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Structure of Populations under Mixed Random and Sib Mating[1]

G. L. Ghai

Iowa State University, Ames, Iowa

Summary. The present investigation relates to various properties of population bred by mixture of breeding systems namely mixed random and sib mating. Expressions have been derived which give the genotypic frequencies in any given generation in terms of the initial values. Under the mating system considered the population will eventually become stable having a certain amount of heterozygosis depending upon the amounts of random and sib mating. The loss of heterozygosity in successive generations has been examined for varying amounts of sib mating in the population.

The formulae have been derived giving the mean and genotypic variance in any given generation of continued mixed mating. The effect of the mating system considered on mean and genotypic variance in successive generations has been discussed in detail in case of (i) absence of dominance and (ii) complete dominance.

In population genetics extensive investigations have been made in respect of various properties of the population under different mating systems like random mating, selfing, sib mating, etc. But the situation where there is complete random mating or complete inbreeding in the population may not always be found and the population may not be bred exactly in the manner postulated in the breeding procedure, i.e., the population may, in fact, be bred by the mixture of breeding systems. For instance, instead of complete inbreeding in the population, some of the individuals may also be obtained by random mating. It would, therefore, be of interest to examine populations under such situations. Recently, Ghai (1964, 1966) has examined the composition and variability of populations under continued mixed random mating and selfing in varying degrees. The purpose of the present investigation is to examine similar properties of the population under another mating system that combines random mating and full sib mating.

As the mating system involves sib mating, the genotypic frequencies of one generation do not help us to calculate these frequencies in the next generation and it is the frequencies of the various types of mating that determine the composition of the next generation. Therefore, we shall have to know not only the genotypic frequencies but also the frequencies of the various types of mating in successive generations.

With respect to one pair of autosomal genes $A-a$, let initially the frequencies of six possible types of mating in the population be:

$$\left.\begin{array}{rl} AA \times AA & f_1^{(0)} = p^4\,, \\ aa \times aa & f_2^{(0)} = q^4\,, \\ AA \times aa & f_3^{(0)} = 2\,p^2\,q^2\,, \\ AA \times Aa & f_4^{(0)} = 4\,p^3\,q\,, \\ aa \times Aa & f_5^{(0)} = 4\,p\,q^3\,, \\ Aa \times Aa & f_6^{(0)} = 4\,p^2\,q^2 \end{array}\right\} \tag{1}$$

giving the initial population as

$$p^2\,AA + 2\,p\,q\,Aa + q^2\,aa\,, \tag{2}$$

where p and q are the frequencies of the alleles A and a respectively.

Let $f_1^{(n)}, f_2^{(n)}, \ldots, f_6^{(n)}$ be the corresponding frequencies of the six types of mating, and D_n, H_n, and R_n as the frequencies of the three genotypes AA, Aa, and aa in the n-th generation of mixed random and sib mating. In each generation let y be the probability of mating at random, and x ($x + y = 1$) the probability of full sib mating.

The relations between the frequencies of the six types of mating in two successive generations of the mixture of breeding systems may be stated in the form of the following equations:

$$\left.\begin{array}{l} f_1^{(n+1)} = y\,D_n^2 + x\,f_1^{(n)} + \left(\dfrac{x}{4}\right) f_4^{(n)} + \left(\dfrac{x}{16}\right) f_6^{(n)}\,, \\ f_2^{(n+1)} = y\,R_n^2 + x\,f_2^{(n)} + \left(\dfrac{x}{4}\right) f_5^{(n)} + \left(\dfrac{x}{16}\right) f_6^{(n)}\,, \\ f_3^{(n+1)} = 2\,y\,D_n\,R_n + \left(\dfrac{x}{8}\right) f_6^{(n)}\,, \\ f_4^{(n+1)} = 2\,y\,D_n\,H_n + \left(\dfrac{x}{2}\right) f_4^{(n)} + \left(\dfrac{x}{4}\right) f_6^{(n)}\,, \\ f_5^{(n+1)} = 2\,y\,H_n\,R_n + \left(\dfrac{x}{2}\right) f_5^{(n)} + \left(\dfrac{x}{4}\right) f_6^{(n)}\,, \\ f_6^{(n+1)} = y\,H_n^2 + x\,f_3^{(n)} + \left(\dfrac{x}{4}\right) f_4^{(n)} + \left(\dfrac{x}{4}\right) f_5^{(n)} + \\ \qquad\qquad + \left(\dfrac{x}{4}\right) f_6^{(n)}\,. \end{array}\right\} \tag{3}$$

