

HOMOZYGOSITY IN A SELFED POPULATION WITH AN ARBITRARY NUMBER OF LINKED LOCI

BY PREM NARAIN

Institute of Agricultural Research Statistics, New Delhi

INTRODUCTION

Quantitative measures of the intensity of inbreeding and degrees of relationship under various systems of mating were first given by Wright (1921) with the aid of path coefficients. The work of Malécot (1948) resulted in essentially the same formulae as that of Wright but his approach was to make use of the probabilities of genes being identical by descent at a locus, the coefficient of inbreeding F of an individual being defined as the probability that the two genes possessed by that individual at a locus are identical by descent. This could be extended directly to cover cases involving more than one locus provided the loci in question are not linked. The exact effect of linkage on the rate of inbreeding, however, did not receive attention until Rajagopalan (1958) studied its effect on the homozygosity of a selfed population using the generation matrix method adopted by Fisher (1949). His study was, however, not general in that it considered only two linked loci. Schnell (1961) considered for the first time, the probabilities of genes being identical by descent with respect to a given set of linked loci and gave generalised concepts of coefficient of inbreeding and panmictic index as inbreeding function (ϕ) and panmictic function (π). But he did not discuss any recurrence relation for a system of mating which would indicate how the homozygosity in a population increases with generation when linkage is operating. In this paper, this has been investigated when the population is inbred by selfing. The study takes into account an arbitrary number of linked loci to give a generalised treatment of the problem.

GENERALISATION OF "COEFFICIENT OF RELATIONSHIP"

Consider two individuals X and Y having genotypes $\frac{a_1 a_2 \dots a_r}{b_1 b_2 \dots b_r}$ and $\frac{c_1 c_2 \dots c_r}{d_1 d_2 \dots d_r}$ respectively where r is the number of loci and the horizontal line indicates that the genes above it lie on one chromosome and those below it lie on the other homologous chromosome. Taking only the i th locus into consideration, the coefficient of relationship between X and Y can be defined as

$$\rho_i^{XY} = \frac{1}{4} [P(a_i = c_i) + P(a_i = d_i) + P(b_i = c_i) + P(b_i = d_i)], \quad (1)$$

where $P(a_i = c_i)$ denotes the probability that a random gene a_i from X is identical by descent with a random gene c_i from Y at the i th locus.

Taking two loci i and j with a recombination value p_{ij} between them, this coefficient of relationship can be defined as

$$\begin{aligned} \rho_{ij}^{XX} = & \frac{1-p_{ij}}{4} \left[P(a_i=c_i; a_j=c_j) + P(b_i=c_i; b_j=c_j) \right. \\ & \left. + P(a_i=d_i; a_j=d_j) + P(b_i=d_i; b_j=d_j) \right] \\ & + \frac{p_{ij}}{4} \left[P(a_i=c_i; b_j=d_j) + P(b_i=c_i; a_j=d_j) \right. \\ & \left. + P(a_i=d_i; b_j=c_j) + P(b_i=d_i; a_j=c_j) \right] \\ & + \frac{p_{ij}(1-p_{ij})}{4} \left[P(a_i=c_i; b_j=c_j) + P(b_i=c_i; a_j=c_j) \right. \\ & + P(a_i=c_i; a_j=d_j) + P(b_i=c_i; b_j=d_j) \\ & + P(a_i=d_i; a_j=c_j) + P(b_i=d_i; b_j=c_j) \\ & \left. + P(a_i=d_i; b_j=d_j) + P(b_i=d_i; a_j=d_j) \right], \end{aligned} \tag{2}$$

where $P(a_i=c_i; a_j=c_j)$ denotes the probability that a random gene a_i from X is identical by descent with a random gene c_i from Y at the i th locus and a random gene a_j from X is identical by descent with a random gene c_j from Y at the j th locus. Similarly ρ_{ijk}^{XX} in terms of probabilities $P(a_i=c_i; a_j=c_j; a_k=c_k)$ can be defined and finally $\rho_{123 \dots r}^{XX}$ can be defined in terms of probabilities $P(a_1=c_1; a_2=c_2; \dots a_r=c_r)$.

