APPLICATIONS OF MATHEMATICS TO BREEDING PROBLEMS II

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INTRODUCTION

Professor H. S. JENNINGS (1916) has published the numerical results for a variety of breeding problems.[1] The present writer (ROBBINS 1917) considered some more general problems, suggested in every case by JENNINGS's paper, and showed how results obtained by JENNINGS came by specializing the general problems. This paper dealt only with a typical Mendelian factor.

The present paper is a continuation of this work. In Part I breeding problems will be considered in which a sex-linked character is involved. Part II consists of problems in breeding parents to offspring, a typical Mendelian character being involved. Each of these problems has been suggested by JENNINGS's work.

PART I. BREEDING PROBLEMS INVOLVING SEX-LINKED CHARACTERS

a. Random mating

For a sex-linked character there are but two types of individuals of the heterozygous sex. They may be indicated by A— and a—, while in the homozygous sex the usual three types, AA, Aa, aa, occur.

[1] The paper referred to deals with problems involving one pair of factors. The same author has since published a paper on two factor problems (JENNINGS 1917).

Limiting the discussion to the case in which the male is the heterozygous sex, consider the problem of random mating in a population,

$$\text{Males: } u\,A\text{—} + v\,a\text{—},$$
$$\text{Females: } r\,AA + s\,Aa + t\,aa.$$

with the restriction that $u + v = r + s + t$. This restriction is for convenience rather than from necessity since it is evident that the proportions will be the same if it is omitted and we assume that each male has an equal chance with every other one of fertilizing a female and that a male may mate with more than one female. It should be stated once for all that in any expression for numbers of different types of individuals, or gametes, it is only the ratio of the coefficients that is of interest. We wish to know how the population will be divided between the possible types after n random matings.

The two types of males in any generation, A— and a—, can occur only by unions of the "bar" (—) of the males with the A and a gametes of the females of the preceding generation. For this reason it is essential to count the A and a gametes in the females of each generation. In the original population the female gametes are,

$$(r+s/2)A + (t+s/2)a.$$

It is convenient to use the notation,

1) $$2r+s=M;\ 2t+s=N;\ r+s+t=u+v=K.$$

Then the female gametes in the original population are in the proportion $MA+Na$, and therefore the males of the first generation are represented by $M\,A\text{—}+N\,a\text{—}$. To form a female, the A or a gamete of the male must unite with A or a gamete of the female. The possible ways in which this can occur gives immediately that the three types of females occur in the proportion

$$Mu\,AA + (Mv + Nu)Aa + Nv\,aa.$$

We will uniformly reduce the proportions so that the sum of the coefficients of the types is unity. Thus we have for the first generation:

$$\text{Males: } \frac{M}{2K}A\text{—} + \frac{N}{2K}a\text{—} = u_1\,A\text{—} + v_1\,a\text{—}.$$

$$\text{Females: } \frac{Mu}{2K^2}AA + \frac{Mv+Nu}{2K^2}Aa + \frac{Nv}{2K^2}aa.$$

Similar argument gives the following results for the second and third generations.

Second generation:

$$\text{Males:}\quad \frac{M+2u}{4K}A\text{—} + \frac{N+2v}{4K}a\text{—} \equiv u_2A\text{—} + v_2a\text{—}.$$

$$\text{Females:}\ \frac{M(M+2u)}{8K^2}AA + \frac{M(N+2v)+N(M+2u)}{8K^2}Aa + \frac{N(N+2v)}{8K^2}aa.$$

$$\equiv u_1u_2AA + (u_1v_2 + v_1u_2)Aa + v_1v_2aa.$$

Third generation:

$$\text{Males:}\quad \frac{3M+2u}{8K}A\text{—} + \frac{3N+2v}{8K}a\text{—} \equiv u_3A\text{—} + v_3a\text{—}.$$

$$\text{Females:}\ \frac{(M+2u)(3M+2u)AA}{32K^2} +$$

$$\frac{(M+2u)(3N+2v)+(N+2v)(3M+2u)}{32K^2}Aa + \frac{(N+2v)(3N+2v)}{32K^2}aa$$

$$\equiv u_2u_3AA + (u_2v_3 + v_2u_3)Aa + v_2v_3aa.$$

In the expressions after the identity signs above, u_n and v_n are to indicate the proportions of A— and a— individuals in the nth generation. It is evident from the second form of the expressions for females that the composition of the females in the nth generation can be written down when the compositions of the males for the nth and $(n-1)$th generations are known.

Inspection shows that $u_3 = (u_1+u_2)/2$ and $v_3 = (v_1+v_2)/2$. This fact or at least the data for another generation or two suggests that we have for all values of n,

$$2)\qquad u_n = \frac{u_{n-1}+u_{n-2}}{2};\quad v_n = \frac{v_{n-1}+v_{n-2}}{2}.$$

We shall prove that this is actually the case, and that the females of the nth generation are represented by $r_nAA + s_nAa + t_naa$ if we let

$$4)\qquad \begin{aligned} r_n &= u_nu_{n-1};\\ s_n &= u_nv_{n-1} + v_nu_{n-1};\\ t_n &= v_nv_{n-1}. \end{aligned}$$

We wish to show that random mating in the population

5) Males: $u_nA— + v_na—$,
Females: $r_nAA + s_nAa + t_naa$,

gives a population obtained by replacing n by $n+1$ in 5). The gametic composition of the females in 5) is

$$(r_n+s_n/2)A + (t_n+s_n/2)a.$$

Substituting the values of r_n, s_n, t_n from 4), this becomes

$$(u_nu_{n-1}+\frac{u_nv_{n-1}+v_nu_{n-1}}{2})A + (v_nv_{n-1}+\frac{u_nv_{n-1}+v_nu_{n-1}}{2})a.$$

