THE DYNAMICS OF POPULATIONS UNDER PARTIAL INBREEDING*

GAURI L. GHAI and OSCAR KEMPTHORNE

Statistical Laboratory, Iowa State University, Ames, Iowa

Introduction

In population genetics situations are not uncommon where outcrossing and inbreeding processes are working simultaneously in varying degrees. For example there are plant species like barley and wheat, rice, lima beans, and etc. which undergo mixed selfing and random mating. The mathematical analysis of a system of a mixed random mating and selfing has been given by Garber (1951), Bennett and Binet (1956) and Ghai (1964). More recently Ghai (1969) has considered models based on a system of mixed random and full-sib mating. Mixed mating systems provide means for maintaining polymorphic variation in the absence of heterozygote advantage. Theoretical effects of such systems on the maintenance of heterozygosity have been previously discussed by Ghai (1966, 1969).

2. Models

In the present paper, theoretical models will be developed for populations under partial inbreeding which include mixed random and (*a*) half-sib mating, (*b*) parent-offspring mating, (*c*) double first cousin mating and (*d*) a general mixture of consanguineous mating systems. We shall be interested in the overall dynamics of the population as well as in its equilibrium state, and in the level of heterozygosity that can be maintained under such systems of mating.

The models to be discussed will apply to diploid populations. The development will be restricted to the segregation of a single locus. We shall assume that there are constant probabilities x and $(1-x)$ of inbreeding and random mating respectively. For example, in the case of mixed random and half-sib mating, x will be the probability of half-sib mating.

In the development of the models we shall use the concept of identity by descent. This will involve two indices, r_{XY} the "coefficient de parente" of two individuals X and Y as defined by Malecot and F_X the coefficient of inbreeding of the individual X. We shall also denote these by r_n and F_n when the individual(s) belong to generation n. We shall further denote the frequencies of the three

*Journal Paper No. J-6827, Iowa Agricultural and Home Economics Experiment Station, Ames, Iowa, Project No. 1669. Supported by National Institute of Health, Grant No. G.M. 13827.

genotypes AA, Aa and aa in generation n by D_n, H_n and R_n respectively and at equili brium by D, H and R, respectively.

(*a*) *Mixed random and half-sib mating :* Consider models of mixed half-sib mating in proportion x, and random mating in the remaining proportion. The appropriate recurrence relations describing the genotypic frequencies under such a system can be derived by considering the following :

$$r_{XY} = x[r_{XY} \mid H.S.]$$

where $r_{XY} \mid H.S.$ denotes the "coefficient de parente'" or coefficient of parentage given X and Y are half-sibs. This will lead to

$$F_{n+2} = x[F_{n+2} \mid H.S.] = \frac{3x}{4} F_{n+1} + \frac{x}{8} F_n + \frac{x}{8}. \tag{1}$$

In the limit when $n \to \infty$

$$F = \lim_{n \to \infty} F_n = \frac{x}{8-7x}. \tag{2}$$

The genotypic distribution at equilibrium is completely determined once we know F which is given explicitly by (2). However, to investigate the dynamics of the population and to specify the genotypic distribution at any given time, say generation n, we have to use Equation (1) along with the relation $H_n = (1 - F_n)H_o$ where $H_o = 2pq$ is the frequency of the heterozygotes in the initial panmictic population, and p and $q(p+q=1)$ are frequencies of the two alleles A and a, respectively. Therefore, the recurrence equation for H_n becomes

$$H_{n+2} - \frac{3x}{4} H_{n+1} - \frac{x}{8} H_n - (1-x)H_o = 0. \tag{3}$$

This can be easily solved to give

$$(H_n - H) = B\lambda^n{}_1 + C\lambda^n{}_2 \tag{4}$$

where

$$H = (1-F)H_o = \frac{16(1-x)}{8-7x} pq \tag{5}$$

and λ_1 and λ_2 are the roots of the characteristic equation

$$\lambda^2 - \frac{3x}{4}\lambda - \frac{x}{8} = 0 \tag{6}$$

which are

$$\lambda_1 = \frac{1}{8}\left(3x + \sqrt{9x^2+8x}\right)$$

$$\lambda_2 = \frac{1}{8}\left(3x - \sqrt{9x^2+8x}\right)$$

and are less than unity. The constants B and C are determined from the initial conditions

$$H_0=2pq$$
$$H_1=(1-x/8)H_0. \tag{7}$$

This will give the solution (4) as

$$H_n=[(1-F)+\frac{(x/8)\lambda_1^{n+1}}{(1-\lambda_1)(\lambda_1-\lambda_2)}-\frac{(x/8)\lambda_2^{n+1}}{(1-\lambda_2)(\lambda_1-\lambda_2)}]H_0. \tag{8}$$