As noted by Schnell (1961), new recombination values are, however, to be introduced when $r > 3$ to enable the gametic frequencies to be expressed as linear functions of recombination values. With four loci, 1, 2, 3 and 4 for instance, there are six recombination values, $p_{12}, p_{23}, p_{34}, p_{13}, p_{14}$ and p_{24} . A new recombination value p_{1234} is required to be introduced measuring recombination between the segments corresponding to 1st and 2nd loci and 3rd and 4th loci. The following relations exist between these recombination parameters as given by Geiringer (1944):-

$$\left. \begin{aligned} p_{13} &= p_{12} + p_{23} - 2c p_{12} \cdot p_{23} \\ p_{24} &= p_{23} + p_{34} - 2c p_{23} \cdot p_{34} \\ p_{14} &= p_{12} + p_{23} + p_{34} - 2c (p_{12} \cdot p_{23} + p_{23} \cdot p_{34} + p_{12} \cdot p_{34}) + 4c p_{12} \cdot p_{23} \cdot p_{34} \\ p_{1234} &= p_{12} + p_{34} - 2c p_{12} \cdot p_{34} \end{aligned} \right\} \tag{3}$$

where c is the coefficient of coincidence.

When c is assumed to be unity, the expression for ρ_{1234}^{XX} involves p_{12}, p_{23} and p_{34} and the various compound probabilities.

INBREEDING FUNCTION AND PANMICTIC FUNCTION

As introduced by Schnell (1961), the inbreeding function ϕ of an individual is defined as the probability that the two gametes that produced the individual contain genes which are identical by descent regarding a given set of loci. Thus, with three loci, for instance,

$$\left. \begin{aligned} \phi_{ijl}^X &= P \begin{pmatrix} a_i = b_i \\ a_j = b_j \\ a_l = b_l \end{pmatrix} \\ \phi_{ijl}^Y &= P \begin{pmatrix} c_i = d_i \\ c_j = d_j \\ c_l = d_l \end{pmatrix} \end{aligned} \right\} \quad (4)$$

Also, the function of inbreeding $\phi^{X \times Y}$ of an offspring resulting from the mating of two individuals X and Y is given by, for a given set of loci,

$$\phi_{ijl}^{X \times Y} = \rho_{ijl}^{XY} \quad (5)$$

The panmictic function π of an individual is defined as the probability that the two gametes producing the individual contain genes which are unlike by descent for a given set of loci. The relations between the two set of functions are, for a given set, say three loci, given by

$$\left. \begin{aligned} \pi_{ijl} &= 1 - \phi_i - \phi_j - \phi_l + \phi_{ij} + \phi_{jl} + \phi_{il} - \phi_{ijl} \\ \phi_{ijl} &= 1 - \pi_i - \pi_j - \pi_l + \pi_{ij} + \pi_{jl} + \pi_{il} - \pi_{ijl} \end{aligned} \right\} \quad (6)$$

As pointed out by Schnell (1961), ϕ and π are particular cases of a more general quantity ξ , the probability that the genes are identical by descent with respect to a given set of loci and also unlike by descent with respect to the remainder of the loci. Thus with three loci, under consideration, $\xi_{ijl}(ij)$ means the probability that the genes are identical by descent at the j th and l th loci but unlike by descent at the i th locus. Obviously then, we have

$$\pi_{ijl} + \xi_{ijl(i)} + \xi_{ijl(j)} + \xi_{ijl(l)} + \xi_{ijl(ij)} + \xi_{ijl(jl)} + \xi_{ijl(il)} + \phi_{ijl} = 1. \quad (7)$$

We have also, the relations given by

$$\left. \begin{aligned} \pi_{ij} &= \xi_{ijl(i)} + \pi_{ijl} \\ \pi_{jl} &= \xi_{ijl(j)} + \pi_{ijl} \\ \pi_{il} &= \xi_{ijl(l)} + \pi_{ijl} \\ \pi_i &= \xi_{ijl(ij)} + \pi_{ij} + \pi_{il} - \pi_{ijl} \\ \pi_j &= \xi_{ijl(jl)} + \pi_{jl} + \pi_{ij} - \pi_{ijl} \\ \pi_l &= \xi_{ijl(il)} + \pi_{il} + \pi_{jl} - \pi_{ijl} \end{aligned} \right\} \quad (8)$$

Similar relations hold with ϕ also.

RECURRENCE RELATIONS

(a) Two loci

Considering only the i th locus, we have already the recurrence relations given in Kempthorne (1957),

$$\left. \begin{aligned} \phi_i^{(n+1)} &= \frac{1}{2} \left(1 + \phi_i^{(n)} \right) \\ \pi_i^{(n+1)} &= \frac{1}{2} \pi_i^{(n)} \end{aligned} \right\} \quad (9)$$

where $\pi_i = 1 - \phi_i$ and $\pi_i^{(n)}$ etc. denotes the value of the function in the n th generation.