Simplifying, and remembering that $u_n+v_n = u_{n-1}+v_{n-1} = 1$, we have,

$$\frac{u_n+u_{n-1}}{2}A + \frac{v_n+v_{n-1}}{2}a.$$

Then the males of the $(n+1)$th generation are represented by

$$\frac{u_n+u_{n-1}}{2}A— + \frac{v_n+v_{n-1}}{2}a—.$$

Thus we have shown that $u_{n+1} = (u_n+u_{n-1})/2$ and $v_{n+1} = (v_n+v_{n-1})/2$. As for the females, consideration of the crosses involved gives for $(n+1)$th generation $(u_{n+1}\,u_n)AA + (u_{n+1}v_n + v_{n+1}u_n)Aa + (v_{n+1}v_n)aa$. Thus $r_{n+1} = u_{n+1}\,u_n$; $s_{n+1} = u_{n+1}v_n + v_{n+1}\,u_n$; $t_{n+1} = v_{n+1}\,v_n$. Q. E. D.

So far we have proved that the fractions giving the proportions of the two types of males in any generation are the averages of the corresponding fractions in the two preceding generations. We have explicit expressions for these fractions for only three generations. To get the general expressions we need to solve the recurrence equation,

6) $$u_n = (u_{n-1}+u_{n-2})/2,$$

subject to the conditions, $u_1 = M/2K$; $u_2 = (M+2u)/4K$. This solution is

7) $$u_n = \frac{u+M}{3K} + \frac{2u-M}{3K}\left(-\frac{1}{2}\right)^n.$$

Similarly,

8) $$v_n = \frac{v+N}{3K} + \frac{2v-N}{3K}\left(-\frac{1}{2}\right)^n.$$

From these values of u_n, v_n we can immediately calculate r_n, s_n, t_n by use of equations 4).

Discussion

1. It should be noticed that these results do not depend directly upon

the values of r, s, t, the numbers determining the nature of the original female population. They are, however, clearly dependent upon the gametic composition of the original female population. Otherwise stated, two original female populations, however different, will give the same results providing that the gametic composition of the two is the same.

2. It is well known that for a non-sex-linked character the proportions in random mating are fixed after the first generation. It should be noted that this is not in general the case for a sex-linked character. A special case will be considered presently in which the proportions are fixed.

3. As the number of generations increases, the population approaches a fixed composition in which all types are present except in very special cases:

$$\lim_{n=\infty} u_n = \frac{u+M}{3K}; \quad \lim_{n=\infty} v_n = \frac{v+N}{3K}.$$

$$\lim_{n=\infty} r_n = \left(\frac{u+M}{3K}\right)^2; \quad \lim_{n=\infty} s_n = 2\frac{(u+M)(v+N)}{9K^2}; \quad \lim_{n=\infty} t_n = \left(\frac{v+N}{3K}\right)^2.$$

Some particular cases: The meaning of these formulae will be made clearer by application to particular cases. Let $u = r$, $v = t$, $s = 0$. Then $M \equiv 2r + s = 2r$ and $N \equiv 2t + s = 2t$; $K \equiv r + s + t = r + t$. Substituting in equation 7), 8) and 4),

$$u_n = \frac{u+M}{3K} = \frac{3r}{3(r+t)} = \frac{r}{r+t}; \; v_n = \frac{t}{r+t},$$

$$r_n = \frac{r^2}{(r+t)^2}; \; s_n = \frac{2rt}{(r+t)^2}; \; t_n = \frac{t^2}{(r+t)^2}.$$

These results were obtained by JENNINGS (1916, § 57).

Again, let $s = 1$, $u = 1$, $r = t = v = 0$. Then $M = N = K = 1$. Substituting in 7) and 8),

$$u_n = \tfrac{2}{3} + \tfrac{1}{3} \cdot (-\tfrac{1}{2})^n = \frac{2^{n+1} - (-1)^{n+1}}{3 \times 2^n}$$

$$v_n = \tfrac{1}{3} - \tfrac{1}{3} \cdot (-\tfrac{1}{2})^n = \frac{2^n - (-1)^n}{3 \times 2^n}.$$

It has been shown by the present writer (ROBBINS 1917) that the nth term of JENNINGS's G series (1916, p. 54) is $G_n = \dfrac{2^n - (-1)^n}{3}$

Using this notation we have,

$$u_n = \frac{G_{n+1}}{2^n}; \; v_n = \frac{G_n}{2^n}.$$

Substituting in equations 4) to obtain the numbers for the female population we have

$$r_n = u_n u_{n-1} = \frac{G_{n+1}\, G_n}{2^{2n-1}};$$

$$s_n = u_n v_{n-1} + v_n u_{n-1} = \frac{G_{n+1}G_{n-1} + G_n^2}{2^{2n-1}} = 1 - r_n - t_n;$$

$$t_n = v_n v_{n-1} = \frac{G_n\, G_{n-1}}{2^{2n-1}}.$$

Using $B_n = 2^n$, these expressions check with those obtained by JENNINGS (1916, § 58). Using the formulae above for the limiting values of u_n, v_n, or taking the limits of the expressions obtained for this particular case,

$$\underset{n=\infty}{\text{Limit}}\; u_n = \frac{u+M}{3K} = \tfrac{2}{3}; \quad \underset{n=\infty}{\text{Limit}}\; v_n = \frac{v+N}{3K} = \tfrac{1}{3}.$$

and

$$\underset{n=\infty}{\text{Limit}}\; r_n = \tfrac{4}{9}; \quad \underset{n=\infty}{\text{Limit}}\; s_n = \tfrac{4}{9}; \quad \underset{n=\infty}{\text{Limit}}\; t_n = \tfrac{1}{9}.$$

