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Mathematical Modeling of Population Genetics

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1 Introduction

Aristotle conducted the first known studies on genetics in his work *Generation of Animals*(9). In 170 A.D. Galen published *On the Natural Faculties* followed by *On Seed* in 180 A.D.(6). Many others in the following centuries contributed to the study of genetics. These included Descartes, Harvey, Hooke, Swammerdam, and Paley(6). In 1859, Darwin became arguably the greatest contributor to genetics by publishing his theory of evolution in his book *The Origin of Species*(9). Up to this point, no genetic experiments had been attempted. In 1894 Roux conducted the first actual science experiments on genetics using frog eggs(9). Mendel, known as the father of genetics, began his famous pea experiment in 1856. Since then, countless others added to the study of genetics. Current studies include heterozygosity in white-tailed deer by Kekkonen(8), adaptation of DNA by Orr(10), sex ratio evolution(1).

This paper focuses on modeling the quantitative factors of population genetics. We begin modeling Mendel's work and building on this work by adding selective variances to the model. This generated data adequately matches prior data from population genetics experiments.

2 Preliminaries

This paper uses the following biological terms.

Definition 1 *(7)Cells that fertilize and replicate to form a new organism are called gametes.*

Examples of gametes include the female ovum and the male sperm of humans. This paper uses the following biological definitions relating to DNA.

Definition 2 *(5)The resulting cell from the union of the two gametes is called a zygote.*

Definition 3 *(5)Haploid cells contain only one set of DNA in an unpaired chromosome.*

Definition 4 *(5)Diploid cells contain two sets of DNA in a paired chromosome.*

Gametes are haploid cells whereas zygotes are diploid.

Definition 5 *(5)A structure in the nucleus of a cell that carries the DNA of the organism is called a chromosome.*

Chromosomes contain all the DNA for an organism. Scientist study chromosomal characteristics for new discoveries in genetics.

Definition 6 *(5)The fundamental unity of heredity is called a gene*

Definition 7 *(5)The position of the gene on the chromosome is called a locus.*

Definition 8 *(3)Different types of genes are called alleles.*

The alleles from each gamete may differ from each other. Both parents each give one set of chromosomes to the offspring. The chromosome's alleles need not be the same. If the alleles differ, the resulting cell is considered a heterozygote. If the alleles do not differ, the resulting cell is considered a homozygote.

Definition 9 *(3)Homozygotes occur when both genes, or alleles, are the same*

Definition 10 *(3)Heterozygotes occur when both genes, or alleles, are different*

Britton gives the following definitions for genotypes and phenotypes.

Definition 11 *(3)The term genotype refers to the genetic make-up of an organism.*

Definition 12 *(3)The physical traits shown in an organism is called the phenotype*

The alleles do not necessarily define the physical characteristics of an organism. The dominance of traits determines if the traits are shown or not shown. The dominant trait shows in mixed alleles, whereas the recessive trait fails to show.

Definition 13 *(3)Dominant traits are expressed in a heterozygote genotype.*

Definition 14 *(3)Recessive trait are not expressed in a heterozygote genotype.*

Example 15 *The brown eye color is considered to be the dominant trait between brown and blue eyes. So if a person had a heterozygote genotype that contained both brown and blue eyes, only brown shows. In order to have a phenotype of blue eyes, a person needs a homozygote genotype with only the recessive trait of blue eyes.*

Example 16 *From previous data, polydactyly, or multi-fingeredness, is expressed in heterozygote situations, thus the trait is dominant. So a parent with a genotype including the trait of polydactyly can expect half of her children to express the trait as well.*

Definition 17 *(3)The probability a trait will survive based on its ability to breed is called survivorship.*

Definition 18 *(3)Any generation that follows after the 1st is called a filial generation.*

Definition 19 *(3)x-linked genes only affect the x-chromosome.*

Definition 20 *(3)Absolute fitness is determined by the favorable reproductions of a specific genotype.*

Definition 21 *(3)Loci with more than one allele in the population are called gene polymorphisms.*

This paper uses the following mathematical terms.