Comparing X with itself, taking into consideration the two loci, we have from (5) and (2)

$$\begin{aligned} \phi_{ij}^{X \times X} &= \rho_{ij}^{XX} \\ &= \frac{p_{ij}^2 + (1-p_{ij})^2}{2} \left[1 + \phi_{ij}^X \right] + p_{ij}(1-p_{ij}) \left[\phi_i^X + \phi_j^X \right]. \end{aligned}$$

Replacing p_{ij} by $\lambda_{ij} = 1 - 2p_{ij}$, the linkage value introduced by Schnell (1961), we get

$$\phi_{ij}^{(n+1)} = \frac{1}{4} \left(1 + \lambda_{ij}^2 \right) \left(1 + \phi_{ij}^{(n)} \right) + \frac{1}{4} \left(1 - \lambda_{ij}^2 \right) \left(\phi_i^{(n)} + \phi_j^{(n)} \right). \tag{10}$$

With the help of the relations

$$\left. \begin{aligned} \phi_{ij} &= 1 - \pi_i - \pi_j + \pi_{ij} \\ \phi_i &= 1 - \pi_i \\ \phi_j &= 1 - \pi_j \end{aligned} \right\} \tag{11}$$

and (9), this can be expressed as

$$\pi_{ij}^{(n+1)} = \left(\frac{k_{ij}}{2} \right) \pi_{ij}^{(n)}, \tag{12}$$

where

$$k_{ij} = \left(1 + \lambda_{ij}^2 \right) / 2.$$

Since π_{ij} can be expressed as $(\pi_j - \xi_{ij(i)})$, the recurrence relation (12) can be written as

$$\pi_j^{(n+1)} - \xi_{ij(i)}^{(n+1)} = \frac{k_{ij}}{2} \left(\pi_j^{(n)} - \xi_{ij(i)}^{(n)} \right),$$

which on using (9), reduces to

$$\xi_{ij(i)}^{(n+1)} - \frac{k_{ij}}{2} \xi_{ij(i)}^{(n)} = \frac{1 - k_{ij}}{2} \pi_{ij}^{(n)}. \tag{13}$$

Replacing n by $(n+1)$ in (13) and then substituting $(1/2) \pi_j^{(n)}$ for $\pi_j^{(n+1)}$, we get

$$\xi_{ij(i)}^{(n+2)} - \frac{k_{ij}}{2} \xi_{ij(i)}^{(n+1)} = \frac{1 - k_{ij}}{4} \pi_j^{(n)}. \tag{14}$$

Eliminating $\pi_j^{(n)}$ between (13) and (14), we get the recurrence relation for $\xi_{ij(i)}$ as

$$\xi_{ij(i)}^{(n+2)} - \frac{1 + k_{ij}}{2} \xi_{ij(i)}^{(n+1)} + \frac{k_{ij}}{4} \xi_{ij(i)}^{(n)} = 0. \tag{15}$$

The recurrence relation for $\xi_{ij(i)}$ is the same as (15), i being replaced by j .

(b) *Three loci*

With three linked loci i, j , and l , there are three linkage values $\lambda_{ij}, \lambda_{jl}$, and λ_{il}

respectively between i th and j th, j th and l th, and i th and l th loci connected by

$$\lambda_{il} = (1-c) (\lambda_{ij} + \lambda_{jl} - 1) + c \lambda_{ij} \lambda_{jl}, \quad (16)$$

where c is the coefficient of coincidence.

When one or two loci are considered, we have the recurrence relations for π -functions as

$$\left. \begin{aligned} \pi_i^{(n+1)} &= \frac{1}{2} \pi_i^{(n)} \\ \pi_{ij}^{(n+1)} &= \frac{k_{ij}}{2} \pi_{ij}^{(n)} \end{aligned} \right\} \quad (17)$$

When all three loci are taken into account and X is compared with itself, using (5), we get

$$\begin{aligned} \phi_{ijl}^{(n+1)} &= \frac{1}{8} \left[1 + \lambda_{ij}^2 + \lambda_{jl}^2 + \lambda_{il}^2 \right] \left[1 + \phi_{ijl}^{(n)} \right] \\ &+ \frac{1}{8} \left[1 + \lambda_{ij}^2 - \lambda_{jl}^2 - \lambda_{il}^2 \right] \left[\phi_i^{(n)} + \phi_{ij}^{(n)} \right] \\ &+ \frac{1}{8} \left[1 - \lambda_{ij}^2 + \lambda_{jl}^2 - \lambda_{il}^2 \right] \left[\phi_j^{(n)} + \phi_{jl}^{(n)} \right] \\ &+ \frac{1}{8} \left[1 - \lambda_{ij}^2 - \lambda_{jl}^2 + \lambda_{il}^2 \right] \left[\phi_i^{(n)} + \phi_{il}^{(n)} \right]. \end{aligned} \quad (18)$$