The frequency of heterozygotes Aa in the $(n+1)$-th generation is given by

$$H_{n+1} = f_3^{(n)} + \frac{1}{2} f_4^{(n)} + \frac{1}{2} f_5^{(n)} + \frac{1}{2} f_6^{(n)}\,. \tag{4}$$

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Substituting the values of f's in the right hand side of (4) from equations (3) we get, in particular

$$H_1 = \left(1 - \frac{x}{4}\right) H_0\,, \quad \text{where} \quad H_0 = 2\,p\,q \tag{5}$$

and

$$H_2 = \left(1 - \frac{x}{2}\right)\left(1 + \frac{x}{4}\right) H_0 \tag{6}$$

and in general, the recurrence relation of H, by the rearrangement of terms takes a simple and convenient form

$$H_{n+3} - \left(1 + \frac{x}{2}\right) H_{n+2} + \left(\frac{x}{4}\right) H_{n+1} + \left(\frac{x}{4}\right) H_n = 0\,. \tag{7}$$

The general expression for H_n from equation (7) comes out as

$$H_n = A\,\lambda_1^n + B\,\lambda_2^n + C\,\lambda_3^n\,, \tag{8}$$

where A, B, and C are determined from the initial conditions and λ_1, λ_2, and λ_3 are three different roots of the cubic equation

$$\lambda^3 - \left(1 + \frac{x}{2}\right)\lambda^2 + \left(\frac{x}{4}\right)\lambda + \left(\frac{x}{4}\right) = 0\,. \tag{9}$$

The roots of this equation are

$$\lambda_1 = \frac{x + \sqrt{x^2 + 4\,x}}{4}\,, \quad \lambda_2 = \frac{x - \sqrt{x^2 + 4\,x}}{4}\,, \quad \lambda_3 = 1$$

with λ_1 and λ_2 being less than unity. Solving for A, B, and C, from the initial conditions, we have

$$A = \frac{\left(\frac{x}{4}\right)\lambda_1 H_0}{(1 - \lambda_1)(\lambda_1 - \lambda_2)}\,, \quad B = \frac{-\left(\frac{x}{4}\right)\lambda_2 H_0}{(1 - \lambda_2)(\lambda_1 - \lambda_2)} \quad \text{and}$$

$$C = \frac{y\,H_0}{(1 - \lambda_1)(1 - \lambda_2)}\,.$$

Hence,

$$H_n = \left[\frac{y}{(1 - \lambda_1)(1 - \lambda_2)} + \frac{\left(\frac{x}{4}\right)\lambda_1^{n+1}}{(1 - \lambda_1)(\lambda_1 - \lambda_2)} - \frac{\left(\frac{x}{4}\right)\lambda_2^{n+1}}{(1 - \lambda_2)(\lambda_1 - \lambda_2)}\right] H_0 \tag{10}$$

which gives the proportion of heterozygotes Aa in the n-th generation of mixed mating.

The proportions of the other genotypes namely the homozygotes AA and aa in the n-th generation are then obtained by

$$D_n = p - \frac{1}{2} H_n\,, \tag{11}$$

$$R_n = q - \frac{1}{2} H_n \tag{12}$$

since the gene frequency does not change from generation to generation.

Under the mating system considered, two opposing forces are acting on the population, sib mating trying to reduce the heterozygosity and random mating trying to regain the initial values. Ultimately a stage would be reached where loss due to one would be balanced by the gain due to the other and the population will eventually reach an equilibrium state which will also have a certain amount of heterozygosis depending upon the amounts of random and sib mating in the population. Therefore, at equilibrium ($n \to \infty$)

$$\left.\begin{aligned} H_\infty &= \frac{y\,H_0}{(1 - \lambda_1)(1 - \lambda_2)} \\ &= 2\,p\,q\left[1 - \frac{x}{4 - 3\,x}\right]. \end{aligned}\right\} \tag{13}$$

It is evident that the smaller the value of x, the more rapidly the population will reach equilibrium state.

