Tested Studies for Laboratory Teaching
Proceedings of the Association for Biology Laboratory Education
Vol. 36, Article 16, 2015

Exploration and Hypothesis Testing of Population Genetics Principles through Computer Simulations

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Adequate coverage of population genetics is difficult due to the ever-increasing breadth of content in most genetics courses. Yet, this field is becoming increasingly important in areas as diverse as anthropology, forensics, ecology, conservation biology and medical genetics. Educators also face the challenge of teaching students to understand stochastic processes, the importance of modeling and to develop and test hypotheses. Using computer simulations, guided exercises and self-designed experiments students will model micro-evolutionary processes. These activities also provide the opportunity to discuss the importance of modeling in scientific research and for student interaction with stochastic processes.

Keywords: Population genetics, Hardy-Weinberg, Selection, Drift, migration, mutation, simulation

Introduction

Population genetics often receives short shrift in the undergraduate curriculum and this is unfortunate as a many topics of emerging importance rely heavily on population genetics underpinnings. These include molecular forensics, genetic genealogy, genomic mapping as in whole genome association studies (WGAS) and conservation biology. An inadequate coverage of these concepts is to the detriment of our students. A proper understanding of the micro-evolutionary processes requires an understanding of population genetics beyond simple Hardy-Weinberg equilibrium. In addition to the theoretical importance of population genetics, it is one of the few subjects at the undergraduate level where students are introduced to stochastic processes and a study of population genetics provides an opportunity for students to generate and test hypotheses using quantitative methods.

The most common approach to teaching population genetics at the undergraduate level relies on an introduction to Hardy Weinberg equilibrium (HWE) and the associated assumptions. Students learn the math and are able to observe allele frequency changes across a few generations. Rarely are students actively engaged with exploring the effects of violating assumptions of Hardy-Weinberg (HW) across many generations, and too often there is no consideration given to interactions when two or more of the Hardy-Weinberg assumptions are violated.

In this multi-part activity students are introduced to the basics of population genetics by providing directed and student designed simulations. During this two-part laboratory experience students explore natural selection and genetic drift and are presented options for including mutation, migration and bottleneck effects into these simulations. These activities can be presented in either order based on the needs of the class and the approach of the instructor. Alternatively, one these labs could be presented as a laboratory exercise and the other as an independent activity. Along the way students will gain experience reading graphical output and will most likely encounter some counterintuitive results that they will find challenging to explain.

In preparation for the lab students should be introduced to the Hardy-Weinberg equation and the assumptions surrounding Hardy-Weinberg equilibrium. It would be helpful if the students had experience calculating allele frequencies from genotype frequencies and predicting genotype frequencies from allele frequencies assuming Hardy-Weinberg conditions (Appendix B). Students should also be familiar with the concept of relative fitness and the relationship of relative fitness of genotype to dominance (Appendix C). For that portion of the lab examining selection, students should be able to calculate change in allele frequency, genotype frequency, and average fitness across at least two generations.

Student Outline

Web PopGen

Lab Part 1:Investigating Microevolution With Computer Modeling - Selection Using "Web Popgen"

Web PopGen is a computer program that simulates the mathematics underlying the

Hardy-Weinberg equation that we discussed in lecture. This is a Flash-based program and so will currently not work on Apple i-Pads (sorry). It should work well on all other computers with

up-to-date flash players. You may access Web PopGen at the following address:

http://www.radford.edu/~rsheehy/Gen_flash/popgen/

General Experimental Method

In these investigations we will violate the Hardy-Weinberg assumptions one at a time in order to predict how populations should evolve in response to different evolutionary forces. Different forces may produce different patterns of evolution, which biologists can then use to determine what forces are working on natural populations.

In these investigations, we will always work with one gene that has only two possible alleles in the population. We always have to start with simplest cases!

Getting Acquainted

First, click on the "?" button in the lower right hand corner for the screen. Read the introductory material about the program. Read about the Display features. Skim through other portions to see what you can get help with when you need it. When you have questions, consult the help information before asking the professor.

Part I: Effect of Selection on a Rare Recessive Trait

Question

The first question we'll ask is "What pattern of evolution results when selection favors a rare recessive trait?

Method

Control Variables

1. One assumption of the Hardy-Weinberg is no migration in or out of populations. Click on the Migration box and make sure the migration rate is zero.

2. Another assumption is that mutations don't produce more of one allele than another. We'll control this by setting both $A_1 => A_2$ and $A_1<=A_2$ mutation rates to 0.

3. A third assumption, no assortative mating, is no problem because the program is currently written to have random mating at all times.

4. A fourth assumption of the Hardy-Weinberg is an infinite population size. That is, there is no sampling error. Click on the box beside "Finite Pop." It will change to "Infinite Pop." Also make sure the "Bottle Neck?" box is NOT checked.