This gives the frequency of Aa genotype in generation n. H, given by (5) is the proportion of heterozygotes that will be present in the population at equilibrium under the mating system considered. This depends upon both the initial heterozygosity and the amount of half-sib mating. The proportions of other genotypes in generation n can be easily derived to give $D_n=p-\frac{1}{2}H_n$ and $R_n=q-\frac{1}{2}H_n$, because the gene frequencies p and q are invariant over time. At equilibrium these will reduce to $D=p-\frac{1}{2}H$ and $R=q-\frac{1}{2}H$.

(*b*) *Mixed random and parent-offspring mating :* In a population with parent-offspring mating in proportion x and random mating in proportion $(1-x)$, we have as before

$$F_{n+2}=x(F_{n+2}|P.O.)$$
$$=\frac{x}{4}(1+F_n+2F_{n+1}) \tag{9}$$

and

$$F=\lim_{n\to\infty}F_n=\frac{x}{4-3x}. \tag{10}$$

The recurrence relation for this is, therefore, given by

$$H_{n+2}-(x/2)H_{n+1}-(x/4)H_n-(1-x)H_o=0 \tag{11}$$

which will give

$$H=\frac{8(1-x)}{4-3x}pq. \tag{12}$$

The recurrence relation (11) is identical with that for a system of mixed random and full-sib mating (Ghai, 1969). Therefore, mixed random mating and parent-offspring mating would yield the same results as obtained under a system of mixed random and full-sib mating which have already been discussed by Ghai (1969). The amount of heterozygosity that would be present in a population at equilibrium under such a system is given by (12). Similar results have also been reported by Karlin (1968) by following the generation matrix approach.

(*c*) *Mixed random and double first cousin mating :* Under this model with double first cousin mating in a fraction x of the population, we have

$$F_{n+3}=(x/8)(1+F_n+2F_{n+1}+4F_{n+2}) \tag{13}$$

which gives at equilibrium

$$F=\lim_{n\to\infty} F_n=x/(8-7x). \tag{14}$$

The recurrence relation for H_n is then given by

$$H_{n+3}-(x/2)H_{n+2}-(x/4)H_{n+1}-(x/8)H_n-(1-x)H_o=0 \tag{15}$$

which gives

$$H=\frac{16(1-x)pq}{8-7x}. \tag{16}$$

Equation (16) gives the proportion of heterozygotes at equilibrium under a system of mixed random and double first cousin mating. This is identical with Equation (5) which gives the amount of heterozygosity at equilibrium under a system of mixed random and half-sib mating. The general recurrence relations for the two systems are quite different and hence will yield different genotypic distribution in generation n. But when n is sufficiently large i.e. at equilibrium, the genotypic distribution of the two systems coincide.

(*d*) *General mixture of consanguineous mating systems :* We shall now consider a general situation where the mating system involves mating at random and mating among relatives with varying degrees of relationship. Let the individuals mate with the following probabilities :

Pr[Random mating]	$=r$
Pr[Selfing]	$=x$
Pr[Full-sib mating]	$=y$
Pr[Half-sib mating]	$=z$

with $r+x+y+z=1$. Matings between parents and offspring, and those between double first cousins are not included because as we have seen earlier, the effect of these matings on the population structure is the same, at least in equilibrium, as that of full-sib and half-sib matings, respectively.

The situation may not seem to be as general and exhaustive to include all kinds of relatives but it does take account of important ones.

The recurrence relation in this case will come out to be

$$F_{n+2}=(x/2)(1+F_{n+1})+(y/4)(1+F_n+2F_{n+1}) \\ +(z/8)(1+F_n+6F_{n+1}). \tag{17}$$

This relationship can be easily verified directly (see Appendix). At equilibrium

$$F=\lim_{n\to\infty} F_n=\frac{4x+2y+z}{8-4x-6y-7z}. \tag{18}$$

This will give the frequency of heterozygotes at equilibrium as

$$H=\frac{16rpq}{8r+4x+2y+z}. \tag{19}$$

Recently Karlin (1968) has given some results of mixed imprinting, fullsib mating, random mating and selfing. He has derived these results following the generation matrix approach.

3. Discussion

The results obtained have bearing on populations which reproduce by mixture of cross-fertilization and inbreeding. The results could also be interpreted as describing the effect of departure from breeding process of complete random mating or of departure from complete inbreeding. It is assumed that population is large and there are no viability or fertility differences.

