 2x)d_n \end{aligned} \right\} \quad (1.2)$$

Now choose λ so that $c_{n+1} + \lambda d_{n+1} \equiv c_n + \lambda d_n$ for all values of n .

$$\text{Then } c_n + \lambda d_n \equiv c_n + \frac{1}{4}(1 - 2x)d_n + \frac{1}{2}\lambda(1 - 2x)d_n$$

$$\therefore \lambda = \frac{1 - 2x}{2 + 4x}$$

Then since $d_\infty = 0$, and $c_1 = 0$, $d_1 = 2$,

$$c_\infty = c_\infty + \lambda d_\infty = c_1 + \lambda d_1 = \frac{1 - 2x}{1 + 2x}$$

Put $y = D_\infty$ (the final proportion of crossover zygotes)

$$\therefore C_\infty + D_\infty = 1, C_\infty - D_\infty = c_\infty \therefore y = \frac{1}{2}(1 - c_\infty)$$

$$\therefore y = \frac{2x}{1 + 2x} \quad (1.3)$$

Hence the proportion of crossover zygotes is approximately equal to twice the mean gametic crossover value when the latter is small, rising to 50 percent with 50 percent crossing over (see figure 1). The actual proportions of the different zygotic types in each generation can be calculated from equations (1.1). Equations (1.2) are not sufficient. The method of solution is given by ROBBINS, and the principal result in our terminology, putting $p = \beta\delta$, the product of the crossover values, is:

$$\begin{aligned} C_n &= \frac{1 - (\frac{1}{2} - x)^n}{1 + 2x} + \frac{1}{2}(\frac{1}{2} - x + p)^{n-1} - (\frac{1}{2})^{n-1} \\ D_n &= \frac{2x + (\frac{1}{2} - x)^n}{1 + 2x} + \frac{1}{2}(\frac{1}{2} - x + p)^{n-1} - (\frac{1}{2})^{n-1} \end{aligned} \quad (1.4)$$

Thus the final proportion of crossover zygotes, D_∞ , depends on x only; the rate of approach to this value depends on p . Indeed if crossing over were restricted to one side of a hermaphrodite, as it is to one sex in the higher insects, we should have $p = 0$, and no crossover zygotes would appear before F_3 . D_n is 0 in F_1 , $\frac{1}{2}p$ in F_2 , rising sharply to $\frac{1}{2}(x + p - 2px + p^2)$ in F_3 , and over half way to its final value in F_4 . Except in F_2 the figures

depend almost entirely on the mean crossover value. Thus with a mean value of 10 percent we have in successive generations the percentages of crossover homozygotes given in table 1.

TABLE 1

| CROSSOVER VALUES PERCENT | F ₂ | F ₃ | F ₄ | F ₅ | F ₆ | F _∞ |
|--------------------------|----------------|----------------|----------------|----------------|----------------|----------------|
| 10, 10 | 0.50 | 5.405 | 9.746 | 12.683 | 14.462 | 16.6 |
| 20, 0 | 0 | 5.0 | 9.5 | 12.55 | 14.395 | 16.6 |

Hence in a plant propagated by self-fertilization, where new combinations are required after a cross, there is a very great advantage in growing on a large progeny as far as F₃, and rather little advantage in growing it beyond F₄. As will appear later, this is also true when double crossing over is taken into account.

BROTHER-SISTER MATING. SEX-LINKED GENES

Two sex-linked genes provide four types of zygotes in the heterogametic sex, and ten in the homogametic. There are thus forty different types of mating. If we consider the results of an original mating $AABB \times ab$, or $aabb \times AB$, the numbers of A and a genes are unequal, and there is a lack of symmetry in the equations, just as there would be in the case last considered if we did not begin with equal numbers of the allelomorphs. We therefore suppose that at the beginning both reciprocal crosses were made in equal numbers. The crossover percentage is taken as 100β , and $\alpha = 1 - \beta$. The fourteen variables of equations (2.1) refer to the proportions of matings of each type. Under the circumstances considered all matings fall into one of fourteen classes having the same frequency in each generation, which is calculable when we know the frequencies in the preceding generation.

| MATINGS | PROPORTION |
|------------------|---|
| $AABB \times AB$ | $C_{n+1} = C_n + \frac{1}{2}I_n + \frac{\alpha^2}{4}M_n + \frac{\beta^2}{4}Q_n$ |
| $aabb \times ab$ | |
| $AAbb \times Ab$ | $D_{n+1} = D_n + \frac{1}{2}J_n + \frac{\alpha^2}{4}P_n + \frac{\beta^2}{4}R_n$ |
| $aaBB \times aB$ | |
| $AABB \times Ab$ | $E_{n+1} = \frac{1}{2}I_n + \frac{\alpha\beta}{4}(M_n + Q_n)$ |
| $AABB \times aB$ | |
| $aabb \times aB$ | |
| $aabb \times Ab$ | |

$$\begin{array}{l}
 AAbb \times AB \\
 AAbb \times ab \\
 aaBB \times AB \\
 aaBB \times ab \\
 \left. \vphantom{\begin{array}{l} AAbb \times AB \\ AAbb \times ab \\ aaBB \times AB \\ aaBB \times ab \end{array}} \right\} F_{n+1} = \frac{1}{4}J_n + \frac{\alpha\beta}{4}(P_n + R_n) \\
 AABb \times ab \\
 aabb \times AB \\
 \left. \vphantom{\begin{array}{l} AABb \times ab \\ aabb \times AB \end{array}} \right\} G_{n+1} = \frac{\alpha^2}{4}M_n + \frac{\beta^2}{4}Q_n \\
 AAbb \times aB \\
 aaBB \times Ab \\
 \left. \vphantom{\begin{array}{l} AAbb \times aB \\ aaBB \times Ab \end{array}} \right\} H_{n+1} = \frac{\alpha^2}{4}P_n + \frac{\beta^2}{4}R_n \\
 AaBB \times AB \\
 AABb \times AB \\
 Aabb \times ab \\
 aABb \times ab \\
 \left. \vphantom{\begin{array}{l} AaBB \times AB \\ AABb \times AB \\ Aabb \times ab \\ aABb \times ab \end{array}} \right\} I_{n+1} = E_n + \frac{1}{4}(I_n + J_n + K_n) + \frac{\alpha\beta}{4}(M_n + Q_n) + \frac{\beta^2}{4}P_n + \frac{\alpha^2}{4}R_n \\
 AaBB \times aB \\
 AABb \times Ab \\
 Aabb \times Ab \\
 aABb \times aB \\
 \left. \vphantom{\begin{array}{l} AaBB \times aB \\ AABb \times Ab \\ Aabb \times Ab \\ aABb \times aB \end{array}} \right\} J_{n+1} = F_n + \frac{1}{4}(I_n + J_n + L_n) + \frac{\alpha\beta}{4}(P_n + R_n) + \frac{\beta^2}{4}M_n + \frac{\alpha^2}{4}Q_n \\
 AaBB \times Ab \\
 AABb \times aB \\
 Aabb \times aB \\
 aABb \times Ab \\
 \left. \vphantom{\begin{array}{l} AaBB \times Ab \\ AABb \times aB \\ Aabb \times aB \\ aABb \times Ab \end{array}} \right\} K_{n+1} = \frac{1}{4}K_n + \frac{\alpha\beta}{4}(P_n + R_n) + \frac{\beta^2}{4}M_n + \frac{\alpha^2}{4}Q_n \\
 AaBB \times ab \\
 AABb \times ab \\
 Aabb \times AB \\
 aABb \times AB \\
 \left. \vphantom{\begin{array}{l} AaBB \times ab \\ AABb \times ab \\ Aabb \times AB \\ aABb \times AB \end{array}} \right\} L_{n+1} = \frac{1}{4}L_n + \frac{\alpha\beta}{4}(M_n + Q_n) + \frac{\beta^2}{4}P_n + \frac{\alpha^2}{4}R_n \\
 AB \cdot ab \times AB \\
 AB \cdot ab \times ab \\
 \left. \vphantom{\begin{array}{l} AB \cdot ab \times AB \\ AB \cdot ab \times ab \end{array}} \right\} M_{n+1} = G_n + \frac{1}{2}L_n + \frac{\alpha^2}{2}M_n + \frac{\beta^2}{2}Q_n \\
 Ab \cdot aB \times Ab \\
 Ab \cdot aB \times aB \\
 \left. \vphantom{\begin{array}{l} Ab \cdot aB \times Ab \\ Ab \cdot aB \times aB \end{array}} \right\} P_{n+1} = H_n + \frac{1}{2}K_n + \frac{\alpha^2}{2}P_n + \frac{\beta^2}{2}R_n \\
 Ab \cdot aB \times AB \\
 Ab \cdot aB \times ab \\
 \left. \vphantom{\begin{array}{l} Ab \cdot aB \times AB \\ Ab \cdot aB \times ab \end{array}} \right\} Q_{n+1} = K_n + \frac{\alpha\beta}{2}(P_n + R_n) \\
 AB \cdot ab \times Ab \\
 AB \cdot ab \times aB \\
 \left. \vphantom{\begin{array}{l} AB \cdot ab \times Ab \\ AB \cdot ab \times aB \end{array}} \right\} R_{n+1} = L_n + \frac{\alpha\beta}{2}(M_n + Q_n).
 \end{array}$$