5. Set the number of generations to 200.

6. All populations will start with the same allele frequencies. You'll see that we can run 5 different populations (5 replicates of our experimental conditions) simultaneously. We will designate A_2 as the recessive allele. Our question asks what happens to an advantageous rare allele, so let's say that A_2 has an initial frequency of 0.05 in the population. What does that mean?

_____

What is the "A_1" (dominant) allele frequency? _____ . Enter the A_1 allele frequency for all 5 populations. Click OK to close the window.

We will compare selection favoring the recessive trait (experimental treatment) with no selection (the control). We will do that by choosing the fitnesses of different phenotypes.

Control Treatment

Run the control treatments first. Let's say that individuals of both the dominant and recessive phenotype have an average survival rate of 36% and then produce an average of 10 offspring per individual. Review your Fitness and Selection Coefficient worksheet to determine what the fitnesses should be if there is no selection. Enter those fitnesses in the boxes. Click Go to run the simulation. Only one line is produced because all 5 populations are doing exactly the same thing. Copy

these graphs to a Word document as described on the handy-dandy Help Page. Crop the image so only one graph is showing. Choose the graph that is most appropriate to your question. Label this Figure 1 and give it a descriptive legend.

Experimental Treatment

To make a good experiment, we change only one thing at a time. Let's say individuals with the recessive phenotype have an average survival rate of 40% and produce an average of 10 offspring per individual, while the dominant phenotype individuals have the same survival rate as in our control (see above).

Calculate the Fitnesses

Enter the fitnesses and click Go. Notice the curve is still changing at 200 generations. One should ask "What's going to happen?" Click Continue to run another 200 generations and find out.

Note that you see you have more complete results, but not all on one graph. Click Reset and change the number of generations to produce graphs with complete curves (but no more generations than necessary). Save graphs to the same Word document. Label this Figure 2 and give it a descriptive legend. To make control and experimental results equivalent, rerun the control at the same number of generations and paste it over (replace) the first graph.

Analysis

Describe the results in the two different figures. Describe not only the result at the end of 200 generations, but also the pattern of evolution -- how the population changed over those 200 generations. To do that, quantify the direction (increase, decrease, no change) and rate of change (remember from algebra that rate is the slope of the line (rise/run); this is most frequently taken at the steepest portion of the line).

Conclusion

In a sentence or two, answer the question of the experiment. Place these concluding sentences under figures 1 and 2.

Part II: How Does the Frequency of an Allele Affect Evolution by Selection?

Now we can follow up the results of the first experiment by seeing if our conclusion about the pattern of evolution is always the same. We might ask "Is the pattern of change the same at any initial frequency of an advantageous recessive allele, whether it's rare or not?"

Plan out an experiment to explore that question.

Hint: Remember that you have 5 populations. Each population can be set to a different initial allele frequency so that you can, in effect, run 5 different experiments at once. Build on what you already know by changing as little as possible from the previous experiment. Present your plan to your instructor.

Play with the frequencies you choose and the generation time until you get good graphs to display in a paper. Copy graphs to the Word document.

Do your analysis. What is going on here? Quantify your impressions by measuring and comparing slopes. Present comparisons of slopes in a table. Run more experiments to confirm what you think is happening. Add those data to your table. Draw a conclusion about the question.

Part III: How Does the Phenotypic Expression of an Allele Affect Evolution by Selection?

We can ask if our conclusions in the previous experiments continue to hold if we modify other parameters of a population. For example, we can ask, "Will an advantageous dominant allele evolve in the same way as an advantageous recessive allele?"

Use your results in Part II as the control set of data. Set up experimental parameters to get equivalent curves when the adaptive allele is a dominant allele. Don't change a bunch of things willy-nilly. Think it through and have a reason for changing anything. Check your plan with your instructor.

Run the program until you get equivalent graphs. Do any other experiments to check your results and conclusions. Copy good graphs to your Word document.

Do your analysis. Quantify comparisons of the patterns of evolution of an advantageous recessive trait with the patterns of evolution of an advantageous dominant trait. Summarize your findings.

Report

Follow the Guidelines for writing research papers (link on D2L) to write a paper on the effect of phenotypic expression on the evolution of a trait.

I won't ask you to do library search, so for your Introduction give background leading to the question(s) of the present research. In this paper, part 1 will be considered previous research. Just summarize what you found in a sentence or two, and then lead the reader to the questions investigated in parts 2 and 3.

The Methods will be whose program you used, how you set parameters for comparing recessive and dominant traits. Specify all the things that were the same, highlight the differences (a table may be useful here).

In the Results you will present and discuss your figures and any tables that resulted from your analysis from Parts II and III (do not include practice graphs of Part I).

The Discussion can just be a reminder to the reader of your question and your summary of what your answer is. Then discuss new questions that this research produced.