The mathematical analysis shows that systems of mixed random and parent offspring mating, and mixed random and full-sib mating yield identical recurrence relations. Therefore, these two systems would lead to the same genotypic distribution. The systems of mixed random and half-sib mating and mixed random and double first cousin mating result in different genotypic distribution in a dynamic population. These distributions, however, coincide when n is sufficiently large i.e. at equilibrium.

Under such mating systems even with high degree of inbreeding, there is a considerable amount of heterozygosity in the population at equilibrium. The level of heterozygosity depends upon the system of mixed mating, the amount of inbreeding and the initial heterozygosity. It may be of interest to compare the relative effects of these mixed mating systems on the maintenance of heterozygosity. The expected heterozygosity relative to the initial heterozygosity in the population at equilibrium under the three systems is depicted graphically in Figure 1. There is practically no loss in heterozygosity when the system of mating deviates from complete random mating by small amounts of inbreeding. In a highly inbred population with say 90-95 percent of inbreeding, the heterozygosity at equilibrium is to the order of 18-9·5 percent of the initial heterozygosity when inbreeding is by selfing. There is about one and a half times as much heterozygosity when inbreeding is by full-sib or parent-offspring mating, and three times as much when inbreeding is by half-sib mating or double first cousin mating.

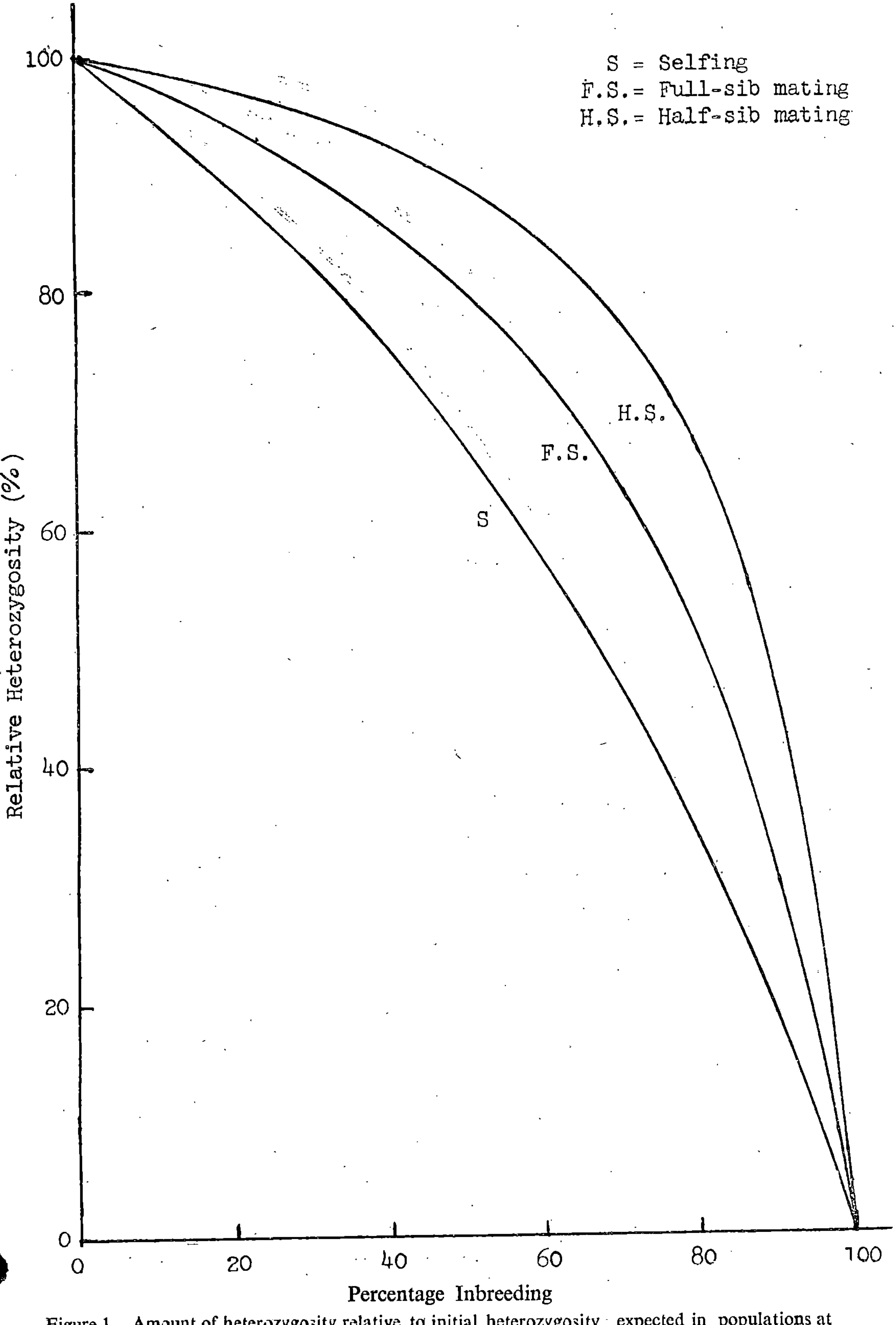


Figure 1. Amount of heterozygosity relative to initial heterozygosity expected in populations at equilibrium under mixed random mating and inbreeding

If x_1, x_2, x_3 are the equivalent amounts of selfing, full-sib or parent-offspring mating, and half-sib or double first cousin mating respectively in the system of mixed mating, which yield the same amount of the heterozygosis in the population at equilibrium, then we have

$$\frac{x_1}{2-x_1}=\frac{x_2}{4-3x_2}=\frac{x_3}{8-7x_3}.$$ This relationship yields

$$x_2=\frac{2x_1}{1+x_1} \text{ and } x_3=\frac{2x_2}{1+x_2}$$

showing that x_3 bears the same relationship with x_2 as x_2 bears with x_1. Thus, for example, 20 per cent of selfing is equivalent to about 33 per cent of full-sib or parent offspring mating which is equivalent to about 50 per cent of half-sib or double first cousin mating in the population in the sense they would give the same final genotypic proportions in the population. Such comparisons, however, shall