(These equations are referred to as 2.1.)

As an illustration of how these equations are derived we may take the distribution of K_n in the following generation. The mating $AaBB \times Ab$ gives $AABb$, $Ab.aB$, AB , and aB offspring in equal numbers. Hence in the next generation the matings $AABb \times AB$, $AABb \times aB$, $Ab.aB \times AB$, and $Ab.aB \times aB$ occur in equal numbers among its progeny. Hence K_n contributes to I_{n+1} , K_{n+1} , Q_{n+1} , P_{n+1} as shown. To reduce the equations (2.1) we put:

$c_n = C_n - D_n, d_n = E_n - F_n, e_n = G_n - H_n, f_n = I_n - J_n, g_n = K_n - L_n,$
 $h_n = M_n - P_n, i_n = Q_n - R_n.$

$$\left. \begin{aligned} \therefore c_{n+1} &= c_n + \frac{1}{2}f_n + \frac{\alpha^2}{4}h_n + \frac{\beta^2}{4}i_n \\ d_{n+1} &= \frac{1}{4}f_n + \frac{\alpha\beta}{4}(h_n + i_n) \\ e_{n+1} &= \frac{\alpha^2}{4}h_n + \frac{\beta^2}{4}i_n \\ f_{n+1} &= d_n + \frac{1}{4}g_n + \frac{\alpha\beta - \beta^2}{4}h_n - \frac{\alpha^2 - \alpha\beta}{4}i_n \\ g_{n+1} &= \frac{1}{4}g_n - \frac{\alpha\beta - \beta^2}{4}h_n + \frac{\alpha^2 - \alpha\beta}{4}i_n \\ h_{n+1} &= e_n - \frac{1}{2}g_n + \frac{\alpha^2}{2}h_n + \frac{\beta^2}{2}i_n \\ i_{n+1} &= \frac{1}{2}g_n - \frac{\alpha\beta}{2}(h_n + i_n) \end{aligned} \right\} \quad (2.2)$$

When $n = 0$, G_n and therefore $e_n = 1$, the other variables are zero. When $n = \infty$, all but C_n, D_n , and consequently c_n vanish. It is required to find the value of c_∞ . To do so we have to find values of $\epsilon, \zeta, \eta, \theta, \phi, \psi$, such that

$$\begin{aligned} c_{n+1} + \epsilon d_{n+1} + \zeta e_{n+1} + \eta f_{n+1} + \theta g_{n+1} + \phi h_{n+1} + \psi i_{n+1} \\ \equiv c_n + \epsilon d_n + \zeta e_n + \eta f_n + \theta g_n + \phi h_n + \psi i_n. \end{aligned}$$

Substituting in the above identity the values of c_{n+1} , etc. and equating coefficients of d_n , etc. we have:

$$\left. \begin{aligned} \epsilon &= \eta \\ \zeta &= \phi \\ \eta &= \frac{1}{2} + \frac{1}{4}\epsilon \\ \theta &= \frac{1}{4}(\eta + \theta - 2\phi + 2\psi) \\ \phi &= \frac{\alpha^2}{4}(1 + \zeta + 2\phi) + \frac{\alpha\beta}{4}(\epsilon - 2\psi) + \frac{2\beta - \beta^2}{4}(\eta - \theta) \\ \psi &= \frac{\beta^2}{4}(1 + \zeta + 2\phi) + \frac{\alpha\beta}{4}(\epsilon - 2\psi) + \frac{\alpha\beta - \alpha^2}{4}(\eta - \theta) \end{aligned} \right\} \quad (2.3)$$

Eliminating $\epsilon = \eta = \frac{2}{3}$, and $\phi = \zeta$, we have

$$\begin{aligned} 9\theta &= 2 - 6\zeta + 6\psi \\ 12(\zeta - \psi) &= (\alpha - \beta)(5 + 9\zeta - 3\theta). \\ 12(\zeta + \psi) &= 1 + 3(\alpha^2 + \beta^2)(3\zeta + \theta) - 6\alpha\beta\psi. \end{aligned}$$

Hence, putting $\beta = x$,

$$\epsilon = \zeta = \frac{2}{3}, \zeta = \phi = \frac{3 - 4x}{3(1 + 4x)}, \quad \theta = 2\psi = \frac{2(4x - 1)}{3(1 + 4\beta)}.$$

Hence, for all values of n ,

$$c_\infty = c_n + \frac{2}{3}(d_n + f_n) + \frac{(3 - 4x)(e_n + h_n)}{3(1 + 4x)} + \frac{(4x - 1)(2g_n + i_n)}{3(1 + 4x)} \quad (2.4)$$

and since $C_n + D_n = 1$, $C_n - D_n = c$

$$\therefore y = D_n = \frac{1}{2}(1 - c_n).$$

In the case here considered $e_0 = 1$

$$\begin{aligned} \therefore c_\infty &= \frac{3 - 4x}{3(1 + 4x)} \\ \therefore y &= \frac{8x}{3(1 + 4x)}. \end{aligned} \quad (2.5)$$

This is plotted in figure 1. It will be seen that if two sex-linked genes give 50 percent crossing over in the homogametic sex, the final proportion of crossover zygotes will be $4/9$. In order to study the rate at which the final values are approached it is necessary to solve the equations (2.2), and also a corresponding set of seven equations for $C_n + D_n$, etc. This is quite possible. Thus it can easily be shown that

$$\begin{aligned} (h_{n+2} - i_{n+2}) - \alpha(h_{n+1} - i_{n+1}) - (\alpha - \beta)(h_n - i_n) &= 0 \\ \therefore h_n - i_n &= \frac{1}{\sqrt{5\alpha^2 - 4\beta^2}} \left[\left(\frac{\alpha + \sqrt{5\alpha^2 - 4\beta^2}}{2} \right)^n - \left(\frac{\alpha - \sqrt{5\alpha^2 - 4\beta^2}}{2} \right)^n \right]. \end{aligned}$$

As, however, any variable, such as C_n , may be the sum of a large number of terms from geometrical series, numerical calculation is easier than algebraic. The expressions given by JENNINGS and ROBBINS for the proportion of heterozygotes in the n th generation are wholly independent of linkage. Hence it is clear that by about F_{10} the population contains only 10 percent of Aa and as many Bb in the homogametic sex, so that equilibrium is nearly reached.

