The Hardy-Weinberg Equilibrium—Some Helpful Suggestions

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In college General Biology curricula, the topic of classical genetics is typically followed by consideration of population and evolutionary genetics. After fundamental genetic principles are studied, students are introduced to the Hardy-Weinberg equilibrium as a continuum of Mendelian Genetics in a population context. Population genetics provides a logical segue to the study of evolution. Populations adhering to the Hardy-Weinberg equilibrium provide a reference for studying evolutionary changes (Journet 1986). With this as a starting point, Darwin's observations can be justified and quantified, as well as expanded upon, to include additional aspects of population and evolutionary genetics.

The Hardy-Weinberg equilibrium is an algebraic mathematical tool for predicting allele frequencies, phenotypes and genotypes in populations (Cummings 1997; Lewis 1997; Mader 1996; Postlethwait & Hopson 1995). Mertens (1992) proposed strategies for introducing the Hardy-Weinberg equilibrium to make it meaningful and more useful to both students and teachers. It has been our experience that students have difficulty with Hardy-Weinberg problem solving. Since students often possess a genuine fear of mathematics, reinforcement of basic mathematical principles when working through Hardy-Weinberg problems will provide a less threatening experience, thereby enabling students to successfully complete problems and concentrate on understanding genetic concepts as they relate to population dynamics (Flannery 1995; Journet 1986).

Various methods, some quite detailed, for presenting the Hardy-Weinberg equilibrium have appeared in journals and textbooks (Cummings 1997; Journet 1986; Lewis 1997; Mader 1996; Postlethwait & Hopson 1995). The Hardy-Weinberg model is presented in a variety of ways in General Biology textbooks. In this paper we offer suggestions for instructors to assist with their presentation of this topic. Regardless of the approach, our suggestions can assist instructors by providing a unified method for explaining the Hardy-Weinberg equilibrium. Our experiences in teaching Mendelian probabilities and the Hardy-Weinberg model confirm that students enrolled in General Biology who have not attained the established level of proficiency in mathematics have difficulty participating in class discussions on this topic and solving homework problems and examination questions.

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Mendel's laws provide the foundation for discussions of evolutionary and population genetics (Dobzhansky et al. 1997). The Hardy-Weinberg equilibrium is a continuation of Mendel's principles, which show that gene frequencies under certain conditions remain constant from one generation to the next, thereby maintaining the allelic composition of the gene pool of the population. During our presentation of the Hardy-Weinberg equilibrium, we link Punnett squares and probability calculations to previous discussions of classical inheritance. We enrich our students' learning experiences by extending basic principles of inheritance, and providing challenging mathematical applications. Instructors can assist students through in-class practice problems. This allows subsequent focus on Hardy-Weinberg theory and applications rather than laboring over arithmetic operations.

We present Hardy-Weinberg theory as a mathematical model demonstrating how allelic and genotypic frequencies remain constant in a large population under specified conditions. Named after its discoverers, Godfrey H. Hardy, a British mathematician, and Wilhelm Weinberg, a German physician, the Hardy-Weinberg equilibrium requires the following conditions (Campbell et al. 1997; Cummings 1997; Journet 1986; Lewis 1997; Mader 1996; Postlethwait & Hopson 1995):

1. No gene flow: There is no migration of individuals into or out of the population.
2. No mutations: Alleles will not change from one generation to the next.
3. No selection: No selective force favors one phenotype over another.
4. No genetic drift: The population is large; random fluctuations are considered negligible.
5. Random mating: Individuals pair by chance, not according to their phenotypes.

If the above assumptions hold true for a given population, and:

p = the frequency of the dominant allele in a population
q = the frequency of the recessive allele in a population,

then: $p + q = 1$ (Equation 1)

and $p^2 + 2pq + q^2 = 1$ (Equation 2)

Equation 1 is called the Gene Pool Equation, and Equation 2 is called the Genotype Equation. In Equation 1 the sum of the frequencies of all of the alleles in a population must equal one (indicating 100%). For example, if $p = 0.2$, then q must equal 0.8. In Equation 2 the sum of the frequencies of individuals with each genotype must add up to the entire population, or one (100%) (Cummings 1997; Lewis 1997; Mader 1993; Postlethwait & Hopson 1995).

Consider the following: Pointy ears are dominant over round ears in an alien population. Let *E* and *e* represent the dominant and recessive alleles, respectively. In a population of 1,000 aliens, 800 have pointy ears ($p = 0.8$; $q = 0.2$). The three possible genotypes in a cross between two heterozygotes are *EE, Ee* and *ee.* We can demonstrate this using a Punnett square:

	E	*e*
E	*EE*	*Ee*
e	*Ee*	*ee*

Using the values for *E* and *e*, $p = 0.8$ and $q = 0.2$, respectively, we can use a Punnett square to calculate the predicted frequencies for each genotype:

	p	q
p	$pp = p^2$	pq
q	pq	$qq = q^2$

$p^2 = 0.64$ or 64%
$pq = 0.16$ or 16%
$q^2 = 0.04$ or 4%

Therefore, using Equation 2:

$$0.64 + (2 \times 0.16) + 0.04 = 1$$
$$64\% + 32\% + 4\% = 100\%$$

Once the components of the equation are determined, students can be challenged with a variety of questions, as well as formulate their own practice problems, including:

1. What percent of the population would you expect to be homozygous dominant? (Answer: 64%)
2. What percent of the population would you expect to be homozygous recessive? (Answer: 4%)
3. What percent of the population would you expect to be heterozygous? (Answer: 32%)
4. What percent of the population would you expect to show the dominant phenotype? (Answer: 96%)

Information ascertained from the answers to these questions allows students to learn additional aspects about a given population, such as knowing the percentage of carriers of a particular genetic disease.

