

Original Article

Mathematical Models in Genetics and Population Inheritance

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Manuscript ID: **Abstract**

JRD -2026-180503

ISSN: 2230-9578

Volume 18

Issue 5

Pp. 24-46

May- 2026

Submitted: 15 Apr. 2026

Revised: 25 Apr. 2026

Accepted: 10 May. 2026

Published: 31 May 2026

Mathematical genetics provides an important quantitative framework for understanding heredity, inheritance, genetic variation, and population evolution. In the present study, several mathematical models associated with genetics are investigated using probability theory, matrix methods, combinatorial techniques, and nonlinear difference equations. The paper mainly focuses on inheritance models, Hardy–Weinberg equilibrium, phenotype and genotype distributions, mutation-selection balance, blood group inheritance, sex-linked characteristics, and inbreeding models. Genetic matrices corresponding to dominant, hybrid, and recessive genotypes are formulated to describe the transmission of hereditary traits across successive generations. The Hardy Weinberg law is derived as an equilibrium condition under random mating, demonstrating the constancy of gene frequencies in stable populations. Mathematical expressions governing phenotype ratios and multiple allele systems are also developed, together with applications to human blood groups. The study further investigates models of genetic improvement through crossbreeding and elimination of recessive traits. Selection and mutation processes are analysed using nonlinear difference equations, and the corresponding equilibrium and stability conditions are discussed in detail. Different inbreeding models, including selfing, sib-mating, implanting, and brother sister mating, are examined to understand the reduction of heterozygosity and long-term genetic variability. The analysis shows that mathematical models play a significant role in explaining hereditary mechanisms, evolutionary dynamics, and population stability. These models possess important applications in agriculture, biotechnology, medicine, animal breeding, and genetic engineering, particularly in the development of disease-resistant and high-yielding species. The present work demonstrates the effectiveness of mathematical techniques in studying complex biological inheritance systems and genetic evolution.

Keywords : Mathematical genetics; Population genetics; Hardy Weinberg law; Genetic matrices; Inheritance models; Selection and mutation; Gene frequencies; Inbreeding models; Phenotype ratios; Blood group inheritance; Sex-linked inheritance; Difference equations; Genetic equilibrium; Crossbreeding; Evolutionary genetics.

Introduction

Investigations in mathematical modelling and study of Genetics has attracted many scientists and researchers in recent years Kerlin [1], Ignatieva et al. [2], Marke [3], Hartl and Clark [4], Nagylaki [5], Nesse [6] Lange [7], Burger [8]. In a family children are generally like the parents. The children resemble the parents either in skin colour or in pattern of hair or eye colour. There may be a family where a child is not like either of the parents. The child differs in some visible character from the parent. Scientists have tried to explain the causes for such similarities or dissimilarities between the parents and off spring. The process through which the parental characters pass to the next generation is called heredity or inheritance. The branch of science which teaches us the mechanism of heredity is known as genetics (Sharma and Anupneha [9]). Since long we were not aware of the mechanism of heredity and we had no clear conception of this mystery of life. However, in the 19th century when people came to know the true nature of germ cells much light was thrown on the mechanism of heredity. One of the pioneers in this field is G.J. Mendel (1822-84), a monk in a monastery at Brunn in Australia. He is called the ‘Father of Heredity’ (Geiringer [10], Crow and Kimura [11]). The knowledge of heredity has its practical applications for the welfare of mankind. This has helped us in plant and animal breedings.

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How to cite this article:

Kumar, M. (2026). Mathematical Models in Genetics and Population Inheritance. *Journal of Research & Development*, 18(5), 24–46. <https://doi.org/10.5281/zenodo.20906365>



Quick Response Code:



Website:

<https://jrdrv.org/>

DOI:

10.5281/zenodo.20906365



In breeding desirable characters present in two parent plants or animals of same or allied species are combined by artificial crossing to produce high-yielding and disease resistance varieties (Ignatieva et al. [2], Akin [12], Teisser [13]). This has wide application in agriculture and it has been possible to produce different varieties of wheat, paddy, cotton, potato, sugarcane and vegetables. The method of production of high yielding crops developed by scientists and biotechnologists have helped a lot to solve the food shortage in India and abroad.

Some useful terms (Kapur [14], Traykov and Trenchev [15])

1. Unit character – Definite external characters of individuals of a cross.
2. Dominant – In a cross there is a character which expresses itself and covers over the other character. The character expressed is called dominant character and is designated by the first letter of the word in capital form. For example, black is a dominant character but is expressed only by writing B.
3. Recessive – It is the character which is present but cannot express itself due to the presence of dominant character. This is shown by the small letter of the word expressing dominant character. For example, white is shown by b or dwarf is shown by t.
4. Allelomorphs or allele – A pair of contrasting characters of which one is dominant and the other is recessive. These two characters are situated in genes at corresponding loci of homologous chromosomes. For example, black and white, tall and dwarf, round and wrinkled.
5. Hybrid – Offspring containing two different unit characters of which one comes from father and the other from mother. For example, offspring formed from tall and short parent (Tt).
6. Homozygote – Where a zygote has similar characters. For example, pure tall TT or pure dwarf tt.
7. Heterozygote – Where this zygote has allelomorphic characters it produces hybrid offspring. For example, hybrid tall which is represented genotypically as Tt.
8. Genotype – Here genetic composition of the individual is considered. Offspring with similar genes or factors (characters) are genotypically alike. For example, TT and TT or tt and tt. TT and TT both are tall and contain similar genes. But TT and Tt are tall externally but one differs from the other in the genetic composition because genetically one is pure tall (TT) and the other is hybrid tall (Tt).
9. Phenotype – Here only externally visible characters are considered and not the genetic composition. Individuals having similar external characters (without considering their genetic composition) are phenotypically alike. For example, TT and Tt both are tall externally but genetically they differ. TT pure tall whereas Tt hybrid tall.

2. Basic Model for Inheritance

(A) Genetic Matrices (Pundir and Pundir [17], Teisser [13], Kapur [14]): Each trait of an individual such as height, eye color, or blood type is determined by a pair of genes, with one gene inherited from each parent. Each gene occurs in two alternative forms, namely the dominant allele G and the recessive allele g . As a result, an individual can possess one of three possible genotypes:

- (i) ($G \cdot G$), identified as the dominant type and denoted by D ;
- (ii) ($G \cdot g$) or ($g \cdot G$), referred to as the heterozygous or hybrid type and represented by H ;
- (iii) ($g \cdot g$), classified as the recessive type and denoted by R .

During reproduction, each offspring receives one allele from each parent, with the inheritance of either allele occurring independently and with equal probability $\frac{1}{2}$.

For example, a cross between a ($G \cdot G$) individual and a ($G \cdot g$) individual yields four equally probable genetic combinations in the offspring.

The probability of this outcome is $\frac{1}{2} \times \frac{1}{2} = \frac{1}{4}$, resulting in a dominant (D) offspring.

- (i) If the offspring receives the allele G from the first parent and the allele g from the second parent, the probability of this outcome is $\frac{1}{2} \times \frac{1}{2} = \frac{1}{4}$. In this case, the resulting genotype is heterozygous (hybrid), denoted by H .
- (i) If the offspring inherits the second allele G from the first parent and the allele G from the second parent, the probability of this combination is again $\frac{1}{4}$. This pairing results in the homozygous dominant genotype, denoted by D .
- (ii) If the offspring receives the alternate G allele from the first parent and the allele g from the second parent, the probability of this particular combination is $\frac{1}{4}$. This genetic pairing results in a heterozygous (hybrid) offspring, denoted by H .

Consequently, the probabilities of the offspring being dominant (D), hybrid (H), and recessive (R) are $\frac{1}{2}$, $\frac{1}{2}$, and 0, respectively. By applying the same line of reasoning, the results summarized in Table 6.1 are obtained, which present the probabilities of obtaining D , H , and R offspring for all possible pairwise crosses among D , H , and R genotypes.

The three basic genetic matrices, corresponding to matings involving D , H , and R , respectively, are derived as follows.

$$A = \begin{bmatrix} 1 & 0 & 0 \\ \frac{1}{2} & \frac{1}{2} & 0 \\ 0 & 1 & 1 \end{bmatrix}, B = \begin{bmatrix} \frac{1}{2} & \frac{1}{2} & 0 \\ \frac{1}{4} & \frac{1}{2} & \frac{1}{4} \\ 0 & \frac{1}{2} & \frac{1}{2} \end{bmatrix}, C = \begin{bmatrix} 0 & 1 & 0 \\ 0 & \frac{1}{2} & \frac{1}{2} \\ 0 & 0 & 1 \end{bmatrix} \quad (2.1)$$

Table 6.1 Results of Crossing by Two Genotypes

	D			H			R		
	D	H	R	D	H	R	D	H	R
D	1	0	0	$\frac{1}{2}$	$\frac{1}{2}$	0	0	1	0
H	$\frac{1}{2}$	$\frac{1}{2}$	0	$\frac{1}{4}$	$\frac{1}{2}$	$\frac{1}{4}$	0	$\frac{1}{2}$	$\frac{1}{2}$
R	0	1	0	0	$\frac{1}{2}$	$\frac{1}{2}$	0	0	1

Each of these matrices satisfies the properties of a stochastic matrix, as all of their entries are non-negative and the sum of the elements in every row is equal to one. This property arises because, for each possible parental combination, the probabilities that the offspring falls into genotype *D*, *H*, or *R* collectively add up to unity.

Consider a population in which the proportions (or probabilities) of individuals exhibiting the dominant (*D*), hybrid (*H*), and recessive (*R*) genotypes are represented by *p*, *q*, and *r*, respectively. These probabilities satisfy the normalization condition

$p + q + r = 1$. Accordingly, the population state can be represented by the probability vector

$$P = (p, q, r) \quad (2.2)$$

is referred to as the probability vector representing the genetic composition of the population.

When every individual in the population is crossed with a parent of dominant genotype, the first transition matrix determines the resulting distribution of genotypes in the offspring generation. In this case, the probability that an offspring belongs to the dominant class (*D*) is given by

$$1 \cdot p + \frac{1}{2} \cdot q + 0 \cdot r = p + \frac{1}{2}q, \quad (2.3)$$

while the probability that the offspring is hybrid (*H*) is

$$0 \cdot p + \frac{1}{2} \cdot q + 1 \cdot r = \frac{1}{2}q + r. \quad (2.4)$$

The probability of obtaining a recessive (*R*) offspring is

$$0 \cdot p + 0 \cdot q + 0 \cdot r = 0. \quad (2.5)$$

Accordingly, when the population is crossed with individuals of pure dominant genotype, the genetic composition of the first offspring generation is obtained by multiplying the initial probability row vector *P* by the first transition matrix *A*. Thus, the resulting probability vector is expressed as *PA*.