BROTHER-SISTER MATING. AUTOSOMAL GENES

We consider the results of an initial mating $AABB \times aabb$ or reciprocally. The gametic series from an $AB.ab$ ♀ is assumed to be $\alpha AB : \beta Ab : \beta aB : \alpha ab$, from $AB.ab$ ♂, $\gamma AB : \delta Ab : \delta aB : \gamma ab$, so that 100β and 100δ are the crossover values. In general these are different, but in mammals β and δ are nearly equal; in the higher insects one of them is zero. There are 100 different types of mating, and owing to the different crossover values in the two sexes, reciprocal crosses do not always yield the same progeny, and therefore the same numbers of matings in the next generation. However, reciprocal crosses occur in the same numbers, and can be grouped together. In the following scheme only one example is given of each type of mating. The total number of types is given in column 2. Thus the following 7 types of mating occur in equal numbers with $AABB \times AAbb$:

$$AAbb \times AABB, aaBB \times AABB, AABB \times aaBB, aabb \times aaBB, \\ aaBB \times aabb, aabb \times AAbb, AAbb \times aabb.$$

In the third column the numbers of each kind of mating in the $(n+1)$ th generation are given in terms of similar numbers in the n th. To save space the suffixes of the latter are omitted, for example, H is written for H_n . The method of calculation is similar to that in the sex-linked case. We thus have equations (3.1):

| Typical mating | Number of types | |
|---------------------|-----------------|---|
| $AABB \times AABB$ | 2 | $C_{n+1} = C_n + H + \frac{1}{4}(\alpha^2 + \gamma^2)L + \frac{1}{4}(\beta^2 + \delta^2)N + \frac{1}{8}Q + \frac{1}{8}R + \frac{1}{8}(\alpha^2 + \gamma^2)U + \frac{1}{8}(\beta^2 + \delta^2)V + \frac{1}{16}\alpha^2\gamma^2W + \frac{1}{16}(\alpha^2\delta^2 + \beta^2\gamma^2)X + \frac{1}{16}\beta^2\delta^2Y.$ |
| $AAbb \times AAbb$ | 2 | $D_{n+1} = D + I + \frac{1}{4}(\alpha^2 + \gamma^2)M + \frac{1}{4}(\beta^2 + \delta^2)P + \frac{1}{8}Q + \frac{1}{8}S + \frac{1}{8}(\beta^2 + \delta^2)U + \frac{1}{8}(\alpha^2 + \gamma^2)V + \frac{1}{16}\beta^2\delta^2W + \frac{1}{16}(\alpha^2\delta^2 + \beta^2\gamma^2)X + \frac{1}{16}\alpha^2\gamma^2Y.$ |
| $AABB \times aabb$ | 2 | $E_{n+1} = \frac{1}{16}\alpha^2\gamma^2W + \frac{1}{16}(\alpha^2\delta^2 + \beta^2\gamma^2)X + \frac{1}{16}\beta^2\delta^2Y.$ |
| $AAbb \times aaBB$ | 2 | $F_{n+1} = \frac{1}{16}\beta^2\delta^2W + \frac{1}{16}(\alpha^2\delta^2 + \beta^2\gamma^2)X + \frac{1}{16}\alpha^2\gamma^2Y.$ |
| $AABB \times AAbb$ | 8 | $G_{n+1} = \frac{1}{16}(\alpha\beta + \gamma\delta)(U + V) + \frac{1}{16}\alpha\beta\gamma\delta(W + 2X + Y).$ |
| $AABB \times AABB$ | 8 | $H_{n+1} = \frac{1}{2}H + \frac{1}{4}(\alpha\beta + \gamma\delta)(L + N) + \frac{1}{8}R + \frac{1}{16}(\alpha^2 + 2\alpha\beta + \gamma^2 + 2\gamma\delta)U + \frac{1}{16}(2\alpha\beta + \beta^2 + 2\gamma\delta + \delta^2)V + \frac{1}{16}\alpha\gamma(\alpha\delta + \beta\gamma)W + \frac{1}{16}(\alpha\gamma + \beta\delta)(\alpha\delta + \beta\gamma)X + \frac{1}{16}\beta\delta(\alpha\delta + \beta\gamma)Y.$ |
| $AAbb \times AAbb$ | 8 | $I_{n+1} = \frac{1}{2}I + \frac{1}{4}(\alpha\beta + \gamma\delta)(M + P) + \frac{1}{8}S + \frac{1}{16}(2\alpha\beta + \beta^2 + 2\gamma\delta + \delta^2)U + \frac{1}{16}(\alpha^2 + 2\alpha\beta + \gamma^2 + 2\gamma\delta)V + \frac{1}{16}\beta\delta(\alpha\delta + \beta\gamma)W + \frac{1}{16}(\alpha\gamma + \beta\delta)(\alpha\delta + \beta\gamma)X + \frac{1}{16}\alpha\gamma(\alpha\delta + \beta\gamma)Y.$ |
| $AABB \times Aabb$ | 8 | $J_{n+1} = \frac{1}{16}(\alpha^2 + \gamma^2)U + \frac{1}{16}(\beta^2 + \delta^2)V + \frac{1}{16}\alpha\gamma(\alpha\delta + \beta\gamma)W + \frac{1}{16}(\alpha\gamma + \beta\delta)(\alpha\delta + \beta\gamma)X + \frac{1}{16}\beta\delta(\alpha\delta + \beta\gamma)Y.$ |
| $AAbb \times AaBB$ | 8 | $K_{n+1} = \frac{1}{16}(\beta^2 + \delta^2)U + \frac{1}{16}(\alpha^2 + \gamma^2)V + \frac{1}{16}\beta\delta(\alpha\delta + \beta\gamma)W + \frac{1}{16}(\alpha\gamma + \beta\delta)(\alpha\delta + \beta\gamma)X + \frac{1}{16}\alpha\gamma(\alpha\delta + \beta\gamma)Y.$ |
| $AABB \times AB.ab$ | 4 | $L_{n+1} = \frac{1}{4}(\alpha^2 + \gamma^2)L + \frac{1}{4}(\beta^2 + \delta^2)N + \frac{1}{8}(\alpha^2 + \gamma^2)U + \frac{1}{8}(\beta^2 + \delta^2)V + \frac{1}{8}\alpha^2\gamma^2W + \frac{1}{8}(\alpha^2\delta^2 + \beta^2\gamma^2)X + \frac{1}{8}\beta^2\delta^2Y.$ |
| $AAbb \times Ab.aB$ | 4 | $M_{n+1} = \frac{1}{4}(\alpha^2 + \gamma^2)M + \frac{1}{4}(\alpha^2 + \delta^2)P + \frac{1}{8}(\beta^2 + \delta^2)U + \frac{1}{8}(\alpha^2 + \gamma^2)V + \frac{1}{8}\beta^2\delta^2W + \frac{1}{8}(\alpha^2\delta^2 + \beta^2\gamma^2)X + \frac{1}{8}\alpha^2\gamma^2Y.$ |