Definition 22 *(2)Two events A and B are said to be independent if the occurrence or nonoccurrence of the first event does not affect the occurrence or nonoccurrence of the second event.*

Definition 23 *(4)A solution ψ of a system*

$$x' = F(t, x)$$

which is defined for $t \geq 0$ is said to be stable (a steady state) if, given any $\varepsilon > 0$, there exists a $\delta > 0$ such that any solution φ of the system satisfying

$$|\varphi(0) - \psi(0)| < \delta$$

satisfies

$$|\varphi(t) - \psi(t)| < \varepsilon$$

where $t \geq 0$. A solution ψ is said to be an interior steady state if $\psi(0)$ lies inside the solution region of the system. A solution ψ is said to be an exterior steady state if $\psi(0)$ lies on the boundary of the solution region.

The following definitions relate to the fitness of the genotype population.

Definition 24 *(3)Relative fitness is determined by the ratio of absolute fitness to the absolute fitness of a theoretical genotype. This fitness can be density-dependent or frequency-dependent, i.e. determined by the size and makeup of the genotype population, and environment.*

Definition 25 *(3)The mean fitness w_p of A is defined by taking a weighted mean over all the homozygotes and half the heterozygotes carrying the allele A.*

3 Primary Results

In the first subsection, a model of Mendel's work with peas is developed. The results of this model are compared to Mendel's results. The second subsection expands this model to include selective variances.

3.1 Mendel's General Model

The first goal is to derive a basic formula for determining the frequency of gamete unions. The basic assumptions include independence of sex ratio and fertility, randomness of mating, survivorship, and the lack of mutation and migration. p defines the frequency of of allele A in a population and q defines the frequency of allele B in the same population. Thus it follows that

$$p + q = 1$$

Now define x, y, z to be the frequencies of the genotype AA, AB, and BB respectively. Since the AB genotype defines a heterozygote, half of the frequency will go towards counting for the A frequency and the other half will go towards the B frequency and so

$$\begin{aligned} p &= x + \frac{1}{2}y \\ q &= z + \frac{1}{2}y \end{aligned}$$

A punnett square summarizes the frequencies.

	$A(p)$	$B(q)$
$A(p)$	p^2	pq
$B(q)$	pq	q^2

From the punnett square, the formula for subsequent generations emerges as

$$p_{n+1} = p_n^2 + \frac{1}{2}\left(2p_n q_n\ \right)$$

with n representing the generation number. Then it follows

$$p_{n+1} = p_n^2 + \frac{1}{2}\left(2p_n q_n\right) = p_n^2 + p_n q_n = p_n\left(p_n + q_n\right) = p_n\left(1\right) = p_n$$

Thus p_n holds independent of p_{n+1} and from now on will only be referred to as p. Similarly

$$q_{n+1} = q_n^2 + \frac{1}{2}\left(2p_n q_n\right) = q_n^2 + p_n q_n = q_n\left(q_n + p_n\right) = q_n\left(1\right) = q_n$$

The Hardy-Weinberg Law follows from this and states allele frequencies p and q remain unchanged from generation to generation. Therefore the filial generations hold the same as in the parental generation and

$$\begin{aligned} x &= p^2 \\ y &= 2pq \\ z &= q^2 \end{aligned}$$

for generations F_1 onward.

Mendel's second law states that traits in one pair of chromosomes are independent of different traits in another pair of chromosomes.

Example 26 *Mating a round (R) yellow (Y) pea and a wrinkled (W) green (G) pea with round and yellow being dominant gives an example of Mendel's second law. Let $F_0 = RRYY + WWGG$ represent the parent generation. The first generation, or F_1, equals $RWYG$ and, since RY holds dominant for all, exhibits RY phenotype. Let F_2 be the following table.*

$F_2 =$

	RY	RG	WY	WG
RY	RY	RY	RY	RY
RG	RY	RG	RY	RG
WY	RY	RY	WY	WY
WG	RY	RG	WY	WG

where the proportions of the phenotypes are defined as

$$RY = \frac{9}{16}; RG = \frac{3}{16}; WY = \frac{3}{16}; WG = \frac{1}{16}$$

Now using Hardy-Weinberg equilibrium we arrive at the following theorem.

Theorem 27 *A population is in Hardy-Weinberg equilibrium if and only if $y^2 = 4xz$ assuming x, y, and z are the usual genotype frequencies.*

Proof. Let p and q represent the frequencies of alleles A and B respectively where $p = x + \frac{1}{2}y$ and $q = z + \frac{1}{2}y$. Note that $p + q = 1$.