Similarly, if the population represented by the probability vector *P* is crossed with pure hybrid or pure recessive individuals, the genotype distributions of the first generation are determined by the matrix products *PB* and *PC*, respectively.

When the initial population is consecutively mated with individuals of dominant, hybrid, dominant, recessive, and hybrid genotypes in that order, the genetic composition of the fifth generation can be determined through successive matrix multiplications. The resulting probability vector for this generation is therefore expressed as *PABACB*

When the population is crossed with dominants, the probability vector of the first generation coincides with the original probability vector if $PA = P$, that is, if

$$(p + \frac{1}{2}q, \frac{1}{2}q + r, 0) = (p, q, r).$$

This condition is satisfied only when $p = 1$, $q = 0$, and $r = 0$, leading to

(2.6)

Similarly, the relations

(2.7)

and

(2.8)

are obtained under the corresponding mating conditions.

Further, if a population characterized by If the initial probability vector P is repeatedly crossed with pure dominant individuals n times, the probability vector representing the genetic composition of the n th generation is obtained by multiplying P with the dominant matrix A successively n times. Mathematically, this is expressed as PA^n . To compute this quantity, it is necessary to evaluate A^n , which can be achieved conveniently by first diagonalizing the matrix A . Since the eigenvalues of A are readily determined, along with their associated eigenvectors $(1, 1, 1)$, $(0, 1, 2)$, and $(0, 0, 1)$, the matrix A can be expressed in a form suitable for this analysis.

$$A = \begin{bmatrix} 1 & 0 & 0 \\ 1 & 1 & 0 \\ 1 & 2 & 1 \end{bmatrix} = \begin{bmatrix} 1 & 0 & 0 \\ 0 & \frac{1}{2} & 0 \\ 0 & 0 & 0 \end{bmatrix} \begin{bmatrix} 1 & 0 & 0 \\ -1 & 1 & 0 \\ 1 & -2 & 1 \end{bmatrix} = SAS^{-1} \quad (2.9)$$

so that

$$= \begin{bmatrix} 1 & 0 & 0 \\ 1 & 1 & 0 \\ 1 & 2 & 1 \end{bmatrix} \begin{bmatrix} 1 & 0 & 0 \\ 0 & \frac{1}{2^n} & 0 \\ 0 & 0 & 0 \end{bmatrix} \begin{bmatrix} 1 & 0 & 0 \\ -1 & 1 & 0 \\ 1 & -2 & 1 \end{bmatrix} = \begin{bmatrix} 1 & 0 & 0 \\ 1 - \frac{1}{2^n} & \frac{1}{2^n} & 0 \\ 1 - \frac{1}{2^{n-1}} & \frac{1}{2^{n-1}} & 0 \end{bmatrix} \quad (2.10)$$

$$PA^n = \left(1 - \frac{q}{2^n} - \frac{r}{2^{n-1}}, \frac{q}{2^n} + \frac{r}{2^{n-1}}, 0 \right) \quad (2.11)$$

As n tends to infinity, the vector PA^n converges to $(1, 0, 0)$. Consequently, when any population is repeatedly and randomly crossed exclusively with dominant individuals, several long-term effects are observed: (i) recessive genotypes eventually disappear from the population, (ii) the proportion of hybrids gradually declines to zero, and (iii) the fraction of dominant individuals approaches unity. Notably, even when the initial population consists entirely of recessives, the proportion of dominants reaches 15/16 by the fifth generation and increases further to 511/512 by the tenth generation. These results demonstrate that a population composed solely of recessives can be systematically converted into a predominantly dominant population over a finite number of generations through successive matings with dominant individuals

Hardy – Weinberg Law (Pundir and Pundir [36])

Consider a population undergoing random mating, or panmixia, characterized by the probability vector P . The probability vectors corresponding to matings with dominant (D), hybrid (H), and recessive (R) individuals are PA , PB , and PC , respectively. Since the proportions of D , H , and R individuals in the population are p , q , and r , the probability vector describing the first filial generation, F_1 , is obtained by appropriately weighting these vectors according to their respective population proportions.

$$pPA + qPB + rPC = \left(\left(p + \frac{1}{2}q \right)^2, 2 \left(p + \frac{1}{2}q \right) \left(r + \frac{1}{2}q \right), \left(r + \frac{1}{2}q \right)^2 \right) \\ = (p', q', r') = P' \text{ (say)} \quad (2.12)$$

The three entries of the probability vector representing the second-generation population, F_2 , are given by

$$\left(p' + \frac{1}{2}q' \right)^2 = \left[\left(p + \frac{1}{2}q \right)^2 + \frac{1}{2} \cdot 2 \left(p + \frac{1}{2}q \right) \left(r + \frac{1}{2}q \right) \right]^2 \\ = \left(p + \frac{1}{2}q \right)^2 \left(p + \frac{1}{2}q + r + \frac{1}{2}q \right)^2 = \left(p + \frac{1}{2}q \right)^2 = p' \quad (2.13)$$

$$\begin{aligned}
 2\left(p' + \frac{1}{2}q'\right)\left(r' + \frac{1}{2}q'\right) &= 2\left[\left(p + \frac{1}{2}q\right)^2 + \left(p + \frac{1}{2}q\right)\left(r + \frac{1}{2}q\right)\right] \\
 &\left[\left(r + \frac{1}{2}q\right)^2 + \left(p + \frac{1}{2}q\right)\left(r + \frac{1}{2}q\right)\right] \\
 &= 2\left(p + \frac{1}{2}q\right)\left(p + \frac{1}{2}q + r + \frac{1}{2}q\right)\left(r + \frac{1}{2}q\right)\left(r + \frac{1}{2}q + p + \frac{1}{2}q\right) \\
 &= 2\left(p + \frac{1}{2}q\right)\left(r + \frac{1}{2}q\right) = q' \quad (2.14)
 \end{aligned}$$

$$\begin{aligned}
 \left(r' + \frac{1}{2}q'\right)^2 &= \left[\left(r + \frac{1}{2}q\right)^2 + \left(p + \frac{1}{2}q\right)\left(r + \frac{1}{2}q\right)\right]2 \\
 &= \left(r + \frac{1}{2}q\right)^2 \left(r + \frac{1}{2}q + p + \frac{1}{2}q\right)^2 = \left(r + \frac{1}{2}q\right)^2 = r' \quad (2.15)
 \end{aligned}$$

Consequently, the probability vector for the second generation F_2 coincides with that of the first generation F_1 . This result indicates that, under random mating, the probability vectors remain unchanged not only for the first generation but also for all subsequent generations. This principle is known as the Hardy Weinberg law, named after the mathematician G. H. Hardy and the geneticist W. Deviations from this equilibrium may arise due to factors such as non-random mating patterns or differential mortality rates among individuals carrying dominant and recessive genes. In practice, however, distinguishing among the three genotypes is often challenging. When the gene G is dominant over g , individuals with genotypes $(G \cdot G)$ and $(G \cdot g)$ exhibit identical observable characteristics and therefore belong to the same phenotype. As a result, although three distinct genotypes exist, only two phenotypic classes are observed with respect to a given gene, namely $\{(G, G), (G, g)\}$ and $\{(g, g)\}$.

Individuals possessing the genotype $(G \cdot G)$ or $(g \cdot g)$ are referred to as homozygous, whereas those with the genotype $(G \cdot g)$ are classified as heterozygous. The Hardy–Weinberg law can also be formulated in terms of gene frequencies. Let P and Q denote the relative frequencies of the alleles G and g within a population, and let (p, q, r) represent the relative frequencies of the genotypes $(G \cdot G)$, $(G \cdot g)$, and $(g \cdot g)$, respectively. Under these definitions, it can be readily seen that

$$P = p + \frac{1}{2}q, \quad Q = \frac{1}{2}q + r \quad (2.18)$$

Given the values of p , q , and r , the corresponding gene frequencies P and Q can be uniquely determined. In contrast, knowledge of P and Q alone does not uniquely specify the genotype frequencies p , q , and r . However, under the assumption of random mating, equations (2.17) and (2.18) lead to

$$P = 1 - \sqrt{r}, \quad Q = \sqrt{r} \quad (2.19)$$

Consider any generation in which the relative frequencies of the genes G and g are P and Q , respectively, with the constraint $P + Q = 1$, and assume that these frequencies are identical in both males and females. Under random mating, the probability that an offspring inherits the gene G from one parent and g from the other is $2PQ$, while the probability that it inherits the gene g from both parents is Q^2 . Consequently, the genotype proportions in the first filial generation F_1 are

$$(G, G): P^2, (G, g): 2PQ, (g, g): Q^2. \quad (2.20)$$

Using relations (6.2.13)– (6.2.15) and (6.2.18), the Hardy–Weinberg proportions are obtained. The relative gene frequencies in F_1 are given by

$$G: 2P^2 + 2PQ = 2P(P + Q) = 2P, g: 2PQ + 2Q^2 = 2Q(P + Q) = 2Q. \quad (2.21)$$

Thus, the gene proportions in the first generation remain identical to those in the original population, and the second filial generation F_2 again exhibits the genotype ratios specified in (2.20). This result provides further confirmation of the Hardy–Weinberg law.