Equations 7) and 8) show clearly that in general the proportions in random mating are not fixed. We have found a special case, however, in which they are fixed. The question naturally arises, what is the condition that must be satisfied in order that the proportions be fixed? From equation 7) we read immediately that for the proportions to be fixed we must have $2u = M$. This condition is also sufficient since if u_n is constant, $v_n (= 1 - u_n)$ is also constant. In other words, *if in the original population the proportion of dominant males equals the proportion of A gametes in the females, the proportions for random mating are fixed.*

b. Assortative mating

Given the population,

Males: $u\,A\text{—} + v\,a\text{—}$,

Females: $r\,AA + s\,Aa + t\,aa$,

what is the composition of the *n*th generation if *A*— males mate with *AA* and *Aa* females and *a*— males mate with *aa* females? It is at once evident that the values of u and v have nothing to do with the future proportions so long as u and v are not zero. We assume that one male may mate with more than one female.

As in the case of random mating, the two types of males in any generation appear in the same proportion as do the two types of female gametes in the preceding generation. In getting the numbers for females it is essential to remember that for assortative mating there will be $r+s$ dominants to t recessives. It is also convenient to notice that the AA females are in number equal to the A female gametes in the preceding generation and that the proportion of heterozygous females is halved at each succeeding generation. These facts enable one to show very easily that the composition of the nth generation is,

$$\text{Males:}\quad \frac{2^n(r+s)-s}{2^nK}A\text{—} + \frac{s+2^nt}{2^nK}a\text{—};$$

$$\text{Females:}\quad \frac{2^n(r+s)-s}{2^nK}AA + \frac{s}{2^nK}Aa + \frac{t}{K}aa.$$

in which $K = r+s+t$.

Discussion

The heterozygous female tends to disappear and in the limiting population the ratio of the dominants to recessives, in males and females alike, is the ratio of dominants to recessives in the original female population, i.e., $r+s$ to t.

In applying these formulae it should be remembered that in deriving them we assumed that neither u nor v was zero. To apply the formulae with safety it is therefore necessary to study the crosses in detail until both dominant and recessive males appear.

A particular case. Let $r = t = 1$; $s = 2$, and assume the existence of both types of males in the original population. This gives,

$$\text{Males:}\quad \frac{3\times 2^{n-1}-1}{2^{n+1}}A\text{—} + \frac{1+2^{n-1}}{2^{n+1}}a\text{—};$$

$$\text{Females:}\quad \frac{3\times 2^{n-1}-1}{2^{n+1}}AA + \frac{1}{2^{n+1}}Aa + \tfrac{1}{4}\,aa.$$

These are the results obtained by JENNINGS (1916, § 60).

If dominants alone are selected, it can readily be shown that the nth generation has the composition,

$$\text{Males:}\quad \left[1 - \frac{s}{2^n(r+s)}\right]A\text{—} + \frac{s}{2^n(r+s)}a\text{—};$$

Females: $[1 - \frac{s}{2^n(r+s)}]AA + \frac{s}{2^n(r+s)}Aa.$

These formulae may also be obtained from the corresponding ones for mating dominants with dominants, recessives with recessives, by setting $t = 0$.

c. Brother and sister mating

i. Random mating

Given a family consisting of

Males: $u\,A\text{—} + v\,a\text{—}$,

Females: $r\,AA + s\,Aa + t\,aa$,

what will be the composition of the nth generation if matings are restricted to brothers with sisters? It is necessary here to consider the different types of families which will arise. These are tabulated below.

Type of cross	Composition of resulting family		Letter indicating type of family
	Males (A—, a—)	Females (AA, Aa, aa)	
$AA \times A$—	(1, 0)	(1, 0, 0)	b
$Aa \times A$—	(½, ½)	(½, ½, 0)	c
$aa \times A$—	(0, 1)	(0, 1, 0)	d
$AA \times a$—	(1, 0)	(0, 1, 0)	e
$Aa \times a$—	(½, ½)	(0, ½, ½)	f
$aa \times a$—	(0, 1)	(0, 0, 1)	g

If we find the number of families of the different types in the nth generation we can readily count up the number of individuals of different types. Let $b_n, c_n \ldots\ldots g_n$ be the proportion of families of type $b, c, \ldots\ldots g$ respectively in the nth generation, so chosen that $b_n + c_n + d_n + e_n + f_n + g_n = 1$. It is useful to study the outcome of brother and sister mating in families of the various types. This study enables us to write down the following recurrence relations:

9) $4b_n = 4b_{n-1} + c_{n-1}$,

10) $4c_n = c_{n-1} + 4e_{n-1} + f_{n-1}$,

11) $4d_n = f_{n-1}$,

12) $4e_n = c_{n-1}$,

13) $4f_n = 4d_{n-1} + c_{n-1} + f_{n-1}$,

14) $4g_n = 4g_{n-1} + f_{n-1}$.