($\rightarrow$) Assume a population is in Hardy-Weinburg equilibrium and thus

$$\begin{aligned} x &= p^2 \\ y &= 2pq \\ z &= q^2 \end{aligned}$$

Then it follows that

$$4xz = 4p^2q^2 = (2pq)^2 = y^2$$

as desired.

($\leftarrow$) Assume $y^2 = 4xz$. By hypothesis since $p + q = 1$ it follows that

$$\begin{aligned} x + y + z &= \left(x + \frac{1}{2}y\right) + \left(z + \frac{1}{2}y\right) = p + q = 1 \\ &\Rightarrow \quad y = 1 - x - z \end{aligned}$$

By substitution we see

$$\begin{aligned} p^2 &= \left(x + \frac{1}{2}y\right)^2 \\ &= x^2 + xy + \frac{1}{4}y^2 \\ &= x^2 + xy + xz \\ &= x^2 + x\left(1 - x - z\right) + xz \\ &= x^2 + x - x^2 - xz + xz \\ &= x \end{aligned}$$

Similarly

$$\begin{aligned} q^2 &= \left(z + \frac{1}{2}y\right)^2 \\ &= z^2 + yz + \frac{1}{4}y^2 \\ &= z^2 + yz + xz \\ &= z^2 + z\left(1 - x - z\right) + xz \\ &= z^2 + z - xz - z^2 + xz \\ &= z \end{aligned}$$

and by substitution of $y^2 = 4xz$

$$\begin{aligned} 2pq &= 2\left(x + \frac{1}{2}y\right)\left(z + \frac{1}{2}y\right) \\ &= 2\left(xz + \frac{1}{2}yz + \frac{1}{2}xy + \frac{1}{4}y^2\right) \\ &= 2\left(\frac{1}{4}y^2 + \frac{1}{2}yz + \frac{1}{2}xy + \frac{1}{4}y^2\right) \\ &= 2\left(\frac{1}{2}y^2 + \frac{1}{2}yz + \frac{1}{2}xy\right) \\ &= y^2 + yz + xy \\ &= y(y + z + x) \\ &= y\left(1\right) \\ &= y \end{aligned}$$

Thus the definition of the Hardy-Weinburg equilibrium is fulfilled as desired. ■

We proceed with an example.

Example 28 *Assume an example of blood types in England produces the frequencies of* $A-32.1\%$, $B-22.4\%$, $AB-7.1\%$, *and* $O-38.4\%$. *First a Punnett square shows the possible blood types:*

	A	B	O
A	A	AB	A
B	AB	B	B
O	A	B	O

Solving with the genotype frequencies,

$$\begin{aligned}
B &= q^2 + 2qr \\
O &= r^2 \\
&\Rightarrow r = \sqrt{O} = \sqrt{38.4\%} = 62.0\% \\
B + O &= q^2 + 2qr + r^2 \\
&= (q+r)^2 \\
&\Rightarrow q + r = \sqrt{B+O} = \sqrt{22.4\% + 38.4\%} = 78.0\% \\
q &= (q+r) - r = 78.0\% - 62.0\% = 16.0\% \\
r + q + p &= 1 \\
&\Rightarrow p = 22.0\% \\
A &= p^2 + 2pr \\
AB &= 2pq
\end{aligned}$$

and so

$$\begin{aligned}
O &= r^2 = (62.0\%)^2 = 38.4\% \\
B &= q^2 + 2qr = (16.0\%)^2 + 2\,(16.0\%)\,(62.0\%) = 22.4\% \\
A &= p^2 + 2pr = (22.0\%)^2 + 2\,(22.0\%)\,(62.0\%) = 32.1\% \\
AB &= 2pq = 2\,(22.0\%)\,(16.0\%) = 7.0\%
\end{aligned}$$

Now to compare data we see

	Data	*Calculated*
A	32.1%	32.1%
B	22.4%	22.4%
AB	7.1%	7.0%
O	38.4%	38.4%

The χ^2 *Goodness of Fit test gives* $\chi^2 = 0.00142857$ *with a P-Value greater than* 0.995. *This means that the given data proves consistent with the random mating assumption.*

According to positive assortative mating, mating occurs more frequently with that of the same genotype. Let x, y, z represent the frequencies of mating

of $AA \times AA, AB \times AB, BB \times BB$**.** The genotypes AA, AB, BB with their frequencies $1:2:1$ result from the mating of $AB \times AB$. Then it follows

$$\begin{aligned} AA &= x_n = \frac{1}{4}\,(\text{total population}) \\ AB &= y_n = \frac{1}{2}\,(\text{total population}) \\ BB &= z_n = \frac{1}{4}\,(\text{total population}) \end{aligned}$$