| Typical mating | Number of types | |
|-----------------------------|-----------------|--|
| <i>AABB</i> × <i>Ab.aB</i> | 4 | $N_{n+1} = \frac{1}{8}R + \frac{1}{8}(\alpha\beta + \gamma\delta)(U+V) + \frac{1}{8}\alpha\beta\gamma\delta(W+2X+Y).$ |
| <i>AAbb</i> × <i>AB.ab</i> | 4 | $P_{n+1} = \frac{1}{8}S + \frac{1}{8}(\alpha\beta + \gamma\delta)(U+V) + \frac{1}{8}\alpha\beta\gamma\delta(W+2X+Y).$ |
| <i>AABb</i> × <i>AAABb</i> | 4 | $Q_{n+1} = 2G + \frac{1}{2}(H+I+J+K) + \frac{1}{4}(\alpha^2 + \gamma^2)(L+M) + \frac{1}{4}(\beta^2 + \delta^2)(N+P) + \frac{1}{4}Q + \frac{1}{8}(R+S+T) + \frac{1}{8}(\alpha^2 + \alpha\beta + \beta^2 + \gamma^2 + \gamma\delta + \delta^2)(U+V) + \frac{1}{16}(\alpha\delta + \beta\gamma)^2(W+Y) + \frac{1}{8}(\alpha\gamma + \beta\delta)^2X.$ |
| <i>AABb</i> × <i>AaBB</i> | 4 | $R_{n+1} = \frac{1}{4}(\beta^2 + \delta^2)L + \frac{1}{4}(\alpha^2 + \gamma^2)N + \frac{1}{8}R + \frac{1}{8}(\beta + \delta)U + \frac{1}{8}(\alpha + \gamma)V + \frac{1}{16}(\alpha\delta + \beta\gamma)^2(W+Y) + \frac{1}{8}(\alpha\gamma + \beta\delta)^2X.$ |
| <i>AABb</i> × <i>Aabb</i> | 4 | $S_{n+1} = \frac{1}{4}(\beta^2 + \delta^2)M + \frac{1}{4}(\alpha^2 + \gamma^2)P + \frac{1}{8}S + \frac{1}{8}(\alpha + \gamma)U + \frac{1}{8}(\beta + \delta)V + \frac{1}{16}(\alpha\delta + \beta\gamma)^2(W+Y) + \frac{1}{8}(\alpha\gamma + \beta\delta)^2X.$ |
| <i>AABb</i> × <i>aaBb</i> | 4 | $T_{n+1} = \frac{1}{8}(\alpha\beta + \gamma\delta)(U+V) + \frac{1}{16}(\alpha\delta + \beta\gamma)^2(W+Y) + \frac{1}{8}(\alpha\gamma + \beta\delta)^2X.$ |
| <i>AABb</i> × <i>AB.ab</i> | 8 | $U_{n+1} = \frac{1}{2}J + \frac{1}{4}(\alpha\beta + \gamma\delta)(L+N) + \frac{1}{8}(S+T) + \frac{1}{8}(\alpha + \gamma)U + \frac{1}{8}(\beta + \delta)V + \frac{1}{8}\alpha\gamma(\beta\gamma + \alpha\delta)W + \frac{1}{8}(\alpha\gamma + \beta\delta)(\alpha\delta + \beta\gamma)X + \frac{1}{8}\beta\delta(\beta\gamma + \alpha\delta)Y.$ |
| <i>AABb</i> × <i>Ab.aB</i> | 8 | $V_{n+1} = \frac{1}{2}K + \frac{1}{4}(\alpha\beta + \gamma\delta)(M+P) + \frac{1}{8}(R+T) + \frac{1}{8}(\beta + \delta)U + \frac{1}{8}(\alpha + \gamma)V + \frac{1}{8}\beta\delta(\beta\gamma + \alpha\delta)W + \frac{1}{8}(\alpha\gamma + \beta\delta)(\alpha\delta + \beta\gamma)X + \frac{1}{8}\alpha\gamma(\beta\gamma + \alpha\delta)Y.$ |
| <i>AB.ab</i> × <i>AB.ab</i> | 1 | $W_{n+1} = 2(E+J) + \frac{1}{2}(\alpha^2 + \gamma^2)L + \frac{1}{2}(\beta^2 + \delta^2)N + \frac{1}{4}(S+T) + \frac{1}{4}(\alpha^2 + \gamma^2)U + \frac{1}{4}(\beta^2 + \delta^2)V + \frac{1}{4}\alpha^2\gamma^2W + \frac{1}{4}(\alpha^2\delta^2 + \beta^2\gamma^2)X + \frac{1}{4}\beta^2\delta^2Y.$ |
| <i>AB.ab</i> × <i>Ab.aB</i> | 2 | $X_{n+1} = \frac{1}{2}T + \frac{1}{2}(\alpha\beta + \gamma\delta)(U+V) + \frac{1}{2}\alpha\beta\gamma\delta(W+2X+Y).$ |
| <i>Ab.aB</i> × <i>Ab.aB</i> | 1 | $Y_{n+1} = 2(F+K) + \frac{1}{2}(\alpha^2 + \gamma^2)M + \frac{1}{2}(\beta^2 + \delta^2)P + \frac{1}{4}(R+T) + \frac{1}{4}(\beta^2 + \delta^2)U + \frac{1}{4}(\alpha^2 + \gamma^2)V + \frac{1}{4}\beta^2\delta^2W + \frac{1}{4}(\alpha^2\delta^2 + \beta^2\gamma^2)X + \frac{1}{4}\alpha^2\gamma^2Y.$ |

Now let $c_n = C_n - D_n$, $d_n = E_n - F_n$, $e_n = H_n - I_n$, $f_n = J_n - K_n$, $g_n = L_n - M_n$, $h_n = N_n - P_n$, $i_n = R_n - S_n$, $j_n = U_n - V_n$, $k_n = W_n - Y_n$.

Hence we have the equations (3.2):

$$\begin{aligned}
 c_{n+1} &= c_n + e_n + \frac{1}{4}(\alpha^2 + \gamma^2)g_n + \frac{1}{4}(\beta^2 + \delta^2)h_n + \frac{1}{8}i_n + \frac{1}{8}(\alpha - \beta + \gamma - \delta)j_n \\
 &\quad + \frac{1}{16}(\alpha^2\gamma^2 - \beta^2\delta^2)k_n. \\
 d_{n+1} &= \frac{1}{16}(\alpha^2\gamma^2 - \beta^2\delta^2)k_n. \\
 e_{n+1} &= \frac{1}{2}e_n + \frac{1}{4}(\alpha\beta + \gamma\delta)(g_n + h_n) + \frac{1}{8}i_n + \frac{1}{16}(\alpha - \beta + \gamma - \delta)j_n \\
 &\quad + \frac{1}{16}(\alpha\gamma - \beta\delta)(\alpha\delta + \beta\gamma)k_n. \\
 f_{n+1} &= \frac{1}{16}(\alpha - \beta + \gamma - \delta)j_n + \frac{1}{16}(\alpha\gamma - \beta\delta)(\alpha\delta + \beta\gamma)k_n. \\
 g_{n+1} &= \frac{1}{4}(\alpha^2 + \gamma^2)g_n + \frac{1}{4}(\beta^2 + \delta^2)h_n + \frac{1}{8}(\alpha - \beta + \gamma - \delta)j_n + \frac{1}{8}(\alpha^2\gamma^2 - \beta^2\delta^2)k_n. \\
 h_{n+1} &= \frac{1}{8}i_n. \\
 i_{n+1} &= \frac{1}{4}(\beta^2 + \delta^2)g_n + \frac{1}{4}(\alpha^2 + \gamma^2)h_n + \frac{1}{8}i_n - \frac{1}{8}(\alpha - \beta + \gamma - \delta)j_n. \\
 j_{n+1} &= \frac{1}{2}f_n + \frac{1}{4}(\alpha\beta + \gamma\delta)(g_n + h_n) - \frac{1}{8}i_n + \frac{1}{8}(\alpha - \beta + \gamma - \delta)j_n \\
 &\quad + \frac{1}{8}(\alpha\gamma - \beta\delta)(\alpha\delta + \beta\gamma)k_n. \\
 k_{n+1} &= 2(d_n + f_n) + \frac{1}{2}(\alpha^2 + \gamma^2)g_n + \frac{1}{2}(\beta^2 + \delta^2)h_n - \frac{1}{4}i_n + \frac{1}{4}(\alpha - \beta + \gamma - \delta)j_n \\
 &\quad + \frac{1}{4}(\alpha^2\gamma^2 - \beta^2\delta^2)k_n.
 \end{aligned}$$

When $n=0$, $E_0 = 1 \therefore d_0 = 1$, the other terms being zero.