Using $P_n = K_3(1+\sqrt{5})^n + K_4(1-\sqrt{5})^n$, the solutions of this system of equations are

$$15)\qquad b_n=\frac{1+K_5}{2}-\frac{3K_1+(-1)^nK_2}{3\times 2^{n+2}}-\frac{P_n+P_{n-1}}{4^n}.$$

$$16)\qquad c_n=\frac{K_1+(-1)^nK_2}{2^{n+1}}+\frac{P_n}{4^n}.$$

$$17)\qquad d_n=-\frac{K_1+(-1)^{n-1}K_2}{2^{n+2}}+\frac{P_{n-1}}{4^n}.$$

$$18)\qquad e_n=\frac{K_1+(-1)^{n-1}K_2}{2^{n+2}}+\frac{P_{n-1}}{4^n}.$$

$$19)\qquad f_n=-\frac{K_1+(-1)^nK_2}{2^{n+1}}+\frac{P_n}{4^n}.$$

$$20)\qquad g_n=\frac{1-K_5}{2}+\frac{3K_1+(-1)^nK_2}{3\times 2^{n+2}}-\frac{P_n+P_{n-1}}{4^n}.$$

The composition of the nth generation is,

Males: $u_n A\text{—} + v_n a\text{—}$,

Females: $r_n AA + s_n Aa + t_n aa$,

in which

$$21)\qquad \begin{aligned} u_n&=\frac{2b_n+c_n+2e_n+f_n}{2}=\frac{1+K_5}{2}-\frac{(-1)^nK_2}{3\times 2^n},\\ v_n&=\frac{c_n+2d_n+f_n+2g_n}{2}=\frac{1-K_5}{2}+\frac{(-1)^nK_2}{3\times 2^n},\end{aligned}$$

$$22)\qquad \begin{aligned} r_n&=\frac{2b_n+c_n}{2}=\frac{1+K_5}{2}+\frac{(-1)^nK_2}{3\times 2^{n+1}}-\frac{P_{n+1}}{4^{n+1}},\\ s_n&=\frac{c_n+2d_n+2e_n+f_n}{2}=\frac{P_{n+1}}{2\times 4^n},\\ t&=\frac{f_n+2g_n}{2}=\frac{1-K_5}{2}-\frac{(-1)^nK_2}{3\times 2^{n+1}}-\frac{P_{n+1}}{4^{n+1}}\end{aligned}$$

Discussion

1. The heterozygous female tends to disappear. This follows from the fact that s_n involves the proper fractions $(1+\sqrt{5})/4$ and $(1-\sqrt{5})/4$ to higher and higher powers as n increases.

2. In the limiting population the ratio of dominants to recessives, in males and females alike, is $(1+K_5)/2$ to $(1-K_5)/2$.

Substituting $n=1$ in equations 15)-20) and solving for $K_1 \ldots\ldots K_5$,

$$K_1 = 2(e_1-d_1)+c_1-f_1.$$
$$K_2 = 2(e_1-d_1)-c_1+f_1.$$
$$K_3 = \frac{1}{\sqrt{5}}\,[(d_1+e_1)(\sqrt{5}-1)+c_1+f_1].$$
$$K_4 = \frac{1}{\sqrt{5}}\,[(d_1+e_1)(\sqrt{5}+1)-c_1-f_1].$$
$$K_5 = b_1-g_1 + \frac{e_1-d_1+c_1-f_1}{3}.$$

In terms of r, s, t, u, v we have

$$b_1 = \frac{ru}{KL};\; c_1 = \frac{su}{KL};\; d_1 = \frac{tu}{KL};\; e_1 = \frac{rv}{KL};\; f_1 = \frac{sv}{KL};\; g_1 = \frac{tv}{KL}.$$

in which $K = r + s + t$ and $L = u + v$.

Particular cases. Consider the problem of brother and sister mating in the family obtained by crossing AA with a—. What we have called the original family will consist in this case of equal numbers of Aa and A— individuals. Thus $r = t = v = 0$; $s = u = 1$. Thus $b_1 = d_1 = e_1 = f_1 = g_1 = 0$; $c_1 = 1$. Calculating the constants, $K_1 = 1$; $K_2 = -1$; $K_3 = \frac{1}{\sqrt{5}}$; $K_4 = -\frac{1}{\sqrt{5}}$; $K_5 = 1/3$.

Substituting in 21) and 22) we have,

$$r_n = 2/3 - \frac{(-1)^n}{3\times 2^{n+1}} - \frac{(1+\sqrt{5})^{n+1}-(1-\sqrt{5})^{n+1}}{\sqrt{5}\times 4^{n+1}};$$

$$s_n = \frac{(1+\sqrt{5})^{n+1}-(1-\sqrt{5})^{n+1}}{2\sqrt{5}\times 4^n};$$

$$t_n = 1/3 + \frac{(-1)^n}{3\times 2^{n+1}} - \frac{(1+\sqrt{5})^{n+1}-(1-\sqrt{5})^{n+1}}{\sqrt{5}\times 4^{n+1}}.$$

The nth term of the Fibonacci series is $F_n = \frac{(1+\sqrt{5})^n-(1-\sqrt{5})^n}{\sqrt{5}\times 2^n}$

Using F_n and G_n we have for the composition of the nth generation

Males: $\frac{G_{n+1}}{2^n} A\text{—} + \frac{G_n}{2^n} a\text{—}$

$$\text{Females: } \frac{2^{n+1}-G_{n+1}-F_{n+1}}{2^{n+1}} AA + \frac{F_{n+1}}{2^n} Aa + \frac{G_{n+1}-F_{n+1}}{2^{n+1}} aa.$$

This problem is worked by JENNINGS (1916, § 69).