(C) Correlation between Genetic Composition of Siblings

As an illustration of the application of the basic model, we examine the correlation between the genetic compositions of offspring produced by the same pair of parents, under the assumptions of random mating and genetic stability of the population. In the original population, let the proportions of dominant, hybrid, and recessive individuals be specified by equation (2.17), that is,

$$P = (1 - \sqrt{r})^2, \quad q = 2\sqrt{r}(1 - \sqrt{r}), \quad r = r$$

Let Y_1 and Y_2 denote two offspring produced by the same parents X_1 and X_2 . By applying the theorems of total probability and compound probability, the required correlation can be derived as follows.

$$\begin{aligned} P(Y_1 = D, Y_2 = D) &= P(Y_1 = D, Y_2 = D; X_1 = D, X_2 = D) + \\ &P(Y_1 = D, Y_2 = D; X_1 = D, X_2 = H) \\ &+ P(Y_1 = D, Y_2 = D; X_1 = H, X_2 = D) + P(Y_1 = D, Y_2 = D; \\ &X_1 = H, X_2 = H) \\ &= P(X_1 = D; X_2 = D) P(Y_1 = D, Y_2 = D/X_1 = D, X_2 = D) \\ &+ P(X_1 = D, X_2 = H) P(Y_1 = D, Y_2 = D/X_1 = D, X_2 = H) \\ &+ P(X_1 = H, X_2 = D) P(Y_1 = D, Y_2 = D/X_1 = H, X_2 = D) \\ &+ P(X_1 = H, X_2 = H) P(Y_1 = D, Y_2 = D/X_1 = H, X_2 = H) \\ &= p^2 \cdot 1 + pq \cdot \frac{1}{4} + pq \cdot \frac{1}{4} + q^2 \cdot \frac{1}{16} = p^2 + \frac{1}{2} pq + \frac{1}{16} q^2 \\ &= (1 - \sqrt{r})^4 + \sqrt{r}(1 - \sqrt{r})^2 + \frac{1}{4} r(1 - \sqrt{r})^2 \\ &= \frac{1}{4} (1 - \sqrt{r})^2 (2 - \sqrt{r})^2 \end{aligned} \quad (2.22)$$

$$\begin{aligned} P(Y_1 = D, Y_2 = H) &= P(Y_1 = H, Y_2 = D) \\ &= \frac{1}{2} \sqrt{r}(1 - \sqrt{r})^2 (2 - \sqrt{r}) \end{aligned}$$

$$P(Y_1 = D, Y_2 = R) = P(Y_1 = R, Y_2 = D) = \frac{1}{4} r(1 - \sqrt{r})^2$$

$$P(Y_1 = H, Y_2 = r) = P(Y_1 = R, Y_2 = H) = \frac{1}{2} r(1 - \sqrt{r})(1 + \sqrt{r})$$

$$P(Y_1 = H, Y_2 = H) = \sqrt{r}(1 - \sqrt{r})(1 + \sqrt{r} - r)$$

$$P(Y_1 = R, Y_2 = r) = \frac{1}{4} r(1 - \sqrt{r})^2$$

By assigning the numerical values 1, 0, and -1 to the genotypes D, H, and R, respectively, the resulting joint (bivariate) probability distribution can be constructed as follows:

Y_1	Y_2	Probability
1	1	$\frac{1}{4} (1 - \sqrt{r})^2 (2 - \sqrt{r})^2$
-1	-1	
0	0	
1	0	$\frac{1}{4} (1 - \sqrt{r})^2$
0	1	
1	-1	$\sqrt{r}(1 - \sqrt{r})(1 + \sqrt{r} - r)$
-1	1	
0	-1	$\frac{1}{2} \sqrt{r}(1 - \sqrt{r})^2 (1 - \sqrt{r})$
-1	0	
		$\frac{1}{2} \sqrt{r}(1 - \sqrt{r})^2 (1 - \sqrt{r})$
		$\frac{1}{4} r(1 - \sqrt{r})^2$

		$\frac{1}{4}r(1-\sqrt{r})^2$
		$\frac{1}{2}r(1-r)$
		$\frac{1}{2}r(1-r)$

The marginal distributions of Y_1 and Y_2 are the same and are given by

Y_1 or Y_2	1	0	-1
Probability	$(1-\sqrt{r})^2$	$2\sqrt{r}(1-r)$	r

From these we easily deduce

$$\bar{Y}_1 = \bar{Y}_2 = 1 - 2\sqrt{r} \quad (2.28)$$

$$\sigma_{Y_1}^2 = \sigma_{Y_2}^2 = 2\sqrt{r}(1-\sqrt{r}) \quad (2.29)$$

$$\text{cov}(Y_1, Y_2) = \sqrt{r}(1-\sqrt{r}) \quad (2.30)$$

$$\rho_{Y_1, Y_2} = \frac{1}{2} \quad (2.31)$$

Consequently, the resulting correlation coefficient is independent of the parameter r , indicating that it assumes the same value for all genes, regardless of their specific frequencies.

(D) Bayes Theorem and Its Applications

At any given time, a set of hypotheses is formulated to explain genetic phenomena, and probabilities are assigned to these hypotheses to quantify the degree of confidence associated with each. These initial probabilities are referred to as a priori probabilities. When an event is observed, the degrees of confidence in the competing hypotheses are revised: the probabilities associated with some hypotheses increase, while those of others decrease. The updated probabilities are known as a posteriori probability. Bayes' theorem provides a formal relationship between a priori and a posteriori probability.

Let $H_1, H_2, \dots, H_n$ represent n mutually exclusive hypotheses, with corresponding prior probabilities $P(H_1), P(H_2), \dots, P(H_n)$. Suppose an event A occurs, and let $P(A | H_1), P(A | H_2), \dots, P(A | H_n)$ denote the conditional probabilities of A under each hypothesis. The goal is to compute the posterior probabilities $P(H_1 | A), P(H_2 | A), \dots, P(H_n | A)$ in terms of the known prior probabilities $P(H_i)$ and conditional probabilities $P(A | H_i)$ for $i = 1, 2, \dots, n$. Using the theorem of compound probability, we have

$$P(AH_i) = P(H_i) P(A|H_i) = P(A) P(H_i | A)$$

so that

$$P(H_i | A) = \frac{P(H_i)P(A | H_i)}{P(A)}, \quad i = 1, 2, \dots, n \quad (2.32)$$

Since the hypotheses $H_1, H_2, \dots, H_n$ are mutually exclusive and collectively exhaustive, the theorem of total probability can be applied, yielding $P(A) = P(AH_1) + P(AH_2) + \dots + P(AH_n) =$

$$\sum_{i=1}^n P(AH_i) = \sum_{i=1}^n P(H_i)P(A | H_i) \quad (2.33)$$

From (6.2.32) and (6.2.33), we get

$$P(H_j | A) = \frac{P(H_j)P(A | H_j)}{\sum_{j=1}^n P(H_j)P(A | H_j)} \quad (2.34)$$

which is the required Bayes theorem.

To demonstrate the application of Bayes' theorem in a genetic context, we examine the probability that a pair of blue-eyed male twins is monovular, that is, derived from a single fertilized egg. In this situation, two competing hypotheses are considered: (i) H_1 : the twins originate from the same egg and are therefore monovular; and (ii) H_2 : the twins arise from different eggs and are thus binovular. To determine the prior probabilities $P(H_1)$ and $P(H_2)$, we recall

the empirical observation that approximately 32 percent of all twin pairs are of unlike sex. Of the remaining 68 percent, it is reasonable to assume that half are monovular and the other half are binovular. Accordingly,

$$P(H_1) = \frac{36}{68} = \frac{9}{17}, P(H_2) = \frac{32}{68} = \frac{8}{17} \quad (2.35)$$

To evaluate the conditional probabilities $P(A | H_1)$ and $P(A | H_2)$, we assume that mating occurs at random and that the population is genetically stable, implying that the proportions of dominant (D), hybrid (H), and recessive (R) genotypes are given by

$$p = (1 - \sqrt{r})^2, \quad q = 2\sqrt{r}(1 - \sqrt{r}), \quad r = r \quad (2.36)$$

Since blue eye color is known to be determined by a recessive gene, the conditional probability that both male twins are recessive, given that they originate from the same egg, is

$$P(A | H_1) = r, \quad (2.37)$$

where r denotes the proportion of recessive individuals in the population.

In contrast, the conditional probability that both boys are recessive when they originate from different eggs is given by

$$P(A | H_2),$$

which corresponds to the probability that two independently formed offspring both express the recessive genotype.

The overall probability is obtained by summing the probabilities of all parental genotype combinations that can produce two children with the bb genotype. Specifically, these combinations include: both parents being Bb ; one parent Bb and the other bb ; the reverse, with the first parent bb and the second Bb ; and finally, both parents being bb . The total probability is the sum of these four individual cases.

$$\begin{aligned} &= q^2 \times \frac{1}{4} \times \frac{1}{4} + qr \times \frac{1}{2} \times \frac{1}{2} + qr \times \frac{1}{2} \times \frac{1}{2} + r^2 \times |x| \\ &= \frac{r(1 - \sqrt{r})^2}{4} + \frac{r\sqrt{r}(1 - \sqrt{r})}{1} + r^2 \\ &= \frac{1}{4}r(1 + r - 2\sqrt{r} + 4\sqrt{r} - 4r + 4r) \frac{1}{4}r(1 + \sqrt{r})^2 \end{aligned} \quad (2.38)$$

By employing equations (6.2.34), (6.2.35), (6.2.37), and (6.2.38), the posterior probabilities $P(H_1 | A)$ and $P(H_2 | A)$ can be determined.

As a second example illustrating the application of Bayes' theorem, consider the following problem. Two individuals with dominant phenotypes mate and produce an offspring that also exhibits a dominant phenotype. The question of interest is to determine the probability that both parents are true dominants. Four possible hypotheses regarding the parental genotypes are considered:

- H_1 : both parents are $(G, G), (G, G)$,
- H_2 : parents are $(G, G), (G, g)$,
- H_3 : parents are $(G, g), (G, G)$,
- H_4 : both parents are $(G, g), (G, g)$.

Let the event A denote the occurrence that the offspring is either (G, G) or (G, g) , that is, phenotypically dominant. The corresponding conditional probabilities are

$$P(A | H_1) = 1, P(A | H_2) = 1, P(A | H_3) = 1, P(A | H_4) = \frac{3}{4}.$$

In the absence of any additional information, Bayes' principle is applied by assuming that all four hypotheses have equal a priori probabilities. Consequently,

3. Further Study of Basic Model for Inheritance of Genetic Characteristics

(a) Phenotype Ratios : For a single gene, there exist four possible genetic configurations, namely $\{(G, G), (G, g), (g, G), (g, g)\}$. These configurations can be classified into three distinct genotypes: dominant (D) corresponding to (G, G) ; hybrid (H) corresponding to (G, g) and (g, G) ; and recessive (R) corresponding to (g, g) . Phenotypically, however, only two observable classes arise: the dominant phenotype, comprising $\{(G, G), (G, g), (g, G)\}$, and the recessive phenotype, consisting solely of (g, g) . Consequently, the ratio of dominant to recessive phenotypes is 3:1.

When two genes are considered simultaneously, the number of possible genetic combinations increases to sixteen, reflecting the greater complexity of multilocus inheritance.

$G_1G_1G_2G_2$	$G_1G_1G_2g_2$	$G_1G_1g_2G_2$	$G_1G_1g_2g_2$
$G_1g_1G_2G_2$	$G_1g_1G_2g_2$	$G_1g_1g_2G_2$	$G_1g_1g_2g_2$
$g_1G_1G_2G_2$	$g_1G_1G_2g_2$	$G_1G_1g_2G_2$	$g_1G_2g_2g_2$
$g_1g_1G_2G_2$	$g_1g_1G_2g_2$	$g_1g_1g_2G_2$	$g_1g_1g_2g_2$

There are 9 genotypes:

D_1D_2, D_1H_2, D_1R_2 H_1D_2, H_1H_2, H_1R_2 R_1D_2, R_1H_2, R_1R_2

These combinations occur with relative frequencies 1,2,1,2,4,2,1,2, and 1, respectively. On the basis of observable characteristics, these genetic combinations can be classified into four distinct phenotypes.