When $n = \infty$, $C_\infty + D_\infty = 1$, and c_∞ is finite, the other terms being zero.

We now have to find $\xi, \eta, \theta, \kappa, \lambda, \mu, \nu, \phi$ so that:

$$c_{n+1} + \zeta d_{n+1} + \eta e_{n+1} + \theta f_{n+1} + \kappa g_{n+1} + \lambda h_{n+1} + \mu i_{n+1} + \nu j_{n+1} + \phi k_{n+1} \\ \equiv c_n + \zeta d_n + \eta e_n + \theta f_n + \kappa g_n + \lambda h_n + \mu i_n + \nu j_n + \phi k_n.$$

The conditions for this to be the case are equations (3.3)

$$\zeta = 2\phi$$

$$\eta = 1 + \frac{1}{2}\eta$$

$$\theta = \frac{1}{2}\nu + 2\phi$$

$$\kappa = \frac{1}{4}(\alpha^2 + \gamma^2)(1 + \kappa + 2\phi) + \frac{1}{4}(\beta^2 + \delta^2)\mu + \frac{1}{4}(\alpha\beta + \gamma\delta)(\eta + \nu).$$

$$\lambda = \frac{1}{4}(\beta^2 + \delta^2)(1 + \kappa + 2\phi) + \frac{1}{4}(\alpha^2 + \gamma^2)\mu + \frac{1}{4}(\alpha\beta + \gamma\delta)(\eta + \nu).$$

$$\mu = \frac{1}{8}(1 + \eta + \lambda + \mu - \nu - 2\phi).$$

$$\nu = \frac{1}{8}(\alpha - \beta + \gamma - \delta)(2 + \eta + \theta + 2x - 2\mu + 2\nu + 4\phi).$$

$$\phi = \frac{1}{16}(\alpha^2\gamma^2 - \beta^2\delta^2)(1 + \zeta + 2\kappa + 4\phi) + \frac{1}{16}(\alpha\gamma - \beta\delta)(\alpha\delta + \beta\gamma)(\eta + \theta + 2\nu).$$

We eliminate $\eta=2$, and $\phi = \frac{1}{2}\zeta$. We also subtract and add together the fourth and fifth of these equations. We put $x = \frac{1}{2}(\beta + \delta)$, the average cross-over value, and also $y = \frac{1}{2}(\alpha\beta + \gamma\delta)$, $z = \alpha\gamma + \beta\delta$, $q = \frac{1}{2} - x$. Hence:

$$2\theta = \nu + 2\zeta.$$

$$\kappa - \lambda = q(1 + \zeta + \kappa - \mu).$$

$$2\kappa + 2\lambda = 1 + y + (1 - y)(\zeta + \kappa) + y\nu.$$

$$7\mu = 3 - \zeta + \lambda - \nu.$$

$$8\nu = q(3 + 2\zeta + \theta + 2\kappa - 2\mu + 2\nu).$$

$$4\zeta = q(3 + \theta + 2\nu) - qz(2 + 3\zeta - \theta + 2\kappa - 2\nu).$$

Omitting some rather tedious algebra, the solution of these equations is:

$$\zeta = \frac{q}{2 - 3q}, \quad \theta = \frac{2q}{2 - 3q}, \quad \kappa = \frac{1}{2 - 3q}, \\ \lambda = \frac{1 - 2q}{2 - 3q}, \quad \mu = \frac{1 - 2q}{2 - 3q}, \quad \nu = \frac{2q}{2 - 3q}$$

as may easily be verified.

$$\therefore c_\infty = c_n + 2c_n + \frac{1}{1 + 6x} [(1 - 2x)(d_n + 2f_n + 2j_n + \frac{1}{2}k_n) \\ + 2g_n + 4x(h_n + i_n)] \tag{3.4}$$

and $y = \frac{1}{2}(1 - c_\infty)$.

In the case considered, $d_0 = 1$, $\therefore c_\infty = \zeta d_0 = 1 - 2x/1 + 6x$. Hence the proportion of crossover zygotes, $y = 4x/1 + 6x$ (3.5).

This is plotted in figure 1. If there is 50 percent crossing over in both sexes, $x = \frac{1}{2}$, $y = \frac{1}{2}$. If there is 50 percent in one sex, and none in the other, $x = \frac{1}{4}$, $y = 5/12$, that is 5/12 only of the zygotes are crossovers.

To solve the equations (3.1) completely, we require, besides the equations (3.2), a group of 13 equations for $C_n + D_n$, etc. and also for the symmetrical terms G_n , Q_n , T_n , and X_n . The full expression for D_n is the sum of a constant term with the n th terms of 19 geometrical series. Their ratios are $\frac{1}{2}$ and the irrational roots of two algebraic equations of the 7th and 11th degrees. These equations can, in part at least, be reduced to quartics, but at least one quartic is irreducible. Hence only numerical calculation is practicable.

PARENTS AND OFFSPRING MATING. SEX-LINKED GENES

In this system of mating a father is mated to his own daughter, a son of this union to his mother and subsequently to his daughter, and so on indefinitely. JENNINGS (1917) has dealt with it in the case of unlinked genes. We consider the results of inbreeding where the matings $AABB \times ab$ and $aabb \times AB$ are made in equal numbers and the daughters (assuming the female sex to be homogametic) backcrossed to the fathers. If the sons were backcrossed to their mothers they would of course give 100 percent non-crossover homozygotes at once. The result of the cross considered, between fathers and F_1 daughters, is the same as if the F_1 were crossed with one another, and their children (F_2) backcrossed to parents. It will be shown later that this latter procedure gives the maximum of crossing over of autosomal genes. The case is fairly simple, since many types of mating are impossible after the first generation. For example $aabb$ mothers have only ab sons. β is the crossover proportion, and $\alpha = 1 - \beta$.

| Typical mating | Number of types | | |
|-------------------|-----------------|---|---------|
| $AABB \times AB$ | 2 | $C_{n+1} = C_n + \frac{1}{2}E_n + \frac{1}{4}\alpha G_n + \frac{1}{4}\beta J_n.$ | } (4.1) |
| $AAbb \times Ab$ | 2 | $D_{n+1} = D_n + \frac{1}{2}F_n + \frac{1}{4}\alpha H_n + \frac{1}{4}\beta I_n.$ | |
| $AABb \times AB$ | 4 | $E_{n+1} = \frac{1}{2}E_n + \frac{1}{4}F_n + \frac{1}{4}\beta G_n + \frac{1}{4}\alpha J_n.$ | |
| $AABb \times Ab$ | 4 | $F_{n+1} = \frac{1}{4}E_n + \frac{1}{2}F_n + \frac{1}{4}\beta H_n + \frac{1}{4}\alpha I_n.$ | |
| $AB.ab \times AB$ | 2 | $G_{n+1} = \frac{3}{4}\alpha G_n + \frac{1}{2}\alpha I_n + \frac{1}{4}\beta J_n.$ | |
| $Ab.aB \times Ab$ | 2 | $H_{n+1} = \frac{3}{4}\alpha H_n + \frac{1}{4}\beta I_n + \frac{1}{2}\beta J_n.$ | |
| $AB.ab \times Ab$ | 2 | $I_{n+1} = \frac{1}{2}\beta(G_n + I_n).$ | |
| $Ab.aB \times AB$ | 2 | $J_{n+1} = \frac{1}{2}\beta(H_n + J_n).$ | |