Thus

$$\begin{aligned} y_{n+1} &= \frac{1}{2}y_n \\ y_{n+2} &= \frac{1}{2}y_{n+1} \\ &= \left(\frac{1}{2}\right)^2 y_n \\ &\vdots \\ y_{n+a} &= \left(\frac{1}{2}\right)^a y_n \end{aligned}$$

as $a \to \infty$, $y_{n+a} \to 0$ and thus the heterozygote population will eventually disappear and only homozygotes would remain. Then it follows that

$$\begin{aligned} p_n &= x_n + \frac{1}{2}y_n \\ &\Rightarrow \quad p_{n+1} = x_{n+1} + \frac{1}{2}y_{n+1} \\ &= x_n + \frac{1}{4}y_n + \frac{1}{2}\left(\frac{1}{2}y_n\right) \\ &= x_n + \frac{1}{2}y_n \\ &= p_n \end{aligned}$$

As n approaches infinity y_n approaches zero and thus

$$x_n = p_n$$

Similarly

$$\begin{aligned} q_n &= z_n + \frac{1}{2}y_n \\ &\Rightarrow \quad q_{n+1} = z_{n+1} + \frac{1}{2}y_{n+1} \\ &= z_n + \frac{1}{4}y_n + \frac{1}{2}\left(\frac{1}{2}y_n\right) \\ &= z_n + \frac{1}{2}y_n \\ &= q_n \end{aligned}$$

As n approaches infinity y_n approaches zero and thus

$$z_n = q_n$$

And thus the heterozygote population no longer exists and the two remaining homozygote populations do not interbreed.

The Hardy-Weinberg law fails to hold when considering X-linked genes. Consider the following example.

Example 29 *Assuming colorblindness holds as a X-linked gene and affects 1 in 20 Caucasian males, the frequency of colorblindness in Caucasian females becomes 1 in 400.*

Theorem 30 *The Hardy-Weinberg law does not hold for X-linked genes.*

Proof. Under the Hardy-Weinberg assumptions, for males with genotypes A and B let the frequencies be defined as m and n and let

$$\begin{aligned} m' &= p \\ n' &= q \end{aligned}$$

where p, q represent corresponding female frequencies. We focus on the female, since the male gives the X-linked gene. Let

$$\begin{aligned} x' &= mp \\ y' &= mp + np \\ z' &= np \end{aligned}$$

Then

$$\begin{aligned} p' &= x' + \frac{1}{2}y' = mp + \frac{1}{2}(mp + np) = m\left(p + \frac{1}{2}q\right) + \frac{1}{2}np \\ p'' &= m'\left(p' + \frac{1}{2}q'\right) + \frac{1}{2}n'p' = p\left(p' + \frac{1}{2}q'\right) + \frac{1}{2}qp' \\ &= p\left(p' + \frac{1}{2}(1 - p')\right) + \frac{1}{2}(1 - p)p' \\ &= p\left(\frac{1}{2} + \frac{1}{2}p'\right) + \frac{1}{2}p' - \frac{1}{2}pp' \\ &= \frac{1}{2}p + \frac{1}{2}pp' + \frac{1}{2}p' - \frac{1}{2}pp' \\ &= \frac{1}{2}p' + \frac{1}{2}p \end{aligned}$$

Solving this equation we get

$$p_n = \frac{2}{3}p_0 + \frac{1}{3}m_0 + \frac{1}{3}(p_0 - m_0)\left(-\frac{1}{2}\right)^n$$

Taking the limit as $n \to \infty$, p_n approaches to the initial frequency of A. ■