It should be apparent that one value of the developments here given is to find the limiting values of the proportions in the composition of the nth generation. To make this clear, suppose we start with a family in which $r = 1$, $s = 2$, $t = 3$, $u = 4$, $v = 5$. (Any other numbers would do equally well.) Then

$$b_1 = \frac{4}{54};\ c_1 = \frac{8}{54};\ d_1 = \frac{12}{54};\ e_1 = \frac{5}{54};\ f_1 = \frac{10}{54};\ g_1 = \frac{15}{54}.$$

$$K_5 = \frac{4}{54} - \frac{15}{54} + \frac{5-12+8-10}{162} = -\frac{7}{27}.$$

$$\frac{1+K_5}{2} = \frac{10}{27};\ \frac{1-K_5}{2} = \frac{17}{27}.$$

Then the limiting proportions are:

$$\text{Males: } \frac{10}{27} A- + \frac{17}{27} a-;$$

$$\text{Females: } \frac{10}{27} AA + \frac{17}{27} aa.$$

This is to show how easily we can get the limiting proportions without calculating a number of terms in the series involved.

ii. Assortative mating

The problem of assortative mating is almost trivial in case of a sex-linked factor. This is because only three types of matings can occur. They are $AA \times A-$, $Aa \times A-$ and $aa \times a-$. The recurrence relations involved are

$$b_n = b_{n-1} + c_{n-1}/2$$
$$c_n = c_{n-1}/2$$
$$g_n = g_{n-1}.$$

The solutions are

$$b_n = b_1 + c_1 - c_1/2^{n-1}.$$
$$c_n = c_1/2^{n-1}.$$
$$g_n = 1 - b_1 - c_1 = g_1.$$

The composition of the nth generation is

Males: $[b_1+c_1-c_1/2^n]A- + [c_1/2^n+g_1]a-$.

Females: $[b_1+c_1-c_1/2^n]AA + c_1/2^n Aa+g_1 aa$.

It is evident that the heterozygous female tends to disappear as n increases indefinitely.

d. Mating parent by offspring

A rather simple problem showing the application of the method of recurrence relations is that of analyzing the population resulting from mating sons to mothers and daughters to fathers. The only possible types of families resulting from such mating are those which we have called b, c, f and g families. A family of type d arises from a cross between aa and $A-$. This cannot occur in the present problem since an aa female cannot be the mother of an $A-$ male, nor can an $A-$ be the father of an aa. For similar reasons no families of type e can occur. The recurrence relations of the problem are as follows:

$$4b_n = 4b_{n-1}+c_{n-1};$$
$$4c_n = 2c_{n-1}+f_{n-1};$$
$$4f_n = c_{n-1}+2f_{n-1};$$
$$4g_n = 4g_{n-1}+f_{n-1}.$$

The solutions are,

$$b_n = \frac{1+K_3}{2} - \frac{K_1+6K_2\times 3^n}{6\times 4^n}.$$

$$c_n = \frac{2K_2\times 3^n+K_1}{2\times 4^n}.$$

$$f_n = \frac{2K_2\times 3^n-K_1}{2\times 4^n}.$$

$$g_n = \frac{1-K_3}{2} + \frac{K_1-6K_2\times 3^n}{6\times 4^n}.$$

The constants have the values,

$$K_1 = 4(c_1-f_1).$$
$$K_2 = 2(c_1+f_1)/3.$$
$$K_3 = b_1-g_1+(c_1-f_1)/3.$$

The composition of the nth generation is

Males: $[b_n+(c_n+f_n)/2]A- + [g_n+(c_n+f_n)/2]a-$.

Females: $[b_n+c_n/2]AA + [(c_n+f_n)/2]Aa + [f_n/2+g_n]aa$.

Substituting the values of $b_n \ldots\ldots g_n$ this becomes:

$$\text{Males:}\quad [\frac{1+K_3}{2}-\frac{K_1}{6\times 4^n}]A\text{—}+[\frac{1-K_3}{2}+\frac{K_1}{6\times 4^n}]a\text{—}.$$

$$\text{Females:}\quad [\frac{1+K_3}{2}+\frac{K_1-2K_2\times 3^{n+1}}{3\times 4^{n+1}}]AA+K_2(3/4)^n Aa+ [\frac{1-K_3}{2}-\frac{K_1+2K_2\times 3^{n+1}}{3\times 4^{n+1}}]aa.$$

It is evident from these results that the heterozygous female tends to disappear and the homozygous types approach the proportion, $(1+K_3)/2$ dominants to $(1-K_3)/2$ recessives.

Consider a particular case. AA is crossed with a— and then the daughters are mated to their father and the sons to their mother. As a result of the original cross we have individuals of types Aa and A— in equal numbers. Now we have the crosses $Aa \times a$— and $AA \times A$— to give what we call our first generation. Thus we have,

$$b_1 = f_1 = 1/2;\ c_1 = g_1 = 0.$$

Evaluating the constants,

$$K_1 = -2;\ K_2 = 1/3;\ K_3 = 1/3.$$

Finally, the population of the nth generation is,

$$\text{Males:}\quad [2/3+\frac{1}{3\times 4^n}]A\text{—}+[1/3-\frac{1}{3\times 4^n}]a\text{—}.$$

$$\text{Females:}\quad [2/3-\frac{1+3^n}{6\times 4^n}]AA+\frac{3^{n-1}}{4^n}Aa+[1/3+\frac{1-3^n}{6\times 4^n}]aa.$$

PART II. BREEDING PARENTS TO OFFSPRING—TYPICAL FACTOR

a. Breeding half of offspring to one parent and half to the other

Suppose a breeding problem is started by making a certain cross and that thereafter half the resulting family is bred to one parent and half to the other. What is the composition of the nth generation, if a typical Mendelian trait is being considered?