$D_1D_2, D_1R_2, R_1D_2, R_1R_2$

with frequencies 9 : 3 : 3 : 1.

We now extend the discussion to the case of n genes. For each individual gene, there are four possible genetic combinations, and therefore the total number of possible combinations for n genes is 4^n . Each gene admits three distinct genotypes, which implies that the total number of genotypes across n genes is 3^n . Similarly, since each gene gives rise to two phenotypes, the total number of phenotypic classes for n genes is 2^n . Moreover, with respect to any single gene, dominant phenotypes occur three times as frequently as recessive phenotypes.

Let us determine the number of dominant phenotypes with respect to r genes. We can select r genes from a total of n in $\binom{n}{r}$ ways. For each such selection, there are three dominant phenotypes and one recessive phenotype. Consequently, the number of individuals that are dominant for the chosen r genes and recessive for the remaining $n - r$ genes is given by

$$\binom{n}{r} 3^r 1^{n-r}.$$

The total frequency of all possible genotype combinations is obtained by summing this expression over all permissible values of r .

$$\sum_{r=0}^n \binom{n}{r} 3^r = (3+1)^n = 4^n \quad (3.1)$$

For a system with n genes, there are a total of 4^n possible genotypes. These can be grouped according to their dominance with respect to the number of genes as follows: for each $r = 0, 1, 2, \dots, n$, there are $\binom{n}{r}$ groups of 3^{n-r} genotypes, each dominant with respect to $n - r$ genes.

Specifically, this gives:

1. one group of 3^n genotypes,
2. $\binom{n}{1}$ groups of 3^{n-1} genotypes each,
3. $\binom{n}{2}$ groups of 3^{n-2} genotypes each,
4. ...,
5. $\binom{n}{r}$ groups of 3^{n-r} genotypes each,
6. and one group of 1 genotype.

The ratios of phenotypes emerge naturally from these groupings. In particular, phenotype frequencies are represented by the coefficients obtained from the binomial expansion of $(3x+y)^n$, whereas genotype frequencies are given by the coefficients in the multinomial expansion of $(x+2y+z)^n$. Furthermore, the frequency of a genotype that is dominant with respect to r genes, hybrid with respect to s genes, and recessive with respect to the remaining $n - r - s$ genes can be formulated in terms of appropriate combinatorial coefficients, as established by Turelli and Barton [122].

(b) Multiple Alleles and Application to Blood Groups

Up to this point, we have discussed cases involving only two alleles, G and g . However, a single genetic locus can have more than two alleles. A well-known example is the gene responsible for human blood groups, which has three alleles: A , B , and O . These three alleles can combine to form a total of nine possible genotypic combinations.

The possible ordered genetic combinations are

$(A, A), (A, B), (A, O), (B, A), (B, B), (B, O), (O, A), (O, B), (O, O)$.

However, these reduce to only six distinct genotypes, since combinations such as (A, B) and (B, A) , (A, O) and (O, A) , and (B, O) and (O, B) are genetically equivalent. As alleles A and B are dominant over allele O , only four phenotypically distinguishable blood groups are observed. These correspond to the following classifications:

1. **Group A:** $(A, A), (A, O), (O, A)$
2. **Group B:** $(B, B), (B, O), (O, B)$
3. **Group AB:** $(A, B), (B, A)$

4. Group O: (O·O)

Accordingly, these phenotypes are designated as blood groups A, B, AB, and O, respectively. Utilizing these genetic combinations, one can systematically determine the possible genotypes and corresponding blood groups of offspring, as presented in Table 3.2. Moreover, Table 3.3 can be derived from Table 3.2 to identify the range of possible paternal blood groups when the blood groups of the mother and child are known.

Table 6.2 Genotypes and Blood Groups of Offspring

Father Mother	A		B		C	
	(A, A)	(A, O)	(B, B)	(B, O)	(A, B)	(O, O)
	(A, A)	(A, A), (A, O)	(A, B)	(A, B), (A, O)	(A, A) (A, B)	(A, O)
(A, A)	A	A	AB	AB, A	A, AB	A
A	(A, A) (A, O)	(A, A), (A, O), (O, O)	(A, B), (B, O)	(A, B), (A, O), (B, O)	(A, A), (A, O), (A, B), (B, O)	(A, O), (O, O)
(A, O)	A	A, O	AB, B	AB, A, B, O	A, AB, B	A, O
	(A, B)	(A, B), (B, O)	(B, B)	(B, B), B, O)	(A, B), (B, B)	(B, O)
(B, B)	AB	AB, B	B	B	AB, B	B
B	(A, B), (A, O)	(A, B), (A, O), (B, O), (O, O)	(B, B), (B, O)	(B, B), (B, O), (O, O)	(A, B), (B, B), (A, O), (B, O)	(B, O), (O, O)
(B, O)	AB, A	AB, A, B, O	B	B, O	AB, B, A	B, O
	(A, A), (A, B)	(A, A), (B, O), (A, O), (A, B)	(A, B), (B, B)	(A, B), (A, O), (B, O)	(A, A) (A, B), (B, B)	(A, O), (B, O)
AB (A, B)	A, AB	A, B, AO	AB, B	AB, A, B	A, AB, B	A, B
	(A, O)	(A, O), (O, O)	(B, O)	(B, O), (O, O)	(A, O), (B, O)	(O, O)
O (O, O)	A	A, O	B	B, O	A, B	O

Table 6.3 Possible blood groups of Father in terms of Blood Groups of Mother and Child

Child Mother	A	B	AB	O
A	A, B, AB, O	B, AB	B, AB	A, B, O
B	A, AB	A, B, AB, O	A, AB	AB, O
AB	A, B, AB, O	A, B, AB, O	A, B, AB	□
O	A, AB	B, AB	□	A, B, O

Table 6.3 is used in certain disputed legal cases to decide whether a certain child born of a certain mother can be the child of a given male.

Let the allele frequencies of *A*, *B*, and *O* in a population be denoted by *p*, *q*, and *r*, respectively. Under the assumption of random mating, the expected proportions of individuals belonging to the four blood groups A, B, AB, and O can be determined from these allele frequencies using standard genetic principles.

$$\text{Blood group A: } p^2 + 2pr$$

$$\text{Blood group B: } q^2 + 2qr$$

$$\text{Blood group AB: } 2pq$$

$$\text{Blood group O: } r^2$$

Conversely, if the distribution of the population according to blood groups is known, the allele frequencies p , q , and r can be estimated using these relations.

(c) Inheritance of Sex-linked Characteristics

In mammals, females have two X sex chromosomes while males have one X and one Y-chromosome. Moreover, many of the genes in the X-chromosome have no complement in the Y-chromosome, in this case, the genotype of the male is determined entirely by the allele occurring in the X-chromosome. Such genes and the characteristics controlled by them are said to be sex linked. For these we have

Female XX	GG	Gg	gg
Male XY	G, g		

The genotype of the male is determined by the single class of the gene since the Y-chromosome carries none of the genes found in the X-chromosome.

If P_n is the proportion of allele G in the females of the n -th generation, then the proportion of G in the males of the n -th generation must be P_{n-1} since all these have come from the $(n-1)$ th generation of the females. Thus, in the n -th generation, females have the proportions P_n , Q_n and males have the proportions P_{n-1} , Q_{n-1} ($P_n + Q_n = P_{n-1} + Q_{n-1} = 1$) and therefore, in the $(n+1)$ th generation for the females, we have

GG	Gg	gg
$P_n P_{n-1}$	$P_n Q_{n-1} + Q_n P_{n-1}$	$Q_n Q_{n-1}$

From this we get

$$P_{n+1} = P_n P_{n-1} + \frac{1}{2}(P_n Q_{n-1} + Q_n P_{n-1}) = P_n P_{n-1} + \frac{1}{2}(P_n - 2P_n P_{n-1} + P_{n-1}) = \frac{1}{2}(P_n + P_{n-1}) \quad (3.2)$$

or

$$P_{n+1} - P_n = -\frac{1}{2}(P_n - P_{n-1}) = \left(-\frac{1}{2}\right)^2 (P_{n-1} - P_{n-2}) = \dots = \left(-\frac{1}{2}\right)^n (P_1 - P_0) \quad (3.3)$$

or

$$\left. \begin{aligned} P_{n+1} &= P_n + \left(-\frac{1}{2}\right)^n (P_1 - P_0) \\ P_n &= P_{n-1} + \left(-\frac{1}{2}\right)^{n-1} (P_1 - P_0) \\ &\vdots \\ P_1 &= P_0 + \left(-\frac{1}{2}\right)^0 (P_1 - P_0) \end{aligned} \right\} \quad (3.4)$$

Adding (6.3.4), We get

$$P_{n+1} = P_0 + \frac{2}{3}(P_1 - P_0) \left[1 - \left(-\frac{1}{2}\right)^{n+1}\right] \quad (3.5)$$

As $n \rightarrow \infty$

$$P_n \rightarrow P_0 + \frac{2}{3}(P_1 - P_0) = \frac{2}{3}P_1 + \frac{1}{3}P_0 = \alpha \quad (3.6)$$

Thus we get the limiting proportions

Female XX	Male XY
GG α^2	G α
Gg $2(1-\alpha)\alpha$	g $1-\alpha$
gg $(1-\alpha)^2$	

Table 6.4 Proportion of Populations according to Blood Groups and Alleles

Population	PART I				PART II		
	Blood Groups				Alleles		
	A	B	AB	O	A	B	O
I	42	8	3	47	0.69	0.25	0.06
II	38	10	3	49	0.70	0.23	0.07
III	34	11	3	52	0.70	0.23	0.07
IV	27	31	3	54	0.70	0.23	0.07
V	27	35	7	31	0.56	0.20	0.24
VI	24	34	9	33	0.50	0.26	0.24

4. Models for Genetic Improvement: Selection and Mutation

(I) Genetic Improvement through Crossbreeding

Previously, we discussed the outcomes of crossing a breed with a dominant, recessive, or hybrid breed over successive generations. Now, we consider a scenario where genes associated with undesirable traits are to be removed from a population and replaced with genes carrying desirable traits.