Making use of (6), (9), and (10) this can be expressed as

$$\pi_{ijl}^{(n+1)} = \frac{1}{8} \left[1 + \lambda_{ij}^2 + \lambda_{jl}^2 + \lambda_{il}^2 \right] \pi_{ijl}^{(n)}. \quad (19)$$

With no interference, $c = 1$ and (16) is simplified. The recurrence relation (19) can then be expressed simply as

$$\pi_{ijl}^{(n+1)} = \left(\frac{k_{ij} k_{jl}}{2} \right) \pi_{ijl}^{(n)}, \quad (20)$$

where

$$k_{ij} = \left(1 + \lambda_{ij}^2 \right) / 2, \text{ and } k_{jl} = \left(1 + \lambda_{jl}^2 \right) / 2.$$

The relations (8) enable π_{ijl} to be expressed in terms of the ξ -function and the π -function of order lower than three and since the recurrence relations for these π -functions, are given by (17), the recurrence relation (20) can ultimately lead to the following recurrence relations for ξ -functions.

$$\xi_{iul(i)}^{(n+2)} - \frac{k_{jl} + k_{ij} k_{jl}}{2} \xi_{iul(i)}^{(n+1)} + \frac{k_{ij} k_{jl}^2}{4} \xi_{iul(i)}^{(n)} = 0; \quad (21)$$

$$\xi_{iul(i)}^{(n+2)} - \frac{k_{il} + k_{ij} k_{jl}}{2} \xi_{iul(i)}^{(n+1)} + \frac{k_{ij} k_{jl} k_{il}}{4} \xi_{iul(i)}^{(n)} = 0; \quad (22)$$

$$\xi_{iul(i)}^{(n+2)} - \frac{k_{ij} + k_{ij} k_{jl}}{2} \xi_{iul(i)}^{(n+1)} + \frac{k_{ij}^2 k_{jl}}{4} \xi_{iul(i)}^{(n)} = 0; \quad (23)$$

$$\xi_{ij(ij)}^{(n+4)} - \frac{1+k_{jl}+k_{il}+k_{ij}k_{jl}}{2} \xi_{ij(ij)}^{(n+3)} + \frac{k_{jl}+k_{il}+k_{ij}k_{jl}+k_{jk_{il}}+k_{ij}k_{il}^2+k_{ij}k_{il}k_{il}}{4} \xi_{ij(ij)}^{(n+2)} - \frac{k_{jk_{il}}+k_{ij}k_{il}^2+k_{ij}k_{jl}k_{il}+k_{ij}k_{ij}^2k_{il}}{8} \xi_{ij(ij)}^{(n+1)} + \frac{k_{ij}k_{ij}^2k_{il}}{16} \xi_{ij(ij)}^{(n)} = 0; \quad (24)$$

$$\xi_{ij(ij)}^{(n+4)} - \frac{1+k_{il}+k_{ij}+k_{ij}k_{jl}}{2} \xi_{ij(ij)}^{(n+3)} + \frac{k_{il}+k_{ij}+k_{ij}k_{jl}-k_{ij}k_{il}+k_{ij}k_{jk_{il}}+k_{ij}^2k_{jl}}{4} \xi_{ij(ij)}^{(n+2)} - \frac{k_{ij}k_{il}+k_{ij}k_{jk_{il}}+k_{ij}^2k_{jl}+k_{ij}^2k_{ij}k_{il}}{8} \xi_{ij(ij)}^{(n+1)} + \frac{k_{ij}^2k_{ij}k_{il}}{16} \xi_{ij(ij)}^{(n)} = 0; \quad (25)$$

$$\xi_{ij(ij)}^{(n+4)} - \frac{1+k_{ij}+k_{jl}+k_{ij}k_{jl}}{2} \xi_{ij(ij)}^{(n+3)} + \frac{k_{ij}+k_{jl}+2k_{ij}k_{il}+k_{ij}^2k_{jl}+k_{ij}k_{ij}^2}{4} \xi_{ij(ij)}^{(n+2)} - \frac{k_{ij}k_{jl}+k_{ij}^2k_{il}+k_{ij}k_{ij}^2+k_{ij}^2k_{ij}^2}{8} \xi_{ij(ij)}^{(n+1)} + \frac{k_{ij}^2k_{ij}^2}{16} \xi_{ij(ij)}^{(n)} = 0. \quad (26)$$