Only five types of families can exist in any generation. The cross $AA \times aa$ cannot occur because neither AA nor aa can have the other as parent. The crosses which occur and the resulting families are tabulated below.

Type of cross	Composition of resulting family (AA, Aa, aa)	Type of family
$AA \times AA$	$(1, 0, 0)$	o
$AA \times Aa$	$(\frac{1}{2}, \frac{1}{2}, 0)$	p
$Aa \times Aa$	$(\frac{1}{4}, \frac{1}{2}, \frac{1}{4})$	r
$Aa \times aa$	$(0, \frac{1}{2}, \frac{1}{2})$	u
$aa \times aa$	$(0, 0, 1)$	v

Our problem now is to consider what results when in a family of each type half the individuals are bred back to one and half to the other of the members of the cross which produced the family. It is evident that families of type o give rise to families of this type only. In families of type p the individuals are equally divided between the types AA and Aa. This family came from a cross between AA and Aa. Breeding AA back to AA gives an o family; breeding AA back to Aa gives a p family; breeding Aa back to AA gives a p family and breeding Aa back to Aa gives an r family. Thus the offspring of a p family will be in families of types o, p, r in the ratio $\frac{1}{4} : \frac{1}{2} : \frac{1}{4}$. Similar detailed consideration of the offspring of families of types r, u, v enable us finally to write down the recurrence relations,

23) $$4o_n = 4o_{n-1} + p_{n-1};$$
24) $$4p_n = 2p_{n-1} + r_{n-1};$$
25) $$4r_n = p_{n-1} + 2r_{n-1} + u_{n-1};$$
26) $$4u_n = 2u_{n-1} + r_{n-1};$$
27) $$4v_n = 4v_{n-1} + u_{n-1}.$$

The solutions of these equations are,

28) $$o_n = \frac{1+K_2}{2} - \frac{K_1}{2^{n+2}} - \frac{P_{n+1}}{2 \times 4^n}.$$

29) $$p_n = \frac{K_1}{2^{n+1}} + \frac{P_n}{4^n}.$$

30) $$r_n = \frac{P_{n+1} - 2P_n}{4^n}.$$

31) $$u_n = -\frac{K_1}{2^{n+1}} + \frac{P_n}{4^n}.$$

32) $$v_n = \frac{1-K_2}{2} + \frac{K_1}{2^{n+2}} - \frac{P_{n+1}}{2 \times 4^n}.$$

in which $P_n = K_3(2+\sqrt{2})^n + K_4(2-\sqrt{2})^n$. Evaluating the constants,

$$K_1 = 2(p_1 - u_1).$$

$$K_2 = o_1 - v_1 + \frac{p_1 - u_1}{2}.$$

33) $$K_3 = \frac{p_1 + u_1 + \sqrt{2}r_1}{2+\sqrt{2}}.$$

$$K_4 = \frac{p_1 + u_1 - \sqrt{2}r_1}{2-\sqrt{2}}.$$

The composition of the nth generation is

34) $$[o_n + p_n/2 + r_n/4]AA + [(p_n + r_n + u_n)/2]Aa + [r_n/4 + u_n/2 + v_n]aa.$$

Substituting from equations 28)-33) into expression 34), the nth generation is

35) $$\left[\frac{1+K_2}{2} - \frac{P_{n+1}}{4^{n+1}}\right]AA + \frac{P_{n+1}}{2\times 4^n}Aa + \left[\frac{1-K_2}{2} - \frac{P_{n+1}}{4^{n+1}}\right]aa.$$

Discussion

The heterozygous individuals tend to disappear regardless of the nature of the original cross. The homozygous types approach a fixed proportion as n increases indefinitely:

$$\frac{1+K_2}{2}AA + \frac{1-K_2}{2}aa.$$

It should be noted that $o_1 \ldots . v_1$ are proportional to the numbers of families of the different types after the first breeding of offspring to parent has occurred.

JENNINGS considered some special cases of this problem but was unable to get a simple expression for the numbers involved. The first case which JENNINGS considers is a cross between AA and aa followed by breeding back to parents. The result of the first cross is a family of individuals all of type Aa. Half of these are bred to AA and half to aa, giving two types of families p, u equal in numbers. Thus, $o_1 = v_1 = r_1 = 0$; $p_1 = u_1 = 1/2$. Substituting in equations 33),

$$K_1 = K_2 = 0;\ K_3 = 1/(2+\sqrt{2});\ K_4 = 1/(2-\sqrt{2}).$$

Substituting these values of the constants in expression 35), and remembering that $P_n = K_3(2+\sqrt{2})^n + K_4(2-\sqrt{2})^n$ we have,

$$(AA)_n = \tfrac{1}{2} - \frac{(2+\sqrt{2})^n+(2-\sqrt{2})^n}{4^{n+1}}$$

$$(Aa)_n = \frac{(2+\sqrt{2})^n+(2-\sqrt{2})^n}{2\times 4^n}$$

$$(aa)_n = \tfrac{1}{2} - \frac{(2+\sqrt{2})^n+(2-\sqrt{2})^n}{4^{n+1}}$$

These formulae give the results which JENNINGS (1916, § 53) has, when we substitute $n = 1, 2, 3, \ldots,$ enable us to calculate the proportions for any value of n independent of other values of n, and give us at once the limits approached. In this case the limiting population is $\tfrac{1}{2}AA + \tfrac{1}{2}aa$.