Let

$$g_1g_1, g_2g_2, g_3g_3, \dots, g_ng_n$$

represent the n pairs of genes that are to be replaced, and

$$G_1G_1, G_2G_2, G_3G_3, \dots, G_nG_n$$

denote the n pairs of desirable genes that will replace them.

An individual carrying the gene pairs in the second set will be considered as belonging to the G -race. This designation does not imply that G is dominant and g is recessive; it merely identifies individuals with the desired genetic composition.

When the initial generation F_0 is crossed with the G -race, the first filial generation F_1 is obtained as

$$G_1g_1, G_2g_2, G_3g_3, \dots, G_ng_n. \quad (4.3)$$

In this generation, one recessive allele g_i in each gene pair is replaced by the corresponding dominant allele G_i . The objective is to eliminate the remaining g_i alleles through repeated crossings with the G -race. These successive crossings produce the generations

$$F_2, F_3, \dots, F_{m+1}, \dots \quad (4.4)$$

At each generation, there is a probability of $\frac{1}{2}$ that a given allele g_i is replaced by G_i , and an equal probability of $\frac{1}{2}$ that it remains unchanged. Consequently, the probability that the $(m+1)$ -th generation still contains the allele g_i is $(\frac{1}{2})^m$.

Furthermore, the probability that exactly r out of the n gene replacements have not occurred follows a binomial distribution and is given by

$${}^nC_0 \left(\frac{1}{2^m}\right)^0 \left(1 - \frac{1}{2^m}\right)^{n-0} = \left(1 - \frac{1}{2^m}\right)^n \quad (4.6)$$

As m becomes very large, the probability converges to one, irrespective of the value of n . Consequently, in the long run, all genes g_i will eventually be replaced by G_i for $i = 1, 2, \dots, n$.

(II) Genetic Improvement through Elimination of Recessives

An alternative approach for enhancing the genetic makeup of plant and animal populations involves the systematic removal of recessive individuals in every generation. This may be achieved, for instance, by eliminating recessive plants or by preventing recessive animals from participating in reproduction, while permitting random mating among the remaining individuals in the population.

Let the proportions of dominant, hybrid, and recessive individuals in the n -th generation be denoted by p_n , q_n , and r_n , respectively. Under the assumption of random mating among the non-eliminated individuals, the genetic composition of the population in the $(n+1)$ -th generation can be determined in terms of these proportions.

$$P_{n+1} = \left(p_n + \frac{1}{2} q_n \right)^2, a_{n+1} = 2 \left(p_n + \frac{1}{2} q_n \right) \left(r_n + \frac{1}{2} q_n \right),$$

$$r_{n+1} = \left(r_n + \frac{1}{2} q_n \right)^2$$
(4.7)

If recessive individuals are systematically removed from the population in the n -th generation, the resulting genetic composition of the population in the $(n+1)$ -th generation can be expressed in terms of the updated proportions of dominants and hybrids after elimination.

$$P_{n+1} = \left(p'_n + \frac{1}{2} q'_n \right)^2, q_{n+1} = 2 \left(p'_n + \frac{1}{2} q'_n \right) \frac{1}{2} q'_n, r_{n+1} = \left(\frac{1}{2} q'_n \right)^2 \quad (4.8)$$

Where $p'_n q'_n$ are the removal of recessive individuals, the adjusted proportions represent the genetic composition of the population in the n -th generation following elimination, and hence the updated frequency distribution can be written as follows.

$$\frac{p'_n}{q'_n} = \frac{p_n}{q_n}, p'_n + q'_n = 1 \quad (4.9)$$

From (6.4.8) and (6.4.9) we get

$$P_{n+1} = \left(1 - \frac{1}{2} q'_n \right)^2, q_{n+1} = q'_n \left(1 - \frac{1}{2} q'_n \right), r_{n+1} = \left(\frac{1}{2} q'_n \right)^2 \quad (4.10)$$

Upon removing the recessive individuals from the population, the resulting genetic composition is given by

$$\frac{p'_{n+1}}{1 - \frac{1}{2} q'_n} = \frac{q'_{n+1}}{q'_n} = \frac{1}{1 + \frac{1}{2} q'_n}$$

or

$$q'_{n+1} = \frac{q'_n}{1 + \frac{1}{2} q'_n} \quad (4.11)$$

This equation represents a difference equation that can be used to solve for the desired quantity. By substituting the relevant values or expressions, we obtain

$$u_n = \frac{1}{q_n} \quad (4.12)$$

In (6.4.11), we get

$$u_{n+1} = u_n + \frac{1}{2} \quad (4.13)$$

whose solution is

$$u_n = A + \frac{1}{2} n \quad (4.14)$$

so that

$$q'_n = \frac{1}{A + \frac{1}{2} n} \quad (4.15)$$

To determine A, we make use of (2.17) of Section 3.2 to get

$$q'_n = \frac{q}{p+q} = \frac{2\sqrt{r}}{1+\sqrt{r}} \quad (4.16)$$

so that

$$A = \frac{1}{2\sqrt{r}} \quad (4.17)$$

Also,

$$q'_n = \frac{2\sqrt{r}}{1+n\sqrt{r}} \quad (4.18)$$

$$r_{n+1} = \left(\frac{1}{2}q'_n\right)^2 = \frac{r}{(1+n\sqrt{r})^2} \quad (4.19)$$

This expression yields the proportion of recessive individuals in the $(n+1)$ -th generation. Knowing the initial proportion of recessives in a genetically stable population, equation (4.19) can be employed to determine the number of generations required to reduce the recessive proportion below any prescribed threshold through systematic elimination at each stage. In this manner, the long-term impact of selective removal of recessives on population structure can be quantitatively assessed. Alternatively, rather than removing all recessive individuals, one may allow a fixed fraction k of the recessive population to remain in each generation. Under this modified strategy, the evolution of the genetic composition is governed by a new set of basic recurrence relations, which describe the resulting proportions of dominants, hybrids, and recessives.

$$p'_n = \frac{1-kr_n}{1-r_n} p_n, \quad q'_n = \frac{1-kr_n}{1-r_n} q_n, \quad r'_n = kr_n \quad (4.20)$$

$$p'_n + q'_n + p'_n = 1 \quad (4.21)$$

$$p_{n+1} = \left(p'_n + \frac{1}{2}q'_n\right)^2 = \left(\frac{1-kr_n}{1-r_n}\right)^2 \left(p_n + \frac{1}{2}q_n\right)^2 \quad (4.22)$$

$$q_{n+1} = 2\left(p'_n + \frac{1}{2}q'_n\right)\left(r'_n + \frac{1}{2}p'_n\right) = 2\left(\frac{1-kr_n}{1-r_n}\right) \quad (4.23)$$

$$\left(p_n + \frac{1}{2}q_n\right)\left(Kr_n + \frac{1-kr_n}{1-r_n}q_n\right)$$

$$r_{n+1} = \left(r'_n + \frac{1}{2}q'_n\right)^2 = \left(kr_n + \frac{1}{2}\frac{1-kr_n}{1-r_n}q_n\right)^2 \quad (4.24)$$

$$p'_{n+1} = \frac{1-kr_{n+1}}{1-r_{n+1}} p_{n+1} = \frac{1-kr_{n+1}}{1-r_{n+1}} \left(p'_n + \frac{1}{2}q'_n\right)^2 \quad (4.25)$$

$$q'_{n+1} = \frac{1-kr_{n+1}}{1-r_{n+1}} q_{n+1} = 2\frac{1-kr_{n+1}}{1-r_{n+1}} \left(p'_n + \frac{1}{2}q'_n\right)^2 \left(r'_n + \frac{1}{2}q'_n\right) \quad (4.26)$$

$$q'_{n+1} = kr_{n+1} = k\left(r'_n + \frac{1}{2}q'_n\right) \quad (4.27)$$

From equations (4.22)– (4.24), we obtain a pair of first-order nonlinear simultaneous difference equations governing the evolution of p_n and q_n . Similarly, equations (4.25)– (4.27) lead to another system of two nonlinear simultaneous difference equations for determining the corresponding variables. Although these formulations fully describe the dynamics of the system, the resulting equations are mathematically intricate, and explicit closed-form solutions are not readily obtainable.

(III) Selection and Mutation

Let P_n and Q_n represent the proportions of the alleles G and g in the n -th generation. Assuming random mating, the frequencies of the genotypes GG , Gg , and gg in the $(n+1)$ -th generation are determined directly from these allele proportions. Suppose the survival probabilities for these genotypes are $S(1-K)$, S , and $S(1-k)$, respectively, where the parameters k and K satisfy $|k| < 1$ and $|K| < 1$. By incorporating these differential survival probabilities, the normalized relative proportions of the genotypes in the $(n+1)$ -th generation can then be calculated.

$$S(1-K)P_n^2, 2SP_nQ_n, S(1-k)Q_n^2 \quad (4.28)$$

so that the relative proportions of G and g in this generation are

$$2S(1-K)P_n^2, 2SP_nQ_n, 2SP_nQ_n + 2S(1-k)Q_n^2 \quad (4.29)$$

and hence

$$\frac{P_{n+1}}{Q_{n+1}} = \frac{(1-K)(P_n^2 / Q_n^2) + (P_n / Q_n)}{(P_n / Q_n) + (1-k)} \quad (4.30)$$

or

$$u_{n+1} = \frac{(1-K)u_n^2 + u_n}{u_n + (1-k)}, u_n = \frac{P_n}{Q_n} \quad (4.31)$$

This relation constitutes a first-order nonlinear difference equation. Once the initial value u_1 is specified, the sequence $\{u_n\}$ can be generated iteratively in a step-by-step manner. The equilibrium (steady-state) solution is obtained by imposing the condition $u_n = u_{n+1} = u$, which leads to the corresponding equilibrium equation.

$$u = \frac{(1-K)u^2 + u}{u + 1 - k} \quad (4.32)$$

or

$$u(uK - k) = 0 \quad (6.4.33)$$

Consequently, the equilibrium solutions are $u = 0$, $u = \frac{k}{K}$, or $u^{-1} = 0$, implying that, in the extreme cases, either the dominant allele or the recessive allele completely survives. Apart from these trivial solutions, the system admits a non-trivial equilibrium given by

$$u = \frac{k}{K}. \quad (4.34)$$

For this equilibrium to be biologically meaningful, it must be positive; therefore, the parameters k and K must have the same sign. This condition indicates that either the heterozygotes possess the highest fitness or they are the least fit relative to the homozygotes. In the special case where $K = k$, the equilibrium frequencies of the genes G and g become equal.