(c) More than three loci

The recurrence relations for the panmictic function π for the two and three loci cases given respectively by (12) and (20) show a general trend. For instance, for the four loci, 1,2,3 and 4 it would be given by

$$\pi_{1234}^{(n+1)} = \frac{1}{1^5} \left(1 + \lambda^2 \frac{1}{12} + \lambda^3 \frac{1}{23} + \lambda^2 \frac{1}{34} + \lambda^2 \frac{1}{13} + \lambda^2 \frac{1}{14} + \lambda^2 \frac{1}{24} + \lambda^2 \frac{1}{1234} \right) \pi_{1234}^{(n)}. \quad (27)$$

With no interference, this would, in view of (3), reduce to

$$\pi_{1234}^{(n+1)} = \left(\frac{k_{12}k_{23}k_{34}}{2} \right) \pi_{1234}^{(n)}, \quad (28)$$

where $k_{ij} = \left(1 + \lambda^2 \right) / 2$, $(ij) = (12), (23), (34)$.

Thus, provided there is no interference, the recurrence relation for $\pi_{123\dots r}$ is given by

$$\pi_{123\dots r}^{(n+1)} = \left(\frac{k_{12}k_{23}\dots k_{(r-1)r}}{2} \right) \pi_{123\dots r}^{(n)} \quad (29)$$

where $k_{ij} = \frac{1 + \lambda^2}{2} = \frac{1 + (1 - 2p_{ij})^2}{2}$, p_{ij} being the probability of recombination between i th and $j = (i+1)$ th loci.

SOLUTIONS FOR RECURRENCE RELATIONS

(a) Two loci

If we initially start with a double heterozygote,

$$\left. \begin{aligned} \pi_{ij}^{(0)} &= \pi_i^{(0)} = \pi_j^{(0)} = 1 \\ \xi_{ij(ij)}^{(0)} &= \xi_{ij(ij)}^{(0)} = 0. \\ \phi_{ij}^{(0)} &= 0. \end{aligned} \right\} \quad (30)$$

Then the recurrence relations for π -functions given by (9) and (12) lead to the solutions

$$\left. \begin{aligned} \pi_i^{(n)} &= \left(\frac{1}{2}\right)^n \\ \pi_j^{(n)} &= \left(\frac{1}{2}\right)^n \\ \pi_{ij}^{(n)} &= \left(\frac{k_{ij}}{2}\right)^n \end{aligned} \right\} \quad (31)$$

The inbreeding function $\phi_{ij}^{(n)}$ after n generations of selfing would then, in view of (11), be given by

$$\phi_{ij}^{(n)} = 1 - 2\left(\frac{1}{2}\right)^n + \left(\frac{k_{ij}}{2}\right)^n \quad (32)$$

This result agrees with that given by Rajagopalan (1958).

Since $\xi_{ij(i)}$ and $\xi_{ij(j)}$ can be expressed respectively as $(\pi_{ij} - \pi_j)$ and $(\pi_{ij} - \pi_i)$, the solutions for ξ -functions can also be obtained with the help of (31) as given below.

$$\left. \begin{aligned} \xi_{ij(i)}^{(n)} &= \left(\frac{1}{2}\right)^n - \left(\frac{k_{ij}}{2}\right)^n \\ \xi_{ij(j)}^{(n)} &= \left(\frac{1}{2}\right)^n - \left(\frac{k_{ij}}{2}\right)^n \end{aligned} \right\} \quad (33)$$

(b) *Three loci*

Again, initially starting with an individual heterozygous for all the three loci, the values of all the π -functions are unity whereas those of ξ - and ϕ -functions are zero in the zero-th generation. The solutions for the recurrence relations for π -functions given by (17) and (20) are

$$\left. \begin{aligned} \pi_i^{(n)} &= \left(\frac{1}{2}\right)^n \\ \pi_j^{(n)} &= \left(\frac{1}{2}\right)^n \\ \pi_l^{(n)} &= \left(\frac{1}{2}\right)^n \\ \pi_{ij}^{(n)} &= \left(\frac{k_{ij}}{2}\right)^n \\ \pi_{jl}^{(n)} &= \left(\frac{k_{jl}}{2}\right)^n \\ \pi_{il}^{(n)} &= \left(\frac{k_{il}}{2}\right)^n \\ \pi_{ijl}^{(n)} &= \left(\frac{k_{ij} k_{jl}}{2}\right)^n \end{aligned} \right\} \quad (34)$$

The inbreeding function $\phi_{ijl}^{(n)}$ after n generations of selfing would then become, in view of (6),

$$\phi_{ijl}^{(n)} = 1 - 3 \left(\frac{1}{2}\right)^n + \left(\frac{k_{ij}}{2}\right)^n + \left(\frac{k_{jl}}{2}\right)^n + \left(\frac{k_{il}}{2}\right)^n - \left(\frac{k_{ij} \cdot k_{jl}}{2}\right)^n \quad (35)$$

The solutions for ξ -functions can similarly be obtained with the help of (8) and (34).