be meaningful when inbreeding procedures are compared in pairs. It shall be erroneous to conclude that we could replace the fractions of say full-sib and half-sib matings in a general mixture of consanguineous matings by the corresponding equivalent amounts of selfing and then consider the results under the model of mixed random mating and selfing with the augmented probability of selfing.

4. Summary

In this paper theoretical models have been developed for populations under partial consanguineous matings viz., mixed random and (*a*) half-sub mating, (*b*) parent-offspring mating, (*c*) double first cousin mating, and (*d*) mating among relatives with varying degrees of relationship. The genotypic distribution under such mating systems at any given time and at equilibrium are discussed. An important feature of the results is the considerable amount of heterozygosity at equilibrium, that these systems can maintain in predominantly inbred populations. The level of heterozygosity depends upon the system of mixed mating, amount of inbreeding and the initial heterozygosity. The relative effects of different systems of mixed mating on the maintenance of heterozygosity in equilibrium are discussed.

REFERENCES

Bennett, J.H. and Binet, F.E. 1956. Association between Mendelian factors with mixed selfing and random mating. Heredity 10 : 51-55.

Fisher, R.A. 1949. The theory of inbreeding. Oliver and Boyd, Edinburgh.

Garber, M.J. 1951. Approach to genotypic equilibrium with varying percentages of selfing and crossfertilization. J. Heredity 42 : 299-300.

Ghai, G.L. 1964. The genotypic composition and variability in plant populations under mixed self-fertilization and random mating. J. Ind. Socy. Agri. 16 : 94-125.

———. 1966. The loss of heterozygosity under mixed selfing and random mating. J. Ind. Socy. Agri. Stat. 18 : 73-81.

———. 1969. Structure of populations under mixed random and sib mating. Theoretical and Applied Genetics 39 : 179-182.

Karlin, S. 1968. Equilibrium behaviour of population genetics models with nonrandom mating. Part I, J. Applied Probability 5 : 231-313.

Kempthorne, O. 1957. An introduction to genetic statistics. John Wiley and Sons, New York.

Li, C.C. 1955. Population genetics. The University of Chicago Press, Chicago, Illinois.

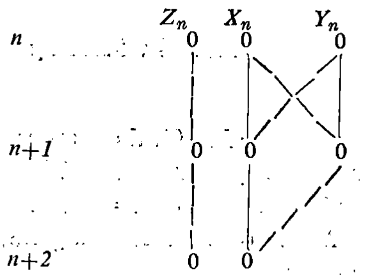
APPENDIX

Suppose there is selfing with probability x and full-sib mating with probability $y(=1-x)$. Then we have

$$F_{n+2}=\left(\frac{x}{2}\right)(1+F_{n+1})+\left(\frac{y}{4}\right)(1+F_n+2F_{n+1})$$

This can be seen by considering the following probabilistic argument.