The frequencies of homozygotes AA and aa at equilibrium are

$$D_\infty = p^2 + \frac{x\,p\,q}{4 - 3\,x}\,, \tag{14}$$

$$R_\infty = q^2 + \frac{x\,p\,q}{4 - 3\,x}\,. \tag{15}$$

Loss of Heterozygosity

Defining the coefficient of inbreeding, F_n, in the n-th generation as the loss in heterozygosity relative to that in the initial population, we have

$$\begin{aligned} F_n &= 1 - H_n/H_0 \\ &= \frac{x/4}{\lambda_1 - \lambda_2}\left[\frac{1 - \lambda_1^{n+1}}{1 - \lambda_1} - \frac{1 - \lambda_2^{n+1}}{1 - \lambda_2}\right] \end{aligned} \tag{16}$$

and in the limiting case ($n \to \infty$) this reduces to

$$F_\infty = 1 - \frac{y}{(1 - \lambda_1)(1 - \lambda_2)} = \frac{x}{4 - 3\,x}\,. \tag{17}$$

This indicates that under this system of mating the heterozygosity is not completely lost except for $x = 1.0$, i.e., complete full-sib mating.

The loss in heterozygosity in successive generations up to 20 generations and in the limiting case has been examined in Table 1 for various combinations of random and sib mating. The values for $x = 1.0$ correspond to the case of complete sib mating. The

Table 1. *Loss of heterozygosity relative to initial heterozygosity (F_n) under mixed random and sib mating*

n	$x =$ .20	.50	.80	.90	1.00
1	.050	.125	.200	.225	.250
2	.055	.156	.280	.326	.375
3	.058	.179	.352	.422	.500
4	.058	.189	.396	.488	.593
5		.194	.429	.539	.671
10			.492	.665	.907
15			.498	.685	.968
20				.690	.986
∞	.058	.200	.500	.692	1.000

x = Probability of sib mating

values for $n = \infty$ correspond to the maximum loss in heterozygosity that can occur under continued mixed random and sib mating. It would be seen that loss of heterozygosity increases with increasing amount of sib mating, but is not proportionate to the increase in the amount of sib mating except in the first generation. There is practically no loss in heterozygosity when the system of mating deviates from complete random mating and the population in successive generations includes some of the individuals obtained by sib mating up to $x = 0.20$. Maximum loss in heterozygosity is of the order of 6% in this case. As the amount of sib mating in the population increases the maximum loss in heterozygosity also rises and in the case of 90% sib mating and 10% random mating it is of the order of 69%. This indicates that the effect of even 10% random mating in the otherwise inbred population is considerable. As against total loss in heterozygosity with complete sib mating (i.e., population eventually becomes completely homozygous), the population retains heterozygosity to the order of 31% with 90% sib mating and 10% random mating. It would also be seen from the table that for a given amount of sib mating most of the expected loss in heterozygosity takes place within the first few generations. Thus in a population mating at random if there is also inbreeding in small amounts, its effect on the population will be negligible, whereas in the case of inbred population the effect of even small amounts of random mating in the population will be substantial.

Mean and Genotypic Variance

If we let d, h, r be the genotypic values of the three genotypes AA, Aa, aa respectively the results can be put in a simple form in terms of $d - r$ and $d - 2h + r$. We therefore use coded genotpyic values as follows:

Genotype	Genotypic Value	Coded Genotypic Value
AA	d	u
Aa	h	$\frac{u-v}{2}$
aa	r	0

where $u = d - r$,

$v = d - 2h + r$.

The mean (μ_n) and genotypic variance (V_n) in generation n are given by

$$\mu_n = p\,u - \frac{1}{2} H_n v \tag{18}$$

and

$$V_n = (4pq - H_n)\frac{u^2}{4} + \frac{p-q}{2} H_n u v + H_n(1 - H_n)\frac{v^2}{4} \tag{19}$$

with $\mu_0 = p\,u - p\,q\,v$ and

$$V_0 = \frac{pq}{2}[u^2 + 2(p-q)\,u\,v + (1 - 2pq)\,v^2].$$

These are general expressions for the mean and genotypic variance. The effect of the mating system considered, on mean and genotypic variance is discussed in detail for two cases (i) absence of dominance, and (ii) complete dominance.

(i) Absence of dominance ($v = 0$). When the average effect of the heterozygote is midway between the two parents, the mean does not change in successive generations and retains its initial value, that is

$$\mu_n = p\,u = \mu_0. \tag{20}$$

The genotypic variance in this case turns out to be

$$V_n = (4pq - H_n)\frac{u^2}{4} = (1 + F_n)\,V_0, \tag{21}$$

where $V_0\left(= \frac{pq}{2} \cdot u^2\right)$ is the corresponding variance in the initial population. The values of F_n are given in Table 1. Since F_n is increasing with n, genotypic variance also increases with n. The genotypic variance also increases with the increasing amount of sib mating, the increase being relatively higher for higher amounts of sib mating in the population.