3.2 Selective Variances

Hardy-Weinberg law fails to account for selection and hence there is no evolution under this law**.** To account for selection, disregard the former assumption of equally fit alleles. The relative fitness of the alleles depends on many factors including density and frequency. We must still assume random mating holds as an assumption to validate the use of a punnett square. Thus the allele frequencies remain p_n and q_n in a population n and the frequencies x_n, y_n, z_n are given by

$$\begin{aligned} x_n &= p_n^2 \\ y_n &= 2p_nq_n \\ z_n &= q_n^2 \end{aligned}$$

Let selection variance be in the ratio $w_x : w_y : w_z$. For AA, AB, BB we have $w_xp_n^2 : 2w_yp_nq_n : w_zq_n^2$. And we can now have the ratio

$$w_xp_n^2 + w_yp_nq_n : w_yp_nq_n + w_zq_n^2$$

Using the frequencies

$$\begin{aligned} p_{n+1} &= f(p_n) = \frac{(w_xp_n + w_yq_n)\,p_n}{w_xp_n^2 + 2w_yp_nq_n + w_zq_n^2} \\ &= \frac{(w_xp_n + w_yq_n)\,(p_n + q_n)p_n}{w_xp_n^2 + 2w_yp_nq_n + w_zq_n^2} \\ &= \frac{((w_xp_n + w_yq_n)\,p_n + (w_xp_n + w_yq_n)\,q_n)\,p_n}{w_xp_n^2 + 2w_yp_nq_n + w_zq_n^2} \\ &= \frac{\left(w_xp_n^2 + w_yq_np_n + w_xp_nq_n + w_yq_n^2\right)p_n}{w_xp_n^2 + 2w_yp_nq_n + w_zq_n^2} \\ &= \frac{w_xp_n^3 + w_yq_np_n^2 + w_xp_n^2q_n + w_yp_nq_n^3}{w_xp_n^2 + 2w_yp_nq_n + w_zq_n^2} \\ &= \frac{w_xp_n^3 + 2w_yp_n^2q_n + w_zp_nq_n^2 + w_xp_n^2q_n - w_yp_n^2q_n + w_yq_np_n^2 + w_yp_nq_n^2 - w_zp_nq_n^2}{w_xp_n^2 + 2w_yp_nq_n + w_zq_n^2} \\ &= p_n + p_nq_n\frac{(w_x - w_y)\,p_n + (w_y - w_z)\,q_n}{w_xp_n^2 + 2w_yp_nq_n + w_zq_n^2} \end{aligned}$$

This defines the Fisher-Haldane-Wright Equation. Find the mean fitness of A:

$$w_p = \frac{w_xp^2 + w_ypq}{p^2 + pq} = \frac{p(w_xp + w_yq)}{p(p+q)} = \frac{(w_xp + w_yq)}{(1)} = w_xp + w_yq$$

Similarly, the following equation shows the mean fitness of B:

$$w_q = \frac{w_ypq + w_zq^2}{pq + q^2} = \frac{q(w_yp + w_zq)}{q(p+q)} = \frac{(w_yp + w_zq)}{(1)} = w_yp + w_zq$$

Now, the overall mean fitness becomes

$$\begin{aligned}
\overline{w} &= w_x p^2 + 2w_y pq + w_z q^2 \\
&= w_x p^2 + w_y pq + w_y pq + w_z q^2 \\
&= p(w_x p + w_y q) + q(w_y p + w_z q) \\
&= pw_p + qw_q
\end{aligned}$$

From dropping the n's in the previous equation and replacing the $n+1$ with the prime notation to denote the next generation, we arrive at

$$p_{n+1} = f(p_n) = \frac{(w_x p_n + w_y q_n)\, p_n}{w_x p_n^2 + 2w_y p_n q_n + w_z q_n^2} = \frac{w_p p}{\overline{w}} = p'$$

Now

$$\begin{aligned}
\delta p &= p' - p \\
&= \frac{w_p p}{\overline{w}} - p \\
&= \frac{w_p p}{\overline{w}} - \frac{p\overline{w}}{\overline{w}} \\
&= \frac{w_p p - p\overline{w}}{\overline{w}} \\
&= \frac{(w_p - \overline{w})\, p}{\overline{w}} \\
&= \frac{\alpha_p p}{\overline{w}}
\end{aligned}$$

where $\alpha_p = w_p - \overline{w}$ defines the mean excess fitness. Further, we see

$$\begin{aligned}
\delta p &= p' - p \\
&= \frac{(w_p - \overline{w})\, p}{\overline{w}} \\
&= \frac{(w_p - (pw_p + qw_q))\, p}{\overline{w}} \\
&= \frac{(w_p - pw_p - qw_q)\, p}{\overline{w}} \\
&= \frac{(w_p\,(1-p) - qw_q)\, p}{\overline{w}} \\
&= \frac{(w_p\,(q) - qw_q)\, p}{\overline{w}} \\
&= pq\frac{w_p - w_q}{\overline{w}} \\
&= pq\frac{(w_x p + w_y q) - (w_y p + w_z q)}{\overline{w}} \\
&= pq\frac{w_x p + w_y q - w_y p - w_z q}{\overline{w}} \\
&= pq\frac{(w_x - w_y)\, p + (w_y - w_z)\, q}{\overline{w}} \qquad (1)
\end{aligned}$$