Generation



We know that

$$F_{n+2}=r_{n+1}=r_{X_{n+1}\ Y_{n+1}}$$

and

$$^rX_{n+1}\ Y_{n+1}=x[rX_{n+1}\ Y_{n+1}/Y=X]+y[^rX_{n+1}\ Y_{n+1}/X,\ Y\ F.S.]$$

where $Y=X$ denotes selfings and $F.S.$ denotes full-sibbing.

Now

$$\left[{}^rX_{n+1}\ Y_{n+1}\ \ Y=X\right]=\frac{1+F_{n+1}}{2} \tag{1}$$

$$[^rX_{n+1}\ Y_{n+1}/X,\ Y\ F.S.]=\tfrac{1}{4}[^rX_nX_n+{}^rY_nY_n+2^rX_nY_n]$$

$$=\frac{1}{4}\left[\frac{1+F_{xn}}{2}+\frac{1+F_{yn}}{2}+2F_{n+1}\right]$$

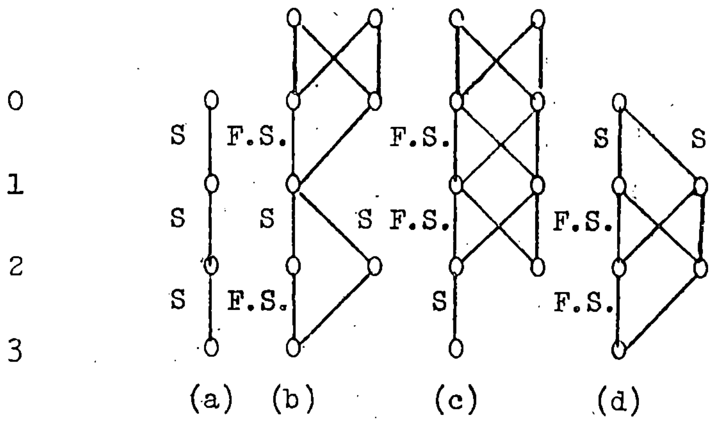
$$=\frac{1}{4}(1+F_n+2F_{n+1}). \tag{2}$$

Therefore

$$F_{n+2}=(x/2)(1+F_{n+1})+(y/4)(1+F_n+2F_{n+1}). \tag{3}$$

The formula (3) can also be verified as follows :

Generation



S=Selfing $F.S.$=Full-sibbing

As we progress from Zeroth generation ($F_0=0$), there are various ways in which the individuals arise to form successive generations. This is shown in the above diagram. In generation 1, $F=1/2$ if selfed or $F=1/4$ if there is ful-sib mating. This would give an average coefficient of inbreeding in generation 1 as

$$F_1=x\left(\frac{1}{2}\right)+y\left(\frac{1}{4}\right)=\frac{1+x}{4}. \tag{4}$$

In generation 2 an individual can arise in the following four ways.

	Mating in Generation		F
	1	2	
(*a*)	S	S	3/4
(*b*)	F.S.	S	5/8
(*c*)	S	F.S.	1/2
(*d*)	F.S.	F.S.	3/8

Therefore

$$\begin{aligned} F_2 &= x^2(3/4)+xy(5/8)+xy(1/2)+y^2(3/8) \\ &= (1/8)(6x^2+9xy+3y^2) \\ &= (3/8)(x+y)(2x+y)=(3/8)(1+x) \end{aligned} \tag{5}$$

which is in agreement if we use the general formula (3). We can now extend the above argument to the individuals of generation 3 which can arise in the following eight ways.

	Mating in Generation			F
	1	2	3	
(*a*)	S	S	S	7/8
(*b*)	S	S	F.S.	3/4
(*c*)	S	F.S.	S	3/4
(*d*)	F.S.	S	S	13/16
(*e*)	S	F.S.	F.S.	5/8
(*f*)	F.S.	S	F.S.	5/8
(*g*)	F.S.	F.S.	S	11/16
(*h*)	F.S.	F.S.	F.S.	1/2

Thus

$$F_3 = x^3(7/8) + x^2y(3/4+3/4+13/16) + xy^2(5/8+5/8+11/16) + y^3(1/2)$$
$$= (1/16)(14x^3+37x^2y+31xy^2+8y^3)$$
$$= (1/16)(14x^2+8y^2+23xy)(x+y)$$
$$= (1/16)\{8(x+y)^2+6x(x+y)+xy\}$$
$$= (1/16)(9+6x+xy). \qquad (6)$$

Again this can be easily seen to be in agreement with the results that would be obtained by using the general formula (3).