(c) *Four loci*

Starting with an individual heterozygous for each of the four loci 1, 2, 3 and 4, the solutions for various π -functions would be given by

$$\left. \begin{aligned} \pi_i^{(n)} &= \left(\frac{1}{2}\right)^n, \quad (i) = (1), (2), (3), (4) \\ \pi_{ij}^{(n)} &= \left(\frac{k_{ij}}{2}\right)^n, \quad (ij) = (12), (23), (34), (13), (14), (24) \\ \pi_{ijl}^{(n)} &= \left(\frac{k_{ij} \cdot k_{jl}}{2}\right)^n, \quad (ijl) = (123), (124), (134), (234) \\ \pi_{1234}^{(n)} &= \left(\frac{k_{12} \cdot k_{23} \cdot k_{34}}{2}\right)^n \end{aligned} \right\} \quad (36)$$

The inbreeding function $\phi_{1234}^{(n)}$ after n generations of selfing would then become

$$\phi_{1234}^{(n)} = 1 - 4\left(\frac{1}{2}\right)^n + \left(\frac{k_{12}}{2}\right)^n + \left(\frac{k_{23}}{2}\right)^n + \left(\frac{k_{34}}{2}\right)^n + \left(\frac{k_{13}}{2}\right)^n + \left(\frac{k_{14}}{2}\right)^n + \left(\frac{k_{24}}{2}\right)^n - \left(\frac{k_{12} \cdot k_{23}}{2}\right)^n - \left(\frac{k_{23} \cdot k_{34}}{2}\right)^n - \left(\frac{k_{13} \cdot k_{34}}{2}\right)^n - \left(\frac{k_{12} \cdot k_{24}}{2}\right)^n + \left(\frac{k_{12} \cdot k_{23} \cdot k_{34}}{2}\right)^n \quad (37)$$

(d) *More than four loci*

The results given by (32), (35) and (37) show a general trend. Thus, provided there is no interference, the inbreeding function ϕ , after n generations of selfing, having started with an individual heterozygous at each of the r loci involved, would be given by

$$\begin{aligned} \phi_{123\dots r}^{(n)} &= 1 - r\left(\frac{1}{2}\right)^n + \Sigma_1 \left(\frac{k_{ij}}{2}\right)^n - \Sigma_2 \left(\frac{k_{ij} \cdot k_{jl}}{2}\right)^n \\ &\quad + \Sigma_3 \left(\frac{k_{ij} \cdot k_{jl} \cdot k_{lm}}{2}\right)^n + \dots \\ &\quad + (-)^r \left(\frac{k_{12} \cdot k_{23} \cdot \dots \cdot k_{(r-1)r}}{2}\right)^n, \end{aligned} \quad (38)$$

where Σ_1 is summation over r_2 values of k given by $k_{12}, k_{23}, \dots, k_{13}, k_{14}, \dots, k_{(r-1)r}$. Similarly Σ_2 is summation over r_3 pairs of k values. The appropriate pair of k values involved would depend on the three loci selected out of r . For instance, if 1st, 4th and 9th loci are forming a trio, the two values will correspond to linkage between 1st and 4th, and 4th and 9th loci. Similar considerations are involved for other summations.

The result given by (38) would reduce to

$$\phi_{123\dots r}^{(n)} = 1 - \left(\frac{1}{2}\right)^n \quad (39)$$

if all the loci are completely linked between themselves leading to all k s being 1, whereas it would reduce to

$$\phi_{123\dots r}^{(n)} = [1 - (\frac{1}{2})^n]^r \tag{40}$$

when there is no linkage between any pairs of loci i.e. all k values are each equal to 1/2.