To find steady state $p = 0$, assume $w_y < w_z$ and $\overline{w} > 0$. Assuming eq. (1) we know

$$\delta p = p_{n+1} - p_n = pq\frac{(w_x - w_y)\,p + (w_y - w_z)\,q}{\overline{w}}$$

Case 31 *If $w_x < w_y$ then $\delta p < 0$.*

Case 32 *Assume $w_x > w_y$. Consider $p \neq 0$ and $q \neq 0$. Since $q = 1 - p$*

$$\begin{aligned} 0 &= (w_x - w_y)\,p + (w_y - w_z)\,(1-p) \\ &= p\,(w_x - w_y - w_y + w_z) + (w_y - w_z) \\ &\Rightarrow \quad w_z - w_y = p\,(w_x - 2w_y + w_z) \\ &\Rightarrow \quad p^* = \frac{w_z - w_y}{w_x - 2w_y + w_z} \end{aligned}$$

Note $f(p^*) = p^*$. Since $\delta p^* = 0$ then p^* exists as an interior stable solution.

Case 33 *If $0 < p < p^*$ then $\delta p < 0$ since $w_x - w_y > 0, p > 0$ implies*

$$0 < (w_x - w_y)\,p < (w_x - w_y)\,p^*$$

Then

$$(w_x - w_y)\,p + (w_y - w_z)\,q < (w_x - w_y)\,p^* + (w_y - w_z)\,q^* = 0$$

Therefore $\delta p < 0$ for $p < p^*$ when $w_x > w_y$ and $\delta p < 0$ if $w_x < w_y$. Thus the iterations are decreasing under these conditions and so $p = 0$ is a steady state solution.

Similarly consider $p = 1$. Assume $w_y < w_z$. Let $p < 1$. Then we need $\delta p > 0$. So

$$(w_x - w_y)\,p + (w_y - w_z)\,q < 0$$

Since we need $w_y - w_z$ to approach 0 we must have $w_x > w_y$ to make $p = 1$ true. This does not mean $w_y > w_z$.

Consider $p^* \in (0, 1)$. Remember

$$p^* = \frac{w_z - w_y}{w_x - 2w_y + w_z} = \frac{w_z - w_y}{(w_x - w_y) + (w_z - w_y)}$$

Case 34 *If $w_y > w_z$ and $w_y > w_x$ then $p^* \neq 0$ and $p^* > 0$ and $p^* < 1$ since $w_z - w_y < 0$ and $w_x - w_y < 0$ and $w_z - w_y < 0$. Thus*

$$0 < \frac{w_z - w_y}{(w_x - w_y) + (w_z - w_y)} < 1$$

Case 35 *Let $w_y < w_z$. If $w_y < w_z$ then $p^* \neq 0$ and $p^* > 0$ and $p^* < 1$ since $w_z - w_y < 0$ and $w_x - w_y > 0$ and $w_z - w_y > 0$. Thus*

$$0 < \frac{w_z - w_y}{(w_x - w_y) + (w_z - w_y)} < 1$$

Under these conditions, p^* is an interior steady state solution.
We now proceed with an example.

Example 36 *Consider Sickle cell anemia. Allele B denotes the disease and allele A denotes normal. Organisms with the genotype AB do not have the disease and have immunity to malaria. Organisms with the genotype BB have the disease and malaria. Organisms with the genotype AA do not have the disease and do not have immunity to malaria. With the relative frequencies of* AA, AB, BB *being* $1, 1+s, 1-t$ *respectively, it is shown the*

$$\begin{aligned} p' &= p + pq\frac{(w_x - w_y)\,p + (w_y - w_z)\,q}{w_x p^2 + 2w_y pq + w_z q^2} \\ &= p + pq\frac{(1-(1+s))\,p + ((1+s)-(1-t))\,q}{1p^2 + 2\,(1+s)\,pq + (1-t)\,q^2} \\ &= p + pq\frac{-sp + (s+t)\,(1-p)}{p^2 + 2pq + 2spq + q^2 - tq^2} \\ &= p + pq\frac{-sp + s + t - sp - tp}{p^2 + 2pq + q^2 + 2spq - tq^2} \\ &= p + pq\frac{s - 2sp + t - tp}{(p+q)^2 + 2spq - tq^2} \\ &= p + pq\frac{s\,(1-2p) + t\,(1-p)}{1 + 2spq - tq^2} \end{aligned}$$