To analyze the stability of the equilibrium solution given in (4.33), we observe from equation (4.31) that

$$u_{n+1} - u_n = \frac{Ku_n}{u_n + 1 - k} \left(\frac{k}{K} - u_n \right) \quad (4.35)$$

or

$$\frac{u_{n+1} - u_n}{k/K - u_n} = \frac{Ku_n}{u_n + 1 - k} \quad (4.36)$$

and

$$\frac{u_{n+1} - k/K}{u_n - k/K} = \frac{u_n(1-K) + (1-k)}{u_n + 1 - k} \quad (4.37)$$

From (6.4.37), we deduce the following results:

- (i) When $0 < k < K < 1$ and $u_n > \frac{k}{K}$, it follows that

$$u_{n+1} < u_n \text{ and } u_{n+1} > \frac{k}{K},$$

which implies that u_{n+1} lies closer to $\frac{k}{K}$ than u_n . Hence, the sequence $\{u_n\}$ decreases monotonically and converges to the equilibrium value $\frac{k}{K}$. Conversely, if $u_n < \frac{k}{K}$, then

$$u_{n+1} > u_n \text{ and } u_{n+1} < \frac{k}{K},$$

so the sequence increases monotonically toward $\frac{k}{K}$. In the former situation, the sequence is monotonically decreasing and bounded below, while in the latter it is monotonically increasing and bounded above. Therefore, in both cases, when $0 < k < K < 1$, the equilibrium solution is asymptotically stable.

- (ii) If both k and K are negative and $\frac{k}{K} < 1$, then equations (6.4.35) and (6.4.37) imply that the quantities

$$u_{n+1} - u_n, u_n - \frac{k}{K}, \text{ and } u_{n+1} - \frac{k}{K}$$

have the same sign. Consequently, if $u_n > \frac{k}{K}$, then $u_{n+1} > \frac{k}{K}$ and $u_{n+1} > u_n$, indicating that u_{n+1} moves farther away from the equilibrium point than u_n . Similarly, if $u_n < \frac{k}{K}$, then $u_{n+1} < \frac{k}{K}$ and $u_{n+1} < u_n$, again showing divergence from the equilibrium. Thus, when both k and K are negative, the equilibrium solution is unstable.

In summary, a stable equilibrium arises when heterozygotes possess the highest fitness, whereas an unstable equilibrium occurs when heterozygotes are the least fit. Equation (6.4.35) may therefore be rewritten as

$$\frac{u_{n+1}u_n}{(n+1)-1} = \frac{Ku_n}{u_n+1-k} \left(\frac{k}{K} - u_n \right) \quad (4.38)$$

When the variation from one generation to the next is negligible compared to the variations in the preceding or subsequent generations such as in cases where K is very small or when the system exhibits minor oscillations around the equilibrium state the discrete difference equation (6.4.38) may be approximated by a corresponding differential equation.

$$\frac{du}{dn} = \frac{Ku}{u+1-k} \left(\frac{k}{K} - u \right) \quad (4.39)$$

which gives, on integration,

$$\left(\frac{1}{k} - \right) \ln u + \left(\frac{1}{K} + \frac{1}{k} - 1 \right) \ln \left| \left(\frac{k}{K} - u \right) \right| = n + \text{constant}$$

This formulation enables us to analyze how the variable u evolves from one generation to the next. In an analogous manner, the interplay between natural selection and mutation can also be examined. Suppose that the survival probabilities of the dominant (D), hybrid (H), and recessive (R) genotypes are $S(1-K)$, $S(1-K)$, and S , respectively, and let μ denote the probability that a mutation from g to G occurs within a single generation. Under these assumptions, the governing relations can be derived accordingly.

$$\begin{aligned} \frac{P_{n+1}}{Q_{n+1}} &= \frac{2S(1-K)P_n + 2S(1-K)P_nQ_n + \mu(2S(1-K)P_nQ_n + 2SQ_n^2)}{(2S(1-K)P_nQ_n + 2SQ_n^2)(1-\mu)} \\ &= \frac{\left(\frac{P_n}{Q_n} + 1 \right) (1-K) \frac{P_n}{Q_n} + \mu \left(\frac{P_n}{Q_n} + 1 - K \frac{P_n}{Q_n} \right)}{\left(\frac{P_n}{Q_n} + 1 - K \frac{P_n}{Q_n} \right) (1-\mu)} \end{aligned} \quad (4.41)$$

$$u_{n+1} = \frac{(u_n+1)(1-K)u_n + \mu(u_n+1-Ku_n)}{(u_n+1-Ku_n)(1-\mu)} \quad (4.42)$$

If we assume that u_n is sufficiently small—which is a reasonable assumption given that mutation rates are typically very low, on the order of 10^{-5} or smaller—then alleles associated with reduced fitness can persist in the population only at very low frequencies through mutation. Under this approximation, equation (6.4.42) may be simplified and rewritten in the following form.

$$u_{n+1} = u_n(1-K) + \mu \quad (4.43)$$

In equilibrium, this gives

$$U = \mu/K. \quad (4.44)$$

An alternative Discussion of Selection

In Section (6.4.III), the problem of selection was examined using the ratio P_n/Q_n . An equivalent analysis can also be carried out by considering P_n alone. Let σ_1 , σ_2 , and σ_3 represent the survival proportions of the dominant (D), hybrid (H), and recessive (R) genotypes, respectively, from birth until reproductive maturity. Under these assumptions, the following relations are obtained.

$$P_{n+1} = \frac{\sigma_1 P_n^2 + \sigma_2 P_n Q_n}{\sigma_1 P_n^2 + 2\sigma_2 P_n Q_n + \sigma_3 Q_n^2} = f(P_n) \quad (4.45)$$

If $n \rightarrow \infty$, then $P_n \rightarrow P$, $P_{n+1} \rightarrow P$, and $Q_n \rightarrow 1 - P$, so that

$$\sigma_1 P^3 + 2\sigma_2 P^2(1 - P) + \sigma_3(1 - P)^2 P - \sigma_1 P^2 - \sigma_2 P(1 - P) = 0 \quad (4.46)$$

This formulation yields three possible equilibrium states of the system.

$$P = 0, P = 1, P_c = \frac{\sigma_2 - \sigma_3}{2\sigma_2 - \sigma_1 - \sigma_3} \quad (4.47)$$

The third equilibrium solution exists provided that $0 < P_c < 1$, and it is of particular importance because, under this condition, all three genetic forms dominant (D), hybrid (H), and recessive (R) persist in the population. Using this result, equation (4.45) can now be expressed in the following form.

$$\left(P_{n+1} - \frac{\sigma_2 - \sigma_3}{2\sigma_2 - \sigma_1 - \sigma_3} \right) = \frac{\sigma_1 P_n + \sigma_3 Q_n}{\sigma_1 P_n^2 + 2\sigma_2 P_n Q_n + \sigma_3 Q_n^2} \left(P_n - \frac{\sigma_2 - \sigma_3}{2\sigma_2 - \sigma_1 - \sigma_3} \right) \quad (4.48)$$

This also shows that, if $P_n \rightarrow P_e$, then P_{n+1} also approaches P_e . Now

$$\begin{aligned} \frac{\sigma_1 P_n + \sigma_3 Q_n}{\sigma_1 P_n^2 + 2\sigma_2 P_n Q_n + \sigma_3 Q_n^2} &= \frac{\sigma_1 P_n + \sigma_2 Q_n}{(\sigma_1 P_n + \sigma_3 Q_n)(P_n + Q_n) + (2\sigma_2 - \sigma_1 - \sigma_3)P_n Q_n} \\ &= \frac{1}{1 + \frac{2\sigma_2 - \sigma_1 - \sigma_3}{\sigma_1 P_n + \sigma_3 Q_n}} \end{aligned} \quad (4.49)$$

From (6.4.48) and (6.4.49), we deduce the following results.

(i) If $\square_2 > \square_1, \square_3$, Under these conditions, the first factor on the right-hand side of equation (4.48) is less than unity, and consequently the corresponding inequality follows.

$$|P_{n+1} - P_e| < |P_n - P_e| \quad (4.50)$$

As a result, P_n converges to P_e as $n \rightarrow \infty$, irrespective of the initial value P_0 . Hence, the equilibrium state is stable (see Fig. 6.1).

$$\begin{array}{c} \leftarrow \\ \frac{0 \ P_e \ P_{n+1} \ P_n \ P_2 \ P_2 \ P_0 \ 1}{0 \ P_0 \ P_1 \ P_2 \ P_n \ P_{n+1} \ P_e \ 1} \end{array}$$

Fig. 6.1 $\square_2 > \square_1, \square_3$: stable equilibrium

(ii) If $\square_2 < \square_1, \square_3$, In this case, the first factor on the right-hand side of equation (6.4.48) exceeds unity, and as a consequence the subsequent inequality follows.

$$|P_{n+1} - P_e| > |P_n - P_e| \quad (4.51)$$

Consequently, the equilibrium state is unstable. If $P_0 < P_e$, then $P_n \rightarrow 0$, whereas if $P_0 > P_e$, we obtain $P_n \rightarrow 1$ (see Fig. 6.2).

$$\begin{array}{c} \rightarrow \\ \frac{0 \ P_e \ P_0 \ P_1 \ P_2 \ P_n \ P_{n+1} \ 1}{0 \ P_{n+1} \ P_n \ P_2 \ P_1 \ P_0 \ P_e} \end{array} P_0 < P_e$$

Fig. 6.2 $\square_2 < \square_1, \square_3$: unstable equilibrium

These findings are consistent with the results obtained in Section (6.4.III) and demonstrate that the equilibrium state is stable when heterozygotes possess the highest survival probability, whereas it becomes unstable when heterozygotes have the lowest survival advantage. For the equilibrium to remain stable, it is therefore necessary that the following condition be satisfied.

$$\begin{aligned} 2\sigma_2 - \sigma_1 - \sigma_3 &> \frac{\sigma_2 - \sigma_3}{2\sigma_2 - \sigma_1 - \sigma_3} > 0, \sigma_2 - \sigma_3 > 0 \\ \frac{\sigma_2 - \sigma_3}{2\sigma_2 - \sigma_1 - \sigma_3} &< 1, \sigma_2 - \sigma_3 < 2\sigma_2 - \sigma_1 - \sigma_3, \sigma_2 - \sigma_1 > 0 \end{aligned} \quad (4.52)$$

Hence, for P_e to constitute a for a solution to represent an equilibrium, it is both a necessary and sufficient condition that $\sigma_2 > \sigma_1, \sigma_3$.