MEAN AND VARIANCE OF THE NUMBER OF LOCI HOMOZYGOUS BY DESCENT

As can be seen from the above considerations, when there are more than one locus, there is a distribution of the number of loci homozygous by descent. The proportion of homozygosity by descent for 0, 1, 2, ... loci depend on the k values, and the number of generations a population is inbred. The mean m and variance v of this distribution are given by

$$\left. \begin{aligned} m &= r[1 - (\frac{1}{2})^n], \\ v &= r(\frac{1}{2})^n[1 - r(\frac{1}{2})^n] + 2\sum \left(\frac{k_{ij}}{2}\right)^n \end{aligned} \right\} r=2, 3, \text{ etc.} \tag{41}$$

where \sum implies summation over r_c_2 values of i , i.e. summation is over all the pairs of loci which are distinct. Expressed in terms of ϕ_i and ϕ_{ij} these are given by

$$\left. \begin{aligned} m &= r\phi_i^{(n)} \\ v &= r\phi_i^{(n)} \left(1 - r\phi_i^{(n)}\right) + 2\sum \phi_{ij}^{(n)}. \end{aligned} \right\} \tag{42}$$

RATE OF INBREEDING

Defining the rate of inbreeding in the n th generation as $\delta^{(n)} = \frac{\phi^{(n)} - \phi^{(n-1)}}{1 - \phi^{(n-1)}}$, it may be seen that with one locus it is independent of the generation, whereas with more than one locus, it depends on the generation and the various recombination values. Thus

$$\left. \begin{aligned} \delta_1^{(n)} &= (\frac{1}{2}) \\ \delta_{12}^{(n)} &\simeq (\frac{1}{2}) \left[1 - \frac{1}{2} \left\{ \frac{k_{12}^{n-1} - k_{12}^n}{k_{12}^{n-1} + k_{12}^n} \right\} \right] \\ \delta_{123}^{(n)} &\simeq (\frac{1}{2}) \left[1 - \frac{1}{3} \left\{ \left(\frac{k_{12}^{n-1} - k_{12}^n}{k_{12}^{n-1} + k_{12}^n} \right) + \left(\frac{k_{23}^{n-1} - k_{23}^n}{k_{23}^{n-1} + k_{23}^n} \right) + \left(\frac{k_{13}^{n-1} - k_{13}^n}{k_{13}^{n-1} + k_{13}^n} \right) \right\} \right] \\ &\dots\dots\dots \\ \delta_{123\dots r}^{(n)} &\simeq (\frac{1}{2}) \left[1 - \frac{1}{r} \sum_x \left(\frac{k_{ij}^{n-1} - k_{ij}^n}{k_{ij}^{n-1} + k_{ij}^n} \right) \right]. \end{aligned} \right\} \tag{43}$$

NUMERICAL RESULTS

Tables 1 and 2 respectively give the values of the ξ -function for the case of two and three loci, together with the means, variances and the rate of inbreeding over a period of five generations, assuming certain arbitrary recombination values.

Table 1. Values of ξ -functions upto five generations for two loci with $p_{12} = .30$

n	1	2	3	4	5
ξ					
π_{12}	·2900	·0841	·0244	·0071	·0020
$\xi_{12(1)}$	·2100	·1659	·1006	·0554	·0292
$\xi_{12(2)}$	·2100	·1659	·1006	·0554	·0292
ϕ_{12}	·2900	·5841	·7744	·8821	·9396
m	1·0000	1·5000	1·7500	1·8750	1·9376
v	·5800	·4182	·2363	·1236	·0825
δ_{12}	·2900	·4142	·4576	·4774	·4877

Table 2. Values of ξ -functions upto five generations for three loci with $p_{12} = .30$ and $p_{23} = .20$

n	1	2	3	4	5
ξ					
π_{123}	·1972	·0389	·0077	·0015	·0003
$\xi_{123(1)}$	·1428	·0767	·0316	·0119	·0043
$\xi_{123(2)}$	·0628	·0287	·0099	·0031	·0009
$\xi_{123(3)}$	·0928	·0452	·0167	·0056	·0017
$\xi_{123(12)}$	·0972	·1057	·0758	·0460	·0257
$\xi_{123(23)}$	·1472	·1372	·0907	·0523	·0283
$\xi_{123(13)}$	·0672	·0892	·0690	·0435	·0249
ϕ_{123}	·1928	·4784	·6986	·8361	·9139
m	1·5000	2·2500	2·6250	2·8125	2·9064
v	1·0300	·7221	·3970	·2025	·1004
δ_{123}	·1928	·3538	·4222	·4562	·4747

It is observed from the above tables that the rate of inbreeding increases with further generations of selfing and that it is more for two loci than for three loci in every generation of selfing.

Tables 3 to 7 give the values of the inbreeding function for the case of three loci upto five generations of selfing with various combinations of values of p_{12} and p_{23} .