Putting $c_n = C_n - D_n$, $d_n = E_n - F_n$, $e_n = G_n - H_n$, $f_n = I_n - J_n$

$$\left. \begin{aligned} \therefore c_{n+1} &= c_n + \frac{1}{2}d_n + \frac{1}{4}\alpha e_n - \frac{1}{4}\beta f_n \\ d_{n+1} &= \frac{1}{4}d_n + \frac{1}{4}\beta e_n - \frac{1}{4}\alpha f_n \\ e_{n+1} &= \frac{3}{4}\alpha e_n + \frac{3}{4}(2\alpha - \beta)f_n \\ f_{n+1} &= \frac{1}{2}\beta(e_n + f_n) \end{aligned} \right\} (4.2)$$

Put $c_{n+1} + \zeta d_{n+1} + \eta e_{n+1} + \theta f_{n+1} \equiv c_n + \zeta d_n + \eta e_n + \theta f_n$.

$$\left. \begin{aligned} \therefore \zeta &= \frac{1}{2} + \frac{1}{4}\zeta \\ \eta &= \frac{1}{4}\alpha + \frac{1}{4}\beta\zeta + \frac{3}{4}\alpha\eta + \frac{1}{2}\beta\theta \\ \theta &= -\frac{1}{4}\beta - \frac{1}{4}\alpha\zeta + \frac{1}{4}(2\alpha - \beta)\eta + \frac{1}{2}\beta\theta \end{aligned} \right\} \quad (4.3)$$

Putting $\beta = x$,

$$\begin{aligned} \zeta &= \frac{2}{3}, \quad \eta = \frac{6 - 7x}{3(2 + 3x)}, \quad \theta = \frac{2 - 9x}{3(2 + 3x)} \\ \therefore c_\infty &= c_n + \frac{2}{3}d_n + \frac{(6 - 7x)e_n + (2 - 9x)f_n}{3(2 + 3x)}. \end{aligned} \quad (4.4)$$

In the case considered $e_1 = G_1 = 1$

$$\begin{aligned} \therefore c_\infty &= \frac{6 - 7x}{6 + 9x} \\ \therefore y &= \frac{8x}{6 + 9x}. \end{aligned} \quad (4.5)$$

Hence with 50 percent crossing over in the homogametic sex the final proportion of crossover zygotes is $8/21$. If both sexes of F_1 are crossed back to the parents,

$$y = \frac{4x}{6 + 9x}.$$

In this case it is quite possible to solve the equations (4.1) completely. C_n differs from C_∞ by the sum of six terms of geometric series, whose ratios are

$$\frac{1}{4}, \frac{3}{4}, \frac{2x \pm \sqrt{9 - 26x + 19x^2}}{4}, \frac{2x \pm \sqrt{9 - 26x + 23x^2}}{4}.$$

Even here however the expression is rather complicated.

PARENT AND OFFSPRING MATING. AUTOSOMAL GENES

The mating system is the same as in the last case, except that both sons and daughters in F_1 are crossed back to the parents. This case has been considered, for unlinked genes, by both JENNINGS (1917) and WRIGHT (1921b). If 100β and 100δ are the crossover percentages, and $\alpha + \beta = \gamma + \delta = 1$, we arrive at equations (5.1).

| Typical mating | Number of types | |
|-----------------------------|-----------------|--|
| <i>AABB</i> × <i>AABB</i> | 2 | $C_{n+1} = C + F + \frac{1}{4}(\alpha + \gamma)J + \frac{1}{4}(\beta + \delta)L.$ |
| <i>AAbb</i> × <i>AAbb</i> | 2 | $D_{n+1} = D + G + \frac{1}{4}(\alpha + \gamma)K + \frac{1}{4}(\beta + \delta)M.$ |
| <i>AABb</i> × <i>AABb</i> | 4 | $E_{n+1} = \frac{1}{2}(E + F + G) + \frac{1}{4}(H + I + N + P).$ |
| <i>AABB</i> × <i>AAbb</i> | 8 | $F_{n+1} = \frac{1}{8}E + \frac{1}{2}F + \frac{1}{8}H + \frac{1}{8}(\beta + \delta)J + \frac{1}{8}(\alpha + \gamma)L + \frac{1}{16}(\alpha + \gamma)N + \frac{1}{16}(\beta + \delta)P.$ |
| <i>AAbb</i> × <i>AABb</i> | 8 | $G_{n+1} = \frac{1}{8}E + \frac{1}{2}G + \frac{1}{8}I + \frac{1}{8}(\beta + \delta)K + \frac{1}{8}(\alpha + \gamma)M + \frac{1}{16}(\beta + \delta)N + \frac{1}{16}(\alpha + \gamma)P.$ |
| <i>AABb</i> × <i>AaBB</i> | 4 | $H_{n+1} = \frac{1}{4}H + \frac{1}{8}(\beta + \delta)N + \frac{1}{8}(\alpha + \gamma)P.$ |
| <i>AABb</i> × <i>Aabb</i> | 4 | $I_{n+1} = \frac{1}{4}I + \frac{1}{8}(\alpha + \gamma)N + \frac{1}{8}(\beta + \delta)P.$ |
| <i>AABB</i> × <i>AB.ab</i> | 4 | $J_{n+1} = \frac{1}{4}(\alpha + \gamma)J + \frac{1}{8}(\beta + \delta)L + \frac{1}{8}(\alpha + \gamma)N + \frac{1}{8}\alpha\gamma Q + \frac{1}{16}(\alpha\delta + \beta\gamma)R.$ |
| <i>AAbb</i> × <i>Ab.aB</i> | 4 | $K_{n+1} = \frac{1}{4}(\alpha + \gamma)K + \frac{1}{8}(\beta + \delta)M + \frac{1}{8}(\alpha + \gamma)P + \frac{1}{8}\alpha\gamma S + \frac{1}{16}(\alpha\delta + \beta\gamma)R.$ |
| <i>AABB</i> × <i>Ab.aB</i> | 4 | $L_{n+1} = \frac{1}{8}(\beta + \delta)(L + P) + \frac{1}{16}(\alpha\delta + \beta\gamma)R + \frac{1}{8}\beta\delta S.$ |
| <i>AAbb</i> × <i>AB.ab</i> | 4 | $M_{n+1} = \frac{1}{8}(\beta + \delta)(M + N) + \frac{1}{16}(\alpha\delta + \beta\gamma)R + \frac{1}{8}\beta\delta Q.$ |
| <i>AABb</i> × <i>AB.ab</i> | 8 | $N_{n+1} = \frac{1}{8}I + \frac{1}{8}(\beta + \delta)J + \frac{1}{8}(\alpha + \gamma)M + \frac{1}{16}(4 + \alpha + \gamma)N + \frac{1}{16}(\beta + \delta)P + \frac{1}{8}(\alpha\delta + \beta\gamma)Q + \frac{1}{16}(\alpha\gamma + \beta\delta)R.$ |
| <i>AABb</i> × <i>Ab.aB</i> | 8 | $P_{n+1} = \frac{1}{8}H + \frac{1}{8}(\beta + \delta)K + \frac{1}{8}(\alpha + \gamma)L + \frac{1}{16}(4 + \alpha + \gamma)P + \frac{1}{16}(\beta + \delta)N + \frac{1}{8}(\alpha\delta + \beta\gamma)S + \frac{1}{16}(\alpha\gamma + \beta\delta)R.$ |
| <i>AB.ab</i> × <i>AB.ab</i> | 1 | $Q_{n+1} = \frac{1}{2}(\alpha + \gamma)(J + N) + \frac{1}{2}\alpha\gamma Q + \frac{1}{4}(\alpha\delta + \beta\gamma)R.$ |
| <i>AB.ab</i> × <i>Ab.aB</i> | 2 | $R_{n+1} = \frac{1}{4}(\beta + \delta)(L + M + N + P) + \frac{1}{4}\beta\delta(Q + S) + \frac{1}{4}(\alpha\delta + \beta\gamma)R.$ |
| <i>Ab.aB</i> × <i>Ab.aB</i> | 1 | $S_{n+1} = \frac{1}{2}(\alpha + \gamma)(K + P) + \frac{1}{2}\alpha\gamma S + \frac{1}{4}(\alpha\delta + \beta\gamma)R.$ |