The steady states exist at $p = 0, 1, p^*$ *where*

$$p^* = \frac{s+t}{2s+t}$$

Proof. Using the previous methods we see that

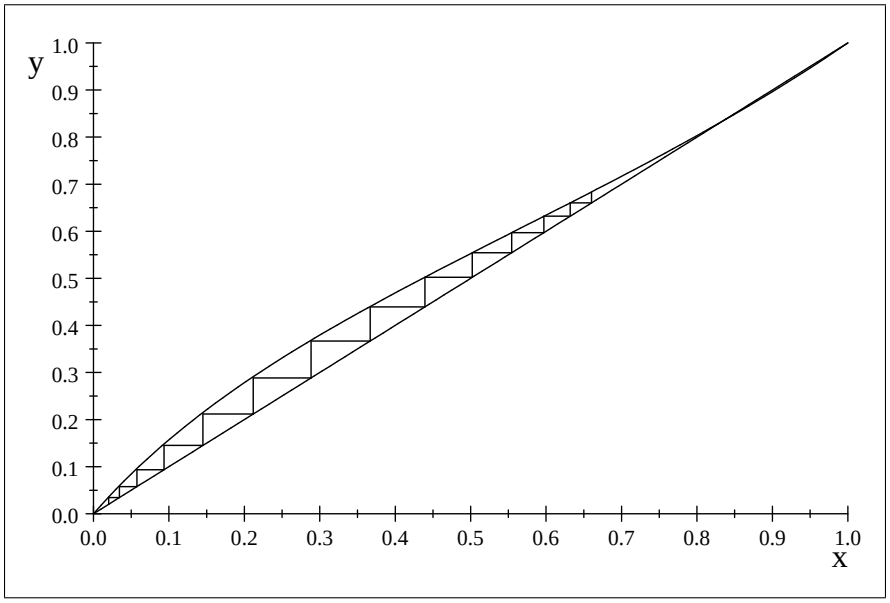
$$\begin{aligned} 0 &= (w_x - w_y)\,p + (w_y - w_z)\,(1-p) \\ &\Rightarrow\ 0 = s\,(1-2p) + t\,(1-p) \\ &\Rightarrow\ 0 = s - 2sp + t - tp \\ &\Rightarrow\ -2sp - tp = -s - t \\ &\Rightarrow\ p\,(2s+t) = s + t \\ &\Rightarrow\ p^* = \frac{s+t}{2s+t} \end{aligned}$$

Thus there exists an interior steady state at

$$p^* = \frac{s+t}{2s+t}$$

■

The cobweb map verifies the existence of a non-oscillatory steady state solution at p^*.



Example 37 *If the frequency of* $BB = .2$ *and* $q^* = .2$ *then* $t = .8$ *and* $p^* = .8$ *and thus*

$$\begin{aligned} p^* &= \frac{s+t}{2s+t} \\ &\Rightarrow \quad 2sp^* + tp^* = s + t \\ &\Rightarrow \quad 2sp^* - s = t - tp^* \\ &\Rightarrow \quad s\left(2p^* - 1\right) = t\left(1 - p^*\right) \\ &\Rightarrow \quad s = \frac{t\left(1-p^*\right)}{2p^* - 1} \\ &\Rightarrow \quad s = \frac{.8\left(1-.8\right)}{2\left(.8\right) - 1} \approx 0.27 \end{aligned}$$

Thus the ratio of frequencies $AA : AB : BB$ *computes as* $1 : 1.27 : 0.2$ *and the chance of a person with genotype* AA *dying from malaria is* 0.21

4 Conclusions and Future Work

This paper developed a formula for modeling the frequencies of alleles under restrictive assumptions. From this, an application of the Hardy-Weinberg law shows that the allele frequencies do not change throughout the generations. We then factored in selection pressure to account for survivorship of alleles which resulted in the Fisher-Haldane-Wright equation. Future work includes studies

of selection pressures limited to specific alleles, studies that include mutation, studies of evolution throughout generations, game theory, strategies of breeding, and many others.

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