During our classroom presentation of the Hardy-Weinberg model, it is apparent that a number of students are unsure of the mathematical calculations. This hesitation with mathematics interferes with their ability to solve problems and analyze results. We are frequently asked to provide additional practice problems. General Biology textbooks usually provide a few example problems. The instructor may find herself/himself searching for additional problems in which the numbers work out without requiring use of a calculator (Lewis 1997; Mader 1993; Postlethwait & Hopson 1995).

Wouldn't it be convenient for instructors to have a table containing p, q, p^2, $2pq$ and q^2 values to facilitate quick, on-the-spot construction of examples? If this table were readily available, problems could be generated quickly and abundantly. Table 1 lists p, q, p^2, $2pq$ and q^2 values for p and $q = 0.1 - 0.9$ in increments of 0.1. More extensive tables could be constructed using p and q values with more significant digits, such as 0.11, 0.12, 0.13, etc. Use of the p and q values in Table 1 to generate problems allows instructors to focus their lesson on the significance of the Hardy-Weinberg equilibrium instead of arithmetic. For example, in a population meeting the requirements of the Hardy-Weinberg equilibrium, if $p = 0.7$, find the frequency of:

a. the recessive allele
b. homozygous dominants
c. heterozygotes (carriers)
d. homozygous recessives
e. dominant phenotypes

in the population. Using Table 1, the answers to a through e are 0.3, 0.49, 0.42, 0.09 and 0.91, respectively. That is, 3% of the population in question contain the recessive allele, 49% are homozygous dominant, 42% are heterozygous (carriers), 9% are homozygous recessive, and 91% display the dominant phenotype.

Suppose a problem states that the frequency of sickle-cell anemia, an autosomal recessive condition is 20% in a given population. We have found that a quick review of conversions between percents and decimals helps guide students through the mechanics of the problem. Conversion of 20% to a decimal for use in Equations 1 and 2 requires dividing by 100 or moving the decimal point two places to the left to obtain 0.2. Likewise, changing a decimal to a percent requires multiplying by 100, or moving the decimal point two places to the right.

Another rule of mathematics is often overlooked by students: When multiplying factors containing decimals, the number of decimal places in the product

Table 1. p, q, p^2 $2pq$ and q^2 values for p and q = 0.1–0.9 in increments of 0.1.

p	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9
q	0.9	0.8	0.7	0.6	0.5	0.4	0.3	0.2	0.1
p^2	0.01	0.04	0.09	0.16	0.25	0.36	0.49	0.64	0.81
$2pq$	0.18	0.32	0.42	0.48	0.50	0.48	0.42	0.32	0.18
q^2	0.81	0.64	0.49	0.36	0.25	0.16	0.09	0.04	0.01

must equal the sum of the decimal places in each of the factors in the problem. For example, this is encountered when multiplying 0.1 by 0.1. The product is 0.01, not 0.1, as students often report erroneously. In addition, encouraging students to familiarize themselves with the perfect squares (n^2) for $n=1$ to $n=25$ will assist them in solving problems more rapidly (Table 2). Confidence with decimal manipulation and swift recognition of perfect squares in Hardy-Weinberg problems empower students to quickly reach solutions, thereby easing any mathematics anxiety.

We propose assisting students with their understanding of the Hardy-Weinberg equilibrium by developing an available pool of questions by the instructor using Table 1, along with reinforcement of multiplication rules for decimals, and a solid familiarity with common perfect squares. Enriching the classroom with mathematics provides for improved scientific literacy and science education, as advocated in the *National Science Education Standards* proposed by the National Research Council (1996). Our approach integrates mathematical applications with biological principles, as well as promoting mathematical understanding.

We were curious to see if Table 1 was as useful to the students as it had been for us. After an introduction to the Hardy-Weinberg model, a sample problem was completed. Students asked questions and requested additional problems to solve. At this point, we distributed Tables 1 and 2 to our classes. Using the tables, students solved Hardy-Weinberg problems with less difficulty. Once the obstacle of arithmetic calculations was overcome, genetic features characterizing the population and the significance of the numbers obtained became the focus of the lesson. Using these suggestions, instructors will be able to present Hardy-Weinberg equilibrium problems more easily. Students will solve problems but, more importantly, understand the significance of the Hardy-Weinberg model to population genetics.

Table 2. Perfect Squares for $n=1$ to $n=25$.

n	n^2	n	n^2
1	1	14	196
2	4	15	225
3	9	16	256
4	16	17	289
5	25	18	324
6	36	19	361
7	49	20	400
8	64	21	441
9	81	22	484
10	100	23	529
11	121	24	576
12	144	25	625
13	169		

Once students become familiar with using Table 1 to solve problems, we encourage them to participate in active and collaborative learning by forming study groups to apply facts and concepts they have learned to new situations. This group process allows them to contemplate the relationship between genetic principles, experimental findings and observations. Does our model have application to *your* population genetics lesson?

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