Let $c_n = C_n - D_n$, $d_n = F_n - G_n$, $e_n = H_n - I_n$, $f_n = J_n - K_n$, $g_n = L_n - M_n$, $h_n = N_n - P_n$, $i_n = Q_n - S_n$. Let $\beta + \delta = 2x$, $\beta\delta = p$.

$$\begin{aligned} \therefore c_{n+1} &= c_n + d_n + \frac{1}{2}(1-x)f_n + \frac{1}{2}xg_n. \\ d_{n+1} &= \frac{1}{2}d_n + \frac{1}{8}c_n + \frac{1}{4}xf_n + \frac{1}{4}(1-x)g_n + \frac{1}{8}(1-2x)h_n. \\ e_{n+1} &= \frac{1}{4}e_n - \frac{1}{4}(1-2x)h_n. \\ f_{n+1} &= \frac{1}{2}(1-x)f_n + \frac{1}{4}xg_n + \frac{1}{4}(1-x)h_n + \frac{1}{8}(1-2x+p)i_n. \\ g_{n+1} &= \frac{1}{4}x(g_n - h_n) - \frac{1}{8}pi_n. \\ h_{n+1} &= -\frac{1}{8}e_n + \frac{1}{4}xf_n - \frac{1}{4}(1-x)g_n + \frac{1}{8}(3-2x)h_n + \frac{1}{4}(x-p)i_n. \\ i_{n+1} &= (1-x)(f_n + h_n) + \frac{1}{2}(1-2x+p)i_n. \end{aligned} \quad (5.2)$$

In order to have $c_n + \zeta d_n + \eta e_n + \theta f_n + \kappa g_n + \lambda h_n + \mu i_n$ independent of n , it is necessary that:

$$\begin{aligned} \zeta &= 1 + \frac{1}{2}\zeta. \\ \eta &= \frac{1}{8}\zeta + \frac{1}{4}\eta - \frac{1}{8}\lambda. \\ \theta &= \frac{1}{2}(1-x) + \frac{1}{4}x\zeta + \frac{1}{2}(1-x)\theta + \frac{1}{4}x\lambda + (1-x)\mu. \\ \kappa &= \frac{1}{2}x + \frac{1}{4}(1-x)\zeta + \frac{1}{4}x(\theta + \kappa) - \frac{1}{4}(1-x)\lambda. \\ \lambda &= \frac{1}{8}(1-2x)\zeta - \frac{1}{4}(1-2x)\eta + \frac{1}{4}(1-x)\theta - \frac{1}{4}x\kappa + \frac{1}{8}(3-2x)\lambda + (1-x)\mu. \\ \mu &= \frac{1}{8}(1-2x+p)\theta - \frac{1}{8}p\kappa + \frac{1}{4}(x-p)\lambda + \frac{1}{2}(1-2x+p)\mu. \end{aligned} \quad (5.3)$$

$$\text{Hence } \zeta = 2, \eta = \frac{2x}{1+4x}, \theta = \frac{2}{1+4x}, \kappa = \frac{4x}{1+4x}, \lambda = \frac{2(1-2x)}{1+4x},$$

$$\mu = \frac{1-2x}{1+4x},$$

as may readily be verified.

$$\therefore c_\infty = c_n + 2d_n + \frac{1}{1+4x} [2f_n + 2x(e_n + 2g_n) + (1-2x)(2h_n + i_n)] \quad (5.4)$$

In the case considered $J_0 = f_0 = \frac{1}{2} \therefore c_\infty = 1/1+4x$

$$\therefore y = \frac{2x}{1+4x} \quad (5.5)$$

Hence with 50 percent crossing over in both sexes, $y = \frac{1}{3}$, with 50 percent crossing over in one only, $y = \frac{1}{4}$. In order to obtain the maximum proportion of crossovers, we should mate F_1 *inter se*, and then mate F_2 back to F_1 of the opposite sex. In this case

$$Q_1 = i_1 = 2, \text{ so } c_\infty = \frac{1-2x}{1+4x}, \text{ and } y = \frac{3x}{1+4x}.$$

Hence when $x = \frac{1}{2}$, $y = \frac{1}{2}$, and with 50 percent crossing over in one sex only, $y = \frac{3}{8}$. The approach to equilibrium involves the solution of equations (5.2) and a set of nine similar equations for $C_n + D_n$, etc. along with E_n and R_n . C_n differs from C_∞ by the sum of terms from 14 geometric series.

INBREEDING WITH ANY INITIAL POPULATION

The five systems of equations (1.1), (2.1), (3.1), (4.1) and (5.1) are true whatever be the initial composition of the population, provided that it contains the genes $A, a, B,$ and b in equal numbers. This is not in general so. But we can render any population symmetrical by adding to it three other suitably chosen populations, these latter being added after one generation of inbreeding, so as not to mate with the group first considered. This addition does not affect the proportion of crossover zygotes, and the proportion of the genes is of course unaltered by inbreeding.

An example will make the method clear. We desire to know the final fate of a population consisting of zygotes in the proportion $1AABB:4aBb$, when mating is at random for one generation, and afterwards brothers and sisters only are mated. After one generation we add to it equal numbers of the children of three populations consisting of ($1AABB:4Aabb$), ($1aabb:$

4AABb) and (1aabb:4AaBB). Hence, out of 100 typical matings of the mixed F₁, 2 are AABB × AABB, 2 aabb × aabb, 4 of each of the 8 types exemplified by AABB × aaBb, 16 of each of the 4 types exemplified by AABb × AABb. Dividing by 50, to give a total of 2:

$$c_1 = C_1 = \frac{1}{25}; f_1 = J_1 = \frac{2}{25}; Q_1 = \frac{8}{25}.$$

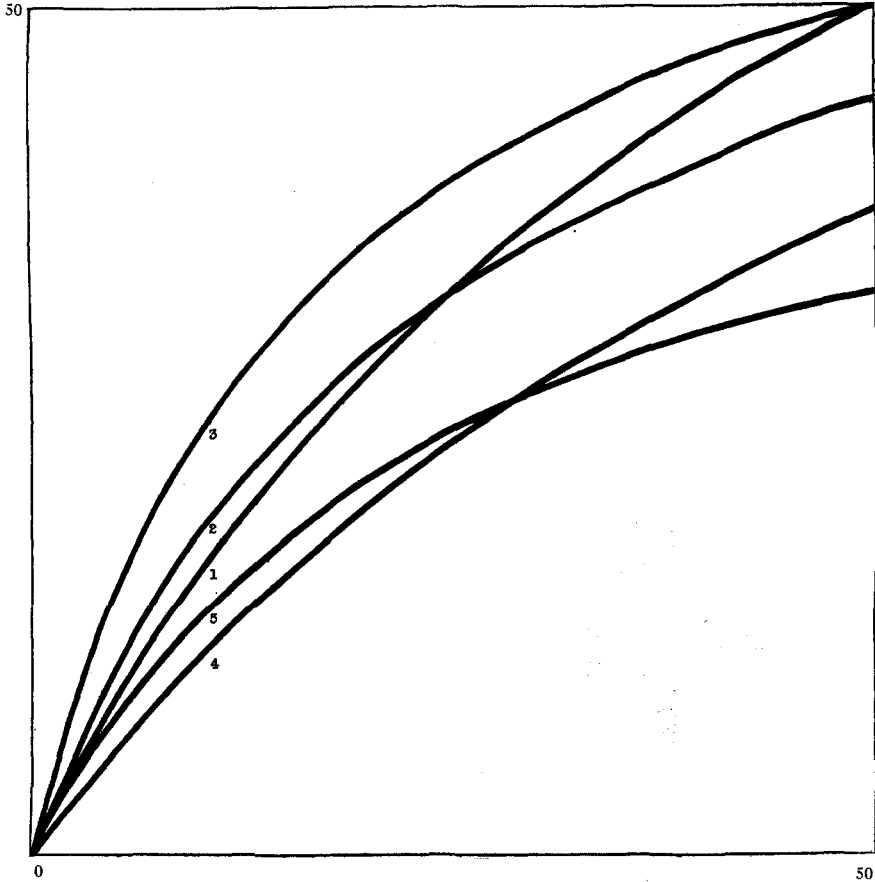


FIGURE 1.—The curves show the percentage of crossover homozygotes at equilibrium (100y), plotted as ordinates against the average crossover value (100x) as abscissa, for the following five systems of mating:

1. Self-fertilization.
2. Brother-sister mating. Sex-linked genes.
3. Brother-sister mating. Autosomal genes.
4. Parent-offspring mating, F₁ daughters backcrossed to father, sex-linked genes.
5. Parent-offspring mating, both F₁ sons and daughters backcrossed to parents, autosomal genes.

Hence by equation (3.4), $c_{\infty} = 1/25 + 2/25 \cdot 2(1 - 2x)/1 + 6x$.

$$\therefore y = \frac{10 + 76x}{25(1 + 6x)}.$$

This is the proportion of crossover zygotes. In the population first considered the ratio $A:a$ is 1:4, that of $B:b$ is 3:2. Hence if $[AABB]$ is the proportion of that type in the final population,

$$[AABB] + [AAbb] = \frac{1}{5}, [AABB] + [aaBB] = \frac{3}{5}, [AAbb] + [aaBB] = y$$

$$\therefore [AABB] = \frac{5 + 22x}{25(1 + 6x)}, [AAbb] = \frac{8x}{25(1 + 6x)},$$

$$[aaBB] = \frac{10 + 68x}{25(1 + 6x)}, [aabb] = \frac{10 + 52x}{25(1 + 6x)}.$$

Similarly the final composition of any other population may be found. It is often more convenient to split it up into groups, and consider each separately. Thus in the above case $1/25$ of the final population is derived from $AABB \times AABB$, that is, is all $AABB$; $16/25$ is derived from the mating $aaBb \times aaBb$, that is, consists of equal numbers of $aaBB$ and $aabb$; $8/25$ is derived from $AABb \times aaBb$, and the reciprocal cross. This gives all four zygotic types in proportions depending on the value of x . It is quite possible to form equations for the results of breeding from a population containing arbitrary numbers of each of the 20 zygotic types, but the expressions obtained are neither short nor elegant.

DOUBLE CROSSING OVER

Consider the inbreeding of zygotes ABC/abc , where the 3 genes A, B, C are linked and in that order. Let p be the proportion of crossing over between AB (that is, $100p$ the crossover value), and let q, r be the same proportions for BC, AC . Then the proportion of double crossovers is obviously $\frac{1}{2}(p+q-r)$. Similarly if, after inbreeding, the proportions of crossover zygotes are $f(p), f(q), f(r)$, the proportion of double crossover zygotes, that is, $aaBBcc$ and $AAbbCC$, is $\frac{1}{2}[f(p)+f(q)-f(r)]$. Now $f(p)$ is always of the form $kp/1+lp$. Hence we have, for the proportion Z of double crossovers,

$$2Z = \frac{kp}{1+lp} + \frac{kq}{1+lq} + \frac{kr}{1+lr}$$

$$\therefore Z = \frac{k(p+q-r+2lpq+l^2pqr)}{2(1+lp)(1+lq)(1+lr)}.$$

Now $\frac{1}{2}(p+q-r)$ is the proportion of gametic double crossovers, and therefore smaller than pq , owing to interference, unless p and q are quite large. Hence since $l > 1$ the last two terms in the nominator are the most important. When p and q are small, r is practically equal to their sum, and $Z = klpq$, approximately.

That is to say whereas the proportion of single gametic crossovers is k times the corresponding gametic value when the latter is small, the proportion of zygotic double crossovers is kl times the proportion of gametic double crossovers calculated if there were no interference, and many more times the real value. The values of k and kl , collected from equations (1.3), (2.5), (3.5), (4.5), (5.5) and their modifications, are given in table 2.

TABLE 2

| TYPE OF INBREEDING | TYPE OF LINKAGE | k | kl |
|---|-----------------|-----|------|
| Self-fertilization | Autosomal | 2 | 4 |
| Brother-sister mating | Autosomal | 4 | 24 |
| Brother-sister mating | Sex-linked | 8/3 | 32/3 |
| Parent-offspring mating | Autosomal | 2 | 8 |
| Parent-offspring mating after F_1 | Autosomal | 3 | 12 |
| Parent-offspring mating both ways | Sex-linked | 2/3 | 1 |
| Parent-offspring mating father-daughter, or after F_1 | Sex-linked | 4/3 | 2 |

DISCUSSION

The method of calculation here employed cannot be applied to most other types of inbreeding. It is wholly inapplicable to the important case where a male is bred to a large group of his half-sisters in each generation. The case of double first cousin matings with autosomal linkage involves the consideration of 10,000 different pairs of mating types, and other systems are still more complex. It may prove possible to solve such problems by an extension of WRIGHT'S (1921a) correlation method, but we have been unable to do so.

Inbreeding may be undertaken for several purposes. It may be desired to obtain and fix as many types as possible after crossing two different varieties, to obtain a pure line of a desired type, or merely a pure line of any sort. In each case it is desirable to encourage crossing over. If the genetics of the organism concerned are known already, this can doubtless be done by *ad hoc* matings. In general this is not possible. The reason why crossing over, that is, recombination, is desirable in all types of inbreeding is as follows. Hybrid vigor may be due partly to heterozygosis as such, but it is probably also in part due to the presence in the hybrid of dominant

genes contributed by the two parents. If so the vigor of an extracted pure line will depend on the numbers of such dominants which are combined in it. In so far as they are linked, the probability of such a combination will depend on the type of mating practised.

It is clear from table 2 that the differences are very considerable. For example a recombination involving three fairly closely linked genes is about 3 times as likely with brother-sister mating as with parent-offspring mating, and six times as likely as with self-fertilization. In the case of sex-linked genes the probability is over 10 times as great with brother-sister mating as with parent-offspring mating. However the disadvantages of the latter are considerably diminished if instead of beginning it by crossing the F_1 to the parents, the first parent-offspring mating is between F_1 and F_2 . If the ideal genotype requires the occurrence of a number of crossings over the differences between different mating systems are greatly increased.

For example if two pure lines of *Drosophila* whose males are of composition $Ab(CdE/CdE)(FgH/FgH)$, and $aB(cDe/cDe)(fGh/fGh)$, respectively, are crossed, the proportion of pure lines finally containing all the dominants is 0.98 percent with brother-sister mating, 0.0372 percent with unrestricted parent-offspring mating, even when all crossover values are 50 percent.

It is clear then that the proportion of homozygosis reached is not the sole possible criterion of intensity of inbreeding. But the difference between different systems due to the considerations here outlined will be far more intense in an organism with high linkage, such as *Apotettix*, *Lebistes*, *Drosophila*, or *Funaria*, than in one with little linkage, such as a mammal or *Triticum vulgare*.

SUMMARY

Formulae are given for the amount of crossing over which is found in the final population when organisms heterozygous for linked genes are inbred according to various systems.

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