Table 3. *Values of the ϕ -function after one generation of selfing for three loci*

P_{12} \ P_{23}	0	.1	.3	.5
0	.5000	.4100	.2900	.2500
.1		.3338	.2322	.2100
.3			.1618	.1450
.5				.1250

Table 4. *Values of the ϕ -function after two generations of selfing for three loci*

P_{12} \ P_{23}	0	.1	.3	.5
0	.7500	.6681	.5841	.5625
.1		.5957	.5186	.5031
.3			.4524	.4381
.5				.4219

Table 5. *Values of the ϕ -function after three generations of selfing for three loci*

P_{12} \ P_{23}	0	.1	.3	.5
0	.8750	.8189	.7744	.7656
.1		.7677	.7246	.7171
.3			.6846	.6776
.5				.6699

Table 6. *Values of the ϕ -function after four generations of selfing for three loci*

P_{12} \ P_{23}	0	.1	.3	.5
0	.9375	.9033	.8821	.8789
.1		.8711	.8499	.8469
.3			.8298	.8270
.5				.8240

Table 7 Values of the ϕ -function after five generations of selfing for three loci

p_{12}	0	.1	.3	.5
p_{23}				
0	.9688	.9491	.9496	.9385
.1		.9305	.9206	.9197
.3			.9113	.9103
.5				.9093

It is apparent from the above tables that the range of effect of linkage on the homozygosity of a selfed population is maximum after one generation of selfing and goes on decreasing with further generations of selfing. This may be measured as the difference between the values of ϕ -function in the totally linked and unlinked cases. It is .3700 after one generation, .3281 after two generations, .2051 after three generations, .1135 after four generations and .0595 after five generations of selfing for three loci. It is also seen that this range is more with three loci than with two loci in each generation of selfing. The above differences in the values of ϕ -function for two loci are .2500, .1875, .1094, .0586 and .0303 respectively after the 1st, 2nd, 3rd, 4th and 5th generation of selfing.

It is also found in the case of three loci that after one generation of selfing the pairs of values for p_{12} and p_{23} can be ranked, in descending order of their effect on the homozygosity, as (0, 0), (.1, 0), (.1, .1), (.3, 0), (.5, 0), (.3, .1), (.5, .1), (.3, .3), (.5, .3) and (.5, .5). This ranking also holds true after two generations of selfing whereas after three generations, the effect of (.1, .1) and (.3, 0) are almost the same. After four and five generations of selfing, the ranking is (0, 0), (.1, 0), (.3, 0), (.5, 0), (.1, .1), (.3, .1), (.5, .1), (.3, .3), (.5, .3) and (.5, .5). Thus, with two generations of selfing (.1, .1) may be regarded as producing a tighter linkage than (.3, 0) or (.5, 0).

SUMMARY

1. A generalised 'coefficient of relationship' between two individuals X and Y has been defined with any number of linked loci.
2. Recurrence relations for ϕ -, π - and ξ -functions (Schnell, 1961) in the case of two and three loci have been obtained.
3. Solutions for recurrence relations have been given for ϕ -function upto the case of any number of linked loci.
4. It has been found that the effect of linkage on the homozygosity of a selfed population is more with a greater number of linked loci and is maximum after one generation of selfing. With three linked loci, the pairs of values of p_{12} , p_{23} when taken as (.1, .1) exert a greater effect than (.3, 0) or (.5, 0) but this is true only upto two generations of selfing.

5. With more than one locus, the rate of inbreeding is not constant with further generations of selfing. It depends on the number of generations of selfing and the recombination values.

REFERENCES

- FISHER, R. A. (1949). *The Theory of Inbreeding*. Oliver and Boyd: Edinburgh.
- GEIRINGER, H. (1944). On the probability theory of linkage in Mendelian heredity. *Ann. Math. Statist.*, **15**, 25-57.
- KEMPTHORNE, O. (1957). *An Introduction to Genetic Statistics*. John Wiley & Sons: New York.
- MALÉCOT, G. (1948). *Les mathématiques de l'hérédité*. Masson et Cie: Paris.
- RAJAGOPALAN, M. (1958). Effect of linkage on the homozygosity of selfed population. *J. Ind. Soc. Agri. Stat.*, **10**, 64-66.
- SCHNELL, F. W. (1961). Some general formulations of linkage effects in inbreeding. *Genetics*, **46**, 947-957.
- WRIGHT, S. (1921). Systems of mating I-V. *Genetics*, **6**, 111-178.