In the limiting case ($n \to \infty$) it becomes

$$V_\infty = \frac{pq(2-x)}{4-3x}u^2 = \frac{2(2-x)}{(4-3x)}V_0 = (1 + F_\infty)\,V_0. \tag{22}$$

(ii) Complete Dominance ($v = -u$). When allele A is completely dominant over a, equations (18)

Table 2. *Genotypic variance relative to the initial variance (V_n/V_0) in the case of complete dominance*

q	n	$x = .20$	.50	.80	.90	1.00
.2	1	1.207	1.669	2.491	2.918	3.471
	2	1.218	1.704	2.571	3.023	3.609
	3	1.222	1.722	2.627	3.103	3.721
	∞	1.223	1.740	2.750	3.334	4.167
.5	1	1.035	1.109	1.221	1.267	1.311
	2	1.037	1.114	1.230	1.277	1.318
	3	1.038	1.117	1.237	1.284	1.324
	∞	1.038	1.120	1.250	1.302	1.333
.6	1	1.015	1.044	1.078	1.084	1.079
	2	1.016	1.046	1.080	1.085	1.074
	3	1.016	1.047	1.081	1.084	1.070
	∞	1.016	1.048	1.083	1.082	1.042
.7	1	1.000	.997	.976	.955	.916
	2	1.000	.996	.972	.949	.903
	3	1.000	.996	.970	.944	.893
	∞	1.000	.996	.964	.927	.840
.8	1	.989	.961	.899	.858	.795
	2	.988	.959	.892	.847	.777
	3	.988	.958	.887	.839	.762
	∞	.988	.957	.875	.812	.694

x = Probability of sib mating.

and (19) giving the mean and genotypic variance respectively reduce to

$$\mu_n = \left(p + \frac{1}{2} H_n\right) u \qquad (23)$$

and

$$V_n = [4\,p\,q - 2\,(p - q)\,H_n - H_n^2]\,\frac{u^2}{4}$$
$$= V_0 + p\,q\,F_n\,[1 - 2\,q^2 - p\,q\,F_n]\,u^2 \qquad (24)$$

with $V_0 = q^2\,(1 - q^2)\,u^2$.

Now $\mu_{n+1} - \mu_n = -\frac{1}{2}\,(H_n - H_{n+1})\,u < 0$.

This shows that the mean decreases in successive generations for all values of q and x.

Also

$$V_{n+1} - V_n = (H_n - H_{n+1})\,[2\,(p - q) + H_n + H_{n+1}]\left(\frac{u^2}{4}\right).$$

When $q \leq 0.5$, $V_{n+1} - V_n > 0$. For different values of the gene frequency, q, and the amount of sib mating, x, the genotypic variance (V_n) relative to the initial variance (V_0) is given in Table 2 for the first three generations and in the limiting case. It may be seen that limiting values are attained very rapidly within two or three generations.

For values of the frequency of the recessive allele less than or equal to one-half ($q \leq 0.5$), the genotypic variance increases in successive generations and also with increasing amount of sib mating. For $q > 0.7$, the genotypic variance decreases. For $q = 0.6$ and 0.7, the genotypic variance increases up to a certain stage and decreases thereafter.

This shows that in the case of complete dominance, the genotypic variance increases when recessive individuals are less than or equal to one quarter ($q^2 \leq 1/4$) in the initial population but it decreases when they are at least as frequent as the dominant individuals ($q^2 \geq 1/2$).

Zusammenfassung

Die vorliegende Untersuchung bezieht sich auf verschiedene Eigenheiten des Populationsverhaltens unter Einfluß einer Mischung von Paarungssystemen, nämlich der Panmixie und der Geschwisterpaarung. Es wurden Formeln abgeleitet, die die genotypischen Frequenzen in jeder beliebigen Generation in Beziehung zu den Ausgangswerten angeben. Unter dem betrachteten Paarungssystem kann die Population gegebenenfalls stabil werden mit einem bestimmten Heterozygotieanteil, der vom Ausmaß der Panmixie und der Geschwisterpaarung abhängt. Für verschiedene Anteile der Geschwisterpaarung wurde der Verlust der Heterozygotie in aufeinanderfolgenden Generationen untersucht.

Die abgeleiteten Formeln liefern das Mittel und die genotypische Varianz in jeder beliebigen Generation fortgesetzter gemischter Paarung. Die Wirkung des betrachteten Paarungssystems auf Mittel und genotypische Varianz in aufeinanderfolgenden Generationen wurde (1) für den Fall der Abwesenheit der Dominanz und (2) den der vollständigen Dominanz ausführlich diskutiert.

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G. L. GHAI,
Iowa State University,
Ames, Iowa 50010 (USA)