It may be worth while to calculate the limiting population for another special case. The original cross is $AA \times Aa$ giving a p family, half of which is to be bred back to AA and half to Aa. This gives as our first generation $\tfrac{1}{4}o + \tfrac{1}{2}p + \tfrac{1}{4}r$; i.e.,

$$o_1 = \tfrac{1}{4};\ p_1 = \tfrac{1}{2};\ r_1 = \tfrac{1}{4};\ u_1 = v_1 = 0.$$
$$K_2 = o_1 - v_1 + (p_1 - u_1)/2 = \tfrac{1}{4} + \tfrac{1}{4} = \tfrac{1}{2}.$$

Then $(1+K_2)/2 = \tfrac{3}{4}$; $(1-K_2)/2 = \tfrac{1}{4}$ and the limiting population is

$$\tfrac{3}{4}\,AA + \tfrac{1}{4}\,aa,$$

which is at least suggested by JENNINGS's result for the 10th generation (JENNINGS 1916, § 55).

b. Breeding offspring to younger parent

The various problems in breeding offspring to the younger parent may be made to depend upon three special problems of this sort. Only five types of families can occur. A family all members of which are Aa individuals cannot occur since the parents of such a family must be AA and aa and neither of these latter types can be the offspring of the other type. Since o and v families remain pure by this system of breeding, we need only consider the outcome of families of types p, r, u.

Suppose we start by breeding the members of a p family to their AA parent. The first generation will consist of families of types o and p in equal numbers. In later generations the offspring of the o families will be in families of type o. To get the contribution of the p families to the second generation we mate with the Aa parent. Thus it is evident that the problem under consideration can be made to depend upon the one begun by mating a p family to the Aa parent. Then any problem in breeding offspring to the younger parent can be made to depend upon three special problems of mating to the younger parent, the breeding being started in the respective problems by mating,

i. members of an r family to the Aa parent,
ii. members of a p family to the Aa parent,
iii. members of a u family to the Aa parent.

(Of course it is evident that both parents of an r family are of type Aa.)

It should be stated that the results for each of these problems are given by JENNINGS (1916, §§ 52, 47, 50). The excuses for the following pages are that proofs are given, and that the methods used, which have important points of difference from any so far used, may be of use elsewhere.

i. If we mate the members of an r family to either parent, Aa, the first generation consists of families of types p, r, u in the proportion indicated by $\frac{1}{4}p_{AA} + \frac{1}{2}r + \frac{1}{4}u_{aa}$ The subscripts on p and u indicate the type of parent to which we are to breed next. The second generation will be

$$\tfrac{1}{8}\,o + \tfrac{1}{8}\,p_{Aa} + \tfrac{1}{8}\,p_{AA} + \tfrac{1}{4}\,r + \tfrac{1}{8}\,u_{aa} + \tfrac{1}{8}\,u_{Aa} + \tfrac{1}{8}\,v.$$

Notice that because of the symmetry of the problem we will have, $o_n = v_n$; $p_n = u_n$. Notice also that part of the families of type p are bred to the AA parent and part to the Aa parent. This threatens to introduce a complication which it is wise to avoid. There are the same number of p and u families to be bred to Aa. Since p and u families have compositions indicated by ($\frac{1}{2}$, $\frac{1}{2}$, 0) and (0, $\frac{1}{2}$, $\frac{1}{2}$), one of each is equivalent in composition to two families of composition ($\frac{1}{4}$, $\frac{1}{2}$, $\frac{1}{4}$), i.e., two r families. Then so far as the present problem is concerned, the p and u families which are to be bred to the Aa parents may be replaced by r families. Let $\bar{p}_n$ represent the families of type p to be bred to the AA parent. Let $\bar{u}_n$ represent the families of type u to be bred to the aa parent. Let $\bar{r}_n = r_n + p_n - \bar{p}_n + u_n - \bar{u}_n$. Then it is easy to show that

36) $\quad 2o_n = 2o_{n-1} + \bar{p}_{n-1}$;
37) $\quad 4\bar{p}_n = \bar{r}_{n-1}$;
38) $\quad 2\bar{r}_n = \bar{r}_{n-1} + 2\bar{p}_{n-1}$;
39) $\quad \bar{u}_n = \bar{p}_n$;
40) $\quad v_n = o_n$.

If we let $P_n = K_1(1+\sqrt{5})^n + K_2(1-\sqrt{5})^n$, the solutions of this system are,

41) $\bar{p}_n = \bar{u}_n = P_{n-1}/4^n$;

42) $\bar{r}_n = P_n/4^n$;

43) $o_n = v_n = \frac{1}{2} - P_{n+1}/4^{n+1}$.