The sequence $\{P_n\}$ is said to converge to the limit P_e at a geometric rate c if

$$\lim_{n \rightarrow \infty} \frac{|P_n - P_e|}{c^n} < \infty, \quad \lim_{n \rightarrow \infty} \frac{|P_n - P_e|}{c^n} = \infty \quad (4.53)$$

The convergence of the sequence is referred to as algebraic if

$$\lim_{n \rightarrow \infty} n^k |P_n - P_e| = \text{a positive constant.}$$

By applying equations (6.4.53) and (6.4.54), it can be shown that when $\sigma_2 > \sigma_1, \sigma_3$, the convergence of the sequence is geometric, occurring at the rate

$$\frac{1}{1 + \frac{2\sigma_2 - \sigma_1 - \sigma_3}{\sigma_1 P_e + \sigma_3 E_e}} = \frac{\sigma_2(\sigma_2 + \sigma_3) - 2\sigma_3\sigma_3}{\sigma_2^2 - \sigma_1\sigma_3} \quad (4.55)$$

Models for Genetic Inbreeding

(i) Inbreeding model I : Selling

Inbreeding means mating of relative, the degree of inbreeding depending on how close the relations are. The closest form of inbreeding occurs in plants where self-fertilization can take place and then same plant can act both as father and mother. The study of inbreeding has played an important role in improving breeds of plants and animals and in explaining certain moral taboos against marriages of close relatives among human beings.

Let G, g be the alleles corresponding to one locus. In selfing, we allow mating of dominants with dominants only, hybrids with hybrids only, and recessives with recessives only, i.e., we allow.

$$(G, G) \times (G, G), (G, g) \times (G, g), (g, g) \times (g, g),$$

and do not allow

$$(G, G) \times (G, g), (G, G) \times (g, g), (G, g) \times (g, g)$$

Let p_n, q_n, r_n be the proportions of D, H, R in the n -th generation. Then :

- (i) $(G, G) \times (G, G)$ gives all (G, G) :
- (ii) $(G, g) \times (G, g)$ gives one-fourth (G, G) , half (G, g) , half (G, g) and one-fourth (g, g) , and
- (iii) $(g, g) \times (g, g)$ gives all (g, g) ,

$$P_{n+1} = P_n + \frac{1}{4}q_n, \quad q_{n+1} = \frac{1}{2}q_n, \quad r_{n+1} = r_n + \frac{1}{4}q_n \quad (5.1)$$

Now, solving (6.5.1), we obtain

$$q_n = q_0 \left(\frac{1}{2}\right)^n, \quad p_n = p_0 + \frac{1}{2}q_0 \left\{1 - \left(\frac{1}{2}\right)^n\right\},$$

$$r_n = r_0 + \frac{1}{2}q_0 \left\{1 - \left(\frac{1}{2}\right)^n\right\} \quad (5.2)$$

So that, an $n \rightarrow \infty$

$$\frac{1}{2}q_0, \quad q_n \rightarrow 0, \quad r_n \rightarrow r_0 + \frac{1}{2}q_0 \quad (5.3)$$

Thus, by selfing, the heterozygotes tend to disappear rather fast, variability is reduced, and likelihood of homozygous individuals increases.

(ii) Inbreeding Model II: Sib – mating

Here we allow six matings:

$$(G, G) \times (G, G), (g, g) \times (g, g), (G, G) \times (G, g),$$

$$(G, g) \times (g, g), (g, g) \times (G, g), (G, G) \times (g, g)$$

or

$$D \times D, R \times R, D \times H, H \times R, H \times H, D \times H$$

Let $P_n, Q_n, R_n, S_n, T_n, U_n$ be the proportions of these crossings in the n -th generation and let F_n denote the vector

$$F_n (P_n, Q_n, R_n, S_n, T_n, U_n) \quad (5.4)$$

To find F_{n+1} , we note the following:

- (i) $P_n D \times D$ matings give all dominants so that there are $P_n D \times D$ matings in F_{n+1}
- (ii) $Q_n R \times R$ matings yield all recessives, resulting in $Q_n R \times R$ matings in F_{n+1}

- (iii) $R_n D \times H$ matings give $\frac{1}{2} R_n$ dominants and $\frac{1}{2} R_n$ hybrids and, therefore, there are $\frac{1}{4} R_n D \times D$, $\frac{1}{2} R_n D \times H$, and $\frac{1}{4} R_n H \times H$ matings in F_{n+1} .
- (iv) $S_n H \times R$ matings produce $\frac{1}{2} S_n$ hybrids and $\frac{1}{2} S_n$ recessives so that there are $\frac{1}{4} S_n H \times H$, $\frac{1}{2} S_n H \times R$, $\frac{1}{4} S_n R \times R$ matings in F_{n+1} .
- (v) $T_n H \times H$ matings yield $\frac{1}{4} T_n$ dominants, $\frac{1}{2} T_n$ hybrids, and $\frac{1}{4} T_n$ recessives, and hence there are $\frac{1}{16} T_n D \times D$, $\frac{1}{4} T_n D \times H$, $\frac{1}{8} T_n D \times R$, $\frac{1}{4} T_n H \times R$, $\frac{1}{4} T_n H \times H$, $\frac{1}{16} T_n R \times R$ matings in F_{n+1} .
- (vi) $U_n D \times R$ matings give U_n hybrids, and so there are $U_n H \times H$ matings in F_{n+1} .

From (i) – (vi), we get the equations:

$$P_{n+1} = P_n + \frac{1}{4} R_n + \frac{1}{10} T_n, Q_{n+1} = Q_n + \frac{1}{4} S_n + \frac{1}{16} T_n \quad (5.5a)$$

$$R_{n+1} = \frac{1}{2} R_n + \frac{1}{4} T_n, S_{n+1} = \frac{1}{2} S_n + \frac{1}{4} T_n \quad (5.5b)$$

$$T_{n+1} = \frac{1}{4} R_n + \frac{1}{4} S_n + \frac{1}{4} T_n + U_n, U_{n+1} = \frac{1}{8} T_n \quad (5.5c)$$

Equations (6.5.5) can be written as

$$F_{n+1} = F_n C, \quad (5.6)$$

where C is the generation matrix

$$C = \begin{matrix} & \begin{matrix} D \times D & R \times R & D \times H & H \times R & H \times H & D \times R \end{matrix} \\ \begin{matrix} D \times D \\ R \times R \\ D \times H \\ H \times R \\ H \times H \\ D \times R \end{matrix} & \begin{bmatrix} 1 & 0 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 & 0 \\ \frac{1}{4} & 0 & \frac{1}{2} & 0 & \frac{1}{4} & 0 \\ 0 & \frac{1}{4} & 0 & \frac{1}{2} & \frac{1}{4} & 0 \\ \frac{1}{16} & \frac{1}{16} & \frac{1}{4} & \frac{1}{4} & \frac{1}{4} & \frac{1}{8} \\ 0 & 0 & 0 & 0 & 1 & 0 \end{bmatrix} \end{matrix}$$

whose solution is

$$F_n = F_0 C^n \quad (5.8)$$

The behaviour of C^n depends on the eigenvalues and eigenvectors of C .

The eigenvalues are

$$\lambda_1 = \frac{1}{4}, \lambda_2 = \frac{1 - \sqrt{5}}{4}, \lambda_3 = \frac{1 + \sqrt{5}}{4} \\ \lambda_4 = \frac{1}{2}, \lambda_5 = 1, \lambda_6 = 6 \quad (5.9)$$

The last two eigenvalues in equation (5.9) correspond to the absorbing states, implying that, in the long run, the system will consist entirely of either dominant or recessive individuals. The speed at which the system approaches this equilibrium is determined by the largest eigenvalue that is less than one, specifically

We note that (5.5b) and (5.5c) contain four variables only and can therefore be solved separately.

Putting

$$X_n = R_n + S_n, \quad Y_n = R_n - S_n \quad (5.10)$$

we get

$$X_{n+1} = \frac{1}{2} X_n + \frac{1}{2} T_n, \quad Y_{n+1} = \frac{1}{2} Y_n \quad (5.11)$$

$$T_{n+1} = \frac{1}{4} X_n + \frac{1}{4} T_n + U_n, \quad U_{n+1} = \frac{1}{8} T_n \quad (5.12)$$

which give

$$16X_{n+3} - 12X_{n+2} - 2X_{n+1} + X_n = 0, Y_{n+1} = \frac{1}{2}Y_n \quad (5.13)$$

$$X_n = R_n + S_n = 2C_1\lambda_1^n + 2C_2\lambda_2^n + 2C_3\lambda_3^n \quad (5.14)$$

$$X_n = R_n - S_n = 2C_4\lambda_4^n \quad (5.15)$$

$$R_n = C_1\lambda_1^n + C_2\lambda_2^n + C_3\lambda_3^n + C_4\lambda_4^n \quad (5.16)$$

$$S_n = C_1\lambda_1^n + C_2\lambda_2^n + C_3\lambda_3^n - C_4\lambda_4^n \quad (5.17)$$

$$T_n = 2X_{n+1} - X_n = 2C_1(2\lambda_1 - 1)\lambda_1^n + 2C_2(2\lambda_2 - 1)\lambda_2^n + 2C_3(2\lambda_3 - 1)\lambda_3^n \quad (5.18)$$

$$U_n = \frac{1}{8}\{2C_1\lambda_1^{n-1} + 2C_2(2\lambda_2 - 1)\lambda_2^{n-1} + 2C_3(2\lambda_3 - 1)\lambda_3^{n-1}\} \quad (5.19)$$

Also,

$$P_{n+1} - Q_{n+1} = P_n - Q_n + \frac{1}{4}Y_n = P_n - Q_n + \frac{1}{2}C_4(\lambda_4)^n = P_n - Q_n + C_4\left(\frac{1}{2}\right)^{n+1} \quad (5.20)$$

which gives

$$P_n - Q_n = (P_0 - Q_0) + \frac{1}{2}(R_0 - S_0)\{1 - (\frac{1}{2})^n\} \quad (5.21)$$

when $n \rightarrow \infty$, we find that

$$P_n - Q_n \rightarrow P_0 - Q_0 + \frac{1}{2}(R_0 - S_0), P_n + Q_n \rightarrow 1 \quad (5.22)$$

$$X_n \rightarrow 0, Y_n \rightarrow 0, R_n \rightarrow 0, S_n \rightarrow 0, T_n \rightarrow 0, U_n \rightarrow 0, \quad (5.23)$$

$$P_n \rightarrow \frac{1}{2} + \frac{1}{2}(P_0 - Q_0) + \frac{1}{4}(R_0 - S_0), \quad (5.24)$$

$$Q_n \rightarrow \frac{1}{2} - \frac{1}{2}(P_0 - Q_0) - \frac{1}{4}(R_0 - S_0) \quad (5.25)$$

(iii) Inbreeding Model III : Inbreeding with implanting

In this model, the offspring tends to mate with one of the parent types with equal probability so that :

- (i) $P_n \times D \times D$ matings give all dominants and parents are all dominants so that we get $P_n D \times D$ matings in F_{n+1} .
- (ii) $Q_n R \times R$ matings yield all recessives and parents are all recessives, and so we obtain $Q_n R \times R$ matings in F_{n+1} .
- (iii) $R_n D \times H$ matings give $\frac{1}{2} R_n$ dominants, $\frac{1}{2} R_n$ hybrids and, since half the parents are D and the other half of the parents are H , we get $\frac{1}{4} R_n D \times D$, $\frac{1}{2} R_n D \times H$ and $\frac{1}{4} R_n H \times H$ matings in F_{n+1} .
- (iv) $S_n H \times R$ matings yield $\frac{1}{2} S_n$ hybrids, $\frac{1}{2} S_n$ recessives and since half the parents are H and the other half of the parents are R , we obtain $\frac{1}{4} S_n H \times H$, $\frac{1}{2} S_n H \times R$, $\frac{1}{4} S_n R \times R$ matings in F_{n+1} .
- (v) $T_n H \times H$ matings give rise to $\frac{1}{4} T_n$ dominants, $\frac{1}{2} T_n$ hybrids, $\frac{1}{4} T_n$ recessives, since all parents are recessives, we have $\frac{1}{4} T_n D \times D$, $\frac{1}{2} T_n H \times H$, $\frac{1}{4} T_n T_n H \times R$ mating in F_{n+1} .
- (vi) $U_n D \times R$ matings produce U_n hybrids and since half the parents are dominants and the other half are recessives, we get $\frac{1}{2} U_n D \times H$ and $\frac{1}{2} U_n R \times H$ matings in F_{n+1} .

From the foregoing discussion, we have

$$\left. \begin{aligned} P_{n+1} &= P_n + \frac{1}{4}Q_n, Q_{n+1} = Q_n + \frac{1}{4}S_n \\ R_{n+1}^* &= \frac{1}{2}R_n + \frac{1}{4}T_n + \frac{1}{2}U_n, S_{n+1} = \frac{1}{2}S_n + \frac{1}{4}T_n + \frac{1}{4}U_n \\ T_{n+1} &= \frac{1}{4}R_n + \frac{1}{4}S_n + \frac{1}{2}T_n, U_{n+1} = 0 \end{aligned} \right\} \quad (5.26)$$

These equations give

$$F_{n+1} = F_n C, F_n = F_0 C^n \quad (5.27)$$

where C is the matrix

$$C = \begin{bmatrix} 1 & 0 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 & 0 \\ \frac{1}{4} & 0 & \frac{1}{2} & 0 & \frac{1}{4} & 0 \\ 0 & \frac{1}{4} & 0 & \frac{1}{2} & \frac{1}{4} & 0 \\ 0 & 0 & \frac{1}{4} & \frac{1}{4} & \frac{1}{2} & 0 \\ 0 & 0 & \frac{1}{2} & \frac{1}{2} & 0 & 0 \end{bmatrix} \quad (5.28)$$

From (6.5.27) and (6.5.28)

$$R_{n+1} = \frac{1}{2}R_n + \frac{1}{4}T_n, S_{n+1} = \frac{1}{2}S_n + \frac{1}{4}T_n, T_{n+1} = \frac{1}{4}R_n + \frac{1}{4}S_n \quad (5.29)$$

which give

$$R_{n+1} - S_{n+1} = \frac{1}{2}(R_n - S_n), R_n - S_n = C_0 \left(\frac{1}{2} \right)^n \quad (5.30)$$

$$S_{n+2} = \frac{1}{2}S_{n+1} + \frac{1}{4} \left(\frac{1}{4}R_n + \frac{1}{4}S_n \right), 8S_{n+2} - 4S_{n+1} = S_n = C_0 \left(\frac{1}{2} \right)^{n+1} \quad (5.31)$$

$$\left. \begin{aligned} S_n &= C_1 \left(\frac{1-\sqrt{3}}{4} \right)^n + C_2 \left(\frac{1-\sqrt{3}}{4} \right)^n - C_0 \left(\frac{1}{2} \right)^{n+1} \\ R_n &= C_1 \left(\frac{1+\sqrt{3}}{4} \right)^n + C_2 \left(\frac{1-\sqrt{3}}{4} \right)^n + C_0 \left(\frac{1}{2} \right)^{n+1} \end{aligned} \right\} \quad (5.32)$$

$$T_n = \frac{1}{2}C_1 \left(\frac{1-\sqrt{3}}{4} \right)^n + \frac{1}{2}C_2 \left(\frac{1-\sqrt{3}}{4} \right)^n \quad (5.33)$$

$$P_{n+1} - Q_{n+1} = P_n - Q_n + \frac{1}{4}(R_n - S_n) = P_n - Q_n + C_n \left(\frac{1}{2} \right)^{n+2} \quad (5.34)$$

$$P_n - Q_n = P_0 - Q_0 + \frac{R_0 - S_0}{2} \left\{ 1 - \left(\frac{1}{2} \right)^n \right\} \quad (5.35)$$

As $n \rightarrow \infty$, we have

$$\left. \begin{aligned} R_n &\rightarrow S_n \rightarrow 0, T_n \rightarrow 0, U_n \rightarrow 0 \\ P_n + Q_n &\rightarrow 1, P_n - Q_n \rightarrow P_0 - Q_0 + \frac{1}{2}(R_0 - S_0) \\ P_n &\rightarrow \frac{1}{2} + \frac{P_0 - Q_0}{2} + \frac{1}{4}(R_0 - S_0), Q_n \rightarrow \frac{1}{2} - \frac{P_0 - Q_0}{2} - \frac{1}{4}(R_0 - S_0) \end{aligned} \right\} \quad (5.36)$$

These limits are the same as those for the inbreeding model (2). However, the rate of approach to the limits depends on the rate of approach to zero of $((1 + \sqrt{3}) / 4)^n = (3635)^n$

Thus, in all the three phenomena, viz, selfing, sib-mating, and implanting, the heterozygotes are lost in further generations, but at different rates, the respective rate per generation are $\frac{1}{2} (1 + \sqrt{5}) / 4$, and $(1 + \sqrt{3}) / 4$. In general, inbreeding leads to a loss of variability among the members of a population.

(iv) Inbreeding Model IV: Brother-sister mating

We consider A population undergoing mass selection against recessive individuals, where individuals with recessive genotypes are systematically removed or selected against (see section (6.4.III)). In the original population of grandfather-grandmother, the proportions of D, H, R are

$$(1 + \sqrt{r})^2, 2\sqrt{r}(1 - \sqrt{r}), r. \quad (5.37)$$

In the first generation of father-mother, after the recessives have been eliminated, the proportions of D, H, R are

$$\frac{1 - \sqrt{r}}{1 + \sqrt{r}}, \frac{2\sqrt{r}}{1 + \sqrt{r}}, 0 \quad (5.38)$$

From this generation, father f and mother m, neither of whom is recessive, produce a son s and a daughter d. Now the son and the daughter, both of whom are chosen to be non-recessive, marry and produce a child C. Now, if either d or s is dominant, a recessive child cannot be produced so that

$$P[C = r] = P[m = D, f = f = H, d = H, s = H, C = R]$$

$$+ P[m = H, f = D, d = H, s = h, C = R] + P[m = H; f = H, d = H, s = H, C = R]$$

$$\begin{aligned} &= \frac{1 - \sqrt{r}}{1 + \sqrt{r}} \frac{2\sqrt{r}}{1 + \sqrt{r}} \cdot \frac{1}{2} \cdot \frac{1}{2} \cdot \frac{1}{4} + \frac{2 - \sqrt{r}}{1 + \sqrt{r}} \cdot \frac{1 - \sqrt{r}}{1 + \sqrt{r}} \cdot \frac{1}{2} \cdot \frac{1}{2} \cdot \frac{1}{4} \\ &+ \frac{2\sqrt{r}}{1 + \sqrt{r}} \frac{2\sqrt{r}}{1 + \sqrt{r}} \cdot \frac{2}{3} \cdot \frac{2}{2} \cdot \frac{1}{4} = \frac{r}{(4(1 + \sqrt{r})^2)} \left(\frac{1}{\sqrt{r}} + \frac{7}{9} \right) \end{aligned} \quad (5.39)$$

In calculating the third term on the right-hand side of (5.39), we have explicitly taken into account the fact that the d and s are not recessives.

We also calculate the probability of C being recessive if mass selection had preceded unchecked without brother-sister mating. From section (6.4.11), such a probability is

$$\frac{r}{(1 + 2\sqrt{r})^3} \quad (5.40)$$

Thus, we get

$$\begin{aligned} &\frac{P(\text{child is recessive from brother - sister mating})}{P(\text{child is recessive with mass selection against recessive})} \\ &= \frac{(1 - 2\sqrt{r})^2}{(1 + \sqrt{r})^2} \frac{1}{4} \left(\frac{1}{\sqrt{r}} + \frac{7}{9} \right) \end{aligned} \quad (5.41)$$

As a consequence of mass selection, when the frequency of the recessive allele r is extremely small, the ratio becomes very large. For example, if $r = 0.000001$, the ratio is approximately 250. This phenomenon was observed empirically, which led to the societal prohibition of brother-sister marriages. A similar pattern occurs in cases of first-cousin or father-daughter matings, and for the same reason, these types of unions were also considered socially and morally unacceptable.

Conclusion and Application

For the given genetic composition i.e. the proportions of dominants, hybrids and recessives in a certain generation F_0 , and given the permissible matings, here we have presented a method of finding the genetic compositions of the generations $F_1, F_2, \dots, F_n$. In particular, we have established the well known Hardy-Weinberg law which states that, if the matings are random, the generations $F_1, F_2, \dots, F_n$ will have the same genetic composition.

The first application of this knowledge is in the sphere of improving the genetic quality of plants and animals through cross-breeding with better quality plants and animals or breeding and elimination of recessives (or of undesirable plants and animals) in succeeding generations. Thus the investigations made in this chapter have practical applications for the welfare of mankind. This has helped us in plants and animal breedings. In breeding desirable characters present in two parent plants or animals of same or allied species are combined by artificial crossing to produce high-yielding and disease resistant varieties. This has wide uses in agriculture and has been possible to produce several varieties of wheat, paddy, cotton, sugar cane and vegetables. The method of production of high yielding crops developed by scientists and biotechnologists have provided a lot help to solve the food shortage in India and abroad.

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