For our problem $\bar{p}_1 = \frac{1}{4}$; $\bar{r}_1 = \frac{1}{2}$; these values determine K_1 and K_2 to be $K_1 = (1+\sqrt{5})/2\sqrt{5}$ and $K_2 = -(1-\sqrt{5})/2\sqrt{5}$ and P_n becomes $P_n = [(1+\sqrt{5})^{n+1} - (1-\sqrt{5})^{n+1}]/2\sqrt{5}$. Since $\mathrm{F}_n = [(1+\sqrt{5})^n - (1-\sqrt{5}^n]/2^n \times \sqrt{5}$, we have $P_n = 2^n \mathrm{F}_{n+1}$. The composition of the nth generation is

$$[o_n + \frac{\bar{p}_n}{2} + \frac{\bar{r}_n}{4}]AA + [\frac{\bar{p}_n + \bar{r}_n + \bar{u}_n}{2}]Aa + [\frac{\bar{r}_n}{4} + \frac{\bar{u}_n}{2} + v_n]aa.$$

Substituting from the above equations, this becomes,

44) $$[\tfrac{1}{2} - \frac{\mathrm{F}_{n+2}}{2^{n+2}}]AA + \frac{\mathrm{F}_{n+2}}{2^{n+1}} Aa + [\tfrac{1}{2} - \frac{\mathrm{F}_{n+2}}{2^{n+2}}]aa.$$

Incidentally it may be noted that the problem of mating AA with aa, then mating half of progeny back to AA and half to aa and then breeding to the younger parent is essentially the present problem. (Compare JENNINGS 1916, § 45.)

ii. If we mate the members of a p family with the Aa parent, the first generation will be $\frac{1}{2}p_{AA} + \frac{1}{2}r$. The second generation will be

$$\tfrac{1}{4}o + \tfrac{1}{4}p_{Aa} + \tfrac{1}{2} \text{ of result of mating } r \text{ by } Aa.$$

The lack of symmetry in this and later results shows that the method of problem i. cannot be used readily. However, inspection of this expression for the second generation is the key to the situation. Let $(p)_n$ stand for the composition of the nth generation in the problem under discussion and similarly, let $(r)_n$ stand for the composition of the nth generation in problem i. Then from the second generation we read,

45) $(p)_n = \frac{1}{4}o + \frac{1}{4}(p)_{n-2} + \frac{1}{2}(r)_{n-1}$.

Replacing n by $n-2$ we have

46) $(p)_{n-2} = \frac{1}{4}o + \frac{1}{4}(p)_{n-4} + \frac{1}{2}(r)_{n-3}$.

Substituting from 46) into 45),

47) $(p)_n = \frac{1}{4}o + 1/16o + 1/16(p)_{n-4} + \frac{1}{2}(r)_{n-1} + \frac{1}{8}(r)_{n-3}$.

It is evident that this process can be continued until (p) has a subscript zero or unity on the right, according as n is even or odd. If n is even we have,

48) $$(p)_n = \tfrac{1}{4}o + \frac{1}{16}o + \ldots + \frac{o+(p)_0}{2^n} + \tfrac{1}{2}(r)_{n-1} + \tfrac{1}{8}(r)_{n-3} + \ldots + \frac{1}{2^{n-1}}(r)_1.$$

$$= \tfrac{1}{3}[1-(\tfrac{1}{4})^n/2]o + \frac{(p)_0}{2^n} + \tfrac{1}{2}(r)_{n-1} + \tfrac{1}{8}(r)_{n-3} + \ldots + \frac{1}{2^{n-1}}(r)_1.$$

If n is odd,

49) $$(p)_n = \tfrac{1}{3}[1-(\tfrac{1}{4})^{n-1}/2]o + \frac{(p)_1}{2^{n-1}} + \tfrac{1}{2}(r)_{n-1} + \tfrac{1}{8}(r)_{n-3} + \ldots + \frac{1}{2^{n-2}}(r)_2.$$

$(r)_n$ is the result in problem i., and is the distribution given in expression 44). $(AA)_n$, $(Aa)_n$, $(aa)_n$ will be used to represent the proportions of the corresponding types of individuals in the nth generation. If n is even,

50) $$(Aa)_n = [1+F_{n+1}+F_{n-1}+ \ldots + F_5+F_3]/2^{n+1}.$$

The terms of the Fibonacci series satisfy the relation

$F_n = F_{n-1}+F_{n-2}$. Then,
$F_2 = F_1+F_0$;
$F_4 = F_3+F_2 = F_3+F_1+F_0 = F_3+F_1$ since $F_0 = 0$.
$F_6 = F_5+F_4 = F_5+F_3+F_1$; it is seen immediately that

51) $F_{2n} = F_{2n-1}+F_{2n-3}+ \ldots +F_3+F_1$ and similar equations show that,
52) $F_{2n-1} = F_{2n-2}+F_{2n-4}+ \ldots +F_4+F_2+F_1$.

In words these equations are equivalent to: *The sum of any number of successive odd (even) terms of the Fibonacci series, beginning with F_1 (F_2+F_1) is the next higher term.*

Since $F_1 = 1$, this enables us to write 50) in the form

53) $$(Aa)_n = F_{n+2}/2^{n+1}.$$

We have shown that 53) holds when n is even. Exactly similar work with equation 49) shows that 53) is correct for n odd. Calculating the values of $(AA)_n$ and $(aa)_n$ we have,

54) $$(AA)_n = \frac{2^{n+3}+(-1)^n-3F_{n+2}}{3\times 2^{n+2}} = \frac{G_{n+3}-F_{n+2}}{2^{n+2}}$$

55) $$(aa)_n = \frac{2^{n+2} - (-1)^n - 3F_{n+2}}{3 \times 2^{n+2}} = \frac{G_{n+2} - F_{n+2}}{2^{n+2}}.$$

iii. The results for this problem are those for ii. with *AA* and *aa* interchanged.

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