Web PopGen

Part 2: Investigations Dealing with Genetic Drift

Part I: Preliminary Observations

1. This time we will violate a different assumption of the Hardy-Weinberg principle, infinite population size. What an infinite population size does is eliminate all sampling error. Sampling error is chance deviation in the real world from theoretic expectations.

For example, the theoretic probability of getting a head with any coin flip is 0.50, so if we flip a coin 10 times we should theoretically get exactly 5 heads and 5 tails. However, we often get 4, 6, or even 10 heads. Those deviations from the expected 5 heads are sample error.

In the same way, Hardy Weinberg calculations are based on theoretical expectations that may not be met in the real world, for example:

a. The allele frequency calculation p = freq(A1A1) + 0.5 freq(A1A2), assumes that the A1A1 and A1A2 individuals will reproduce at exactly their frequencies in the population. In nature, A1A1 individuals might enter into slightly more mating than expected, just by chance --not because they have any advantageous quality. That's sampling error.

b. The union of gametes to produce offspring genotype frequencies of p^2, 2pq, and q^2 assumes that the gametes will combine at exactly the p and q frequencies. But in nature, just by chance, the allele frequencies involved in making the next generation may not be exactly p and q. As a result, for example, there may be slightly more A1A1 combinations and the frequency of A1A1 offspring will be a little larger than p^2. That's sampling error again.

2. To introduce sampling error, set the population size to 20 ("finite" means an element of chance is involved). Keep all other parameters the same as the Hardy-Weinberg conditions. Set generations to 100. Run 5 populations simultaneously all starting at the same initial frequency.

Notice that population 0 is an infinite population and so represents the control treatment. Notice also that the upper graph tells you the number of populations in which the A1 allele was either fixed or lost. If A1 is fixed, then A2 is lost, as you can see on the lower graph. If not all alleles are fixed or lost, click "continue" to see how many generations it takes.

3. The pattern of evolution that results from sampling error is called genetic drift -- frequencies seem to drift at random. But if we measure averages or percent from lots of populations, we can see that despite the randomness, there are some trends.

Notice that you can measure or count various things, such as:

- the number of populations in which an allele is fixed (or lost).
- the time (generations) to fixation (or loss).
- how often the direction of change (allele frequency increasing or decreasing) changes.
- there is no regular slope, but you can measure the maximum and minimum amount of change in N generations.

4. Draw conclusions (generalizations) about how "drifting" populations tend to evolve

Part II.

We will now conduct an experiment where we, as a class, collect and share data. We will address these three questions:

1) What is the effect of population size on genetic drift?
2) What is the effect of allele frequency on genetic drift?
3) What effect does gene flow have on genetic drift?

We will start with each person collecting data on the length of time until loss or fixation of alleles at various starting allele frequencies and different population sizes. Each person will run each simulation 5 times and record the following information:

a) Number of times A1 allele was fixed.
b) Average time till fixation of A1 allele.
c) Average time of loss of A1 allele.

Experiment 1:

Set number of populations to 10. Set A1 allele frequency to 0.1. Record the above data for each population size.

Experiment 2:

Set number of populations to 10. Set A1 allele frequency to 0.25. Record the above data for each population size.

Experiment 3:

Set number of populations to 10. Set A1 allele frequency to 0.5. Record the above data for each population size.

Experiment 4:

Set number of populations to 10. Set A1 allele frequency to 0.75. Record the above data for each population size.

Experiment 5:

Set number of populations to 10. Set A1 allele frequency to 0.9. Record the following data for each population size.

After collecting your data calculate the means in each column and record these data on the google docs table at the link I sent you earlier. Each experiment appears on a different tab (look at the bottom of the web page). The last row will be the calculated means for each column. Draw conclusions (generalizations) about how "drifting" populations tend to evolve. Write a concise summary of your conclusions based on our group data.

Materials

Computer with Internet access, preferably one per student although some students benefit by working in pairs.

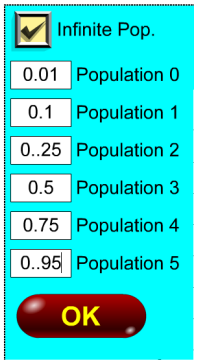
Notes for the Instructor

This lab works best when students have been introduced to the calculation of allele frequency, genotype frequency and relative fitness as well as the principles of genetic drift and natural selection. These may be presented either through directed readings or lecture. Having students work problems for calculating allele and genotype frequencies and for calculating relative fitness before the first lab period is beneficial. During the initial lab period students are introduced to the program and encouraged to explore the program using an initial series of directed experiments that become progressively more student-designed. Once students are familiar with the various settings they may be assigned independent projects, although I have found it useful for students to collaborate on projects. Having a second lab period reserved for the second half of this sequence has encouraged these collaborations.

Students are generally able to figure out how the program works through exploration, but it may be helpful to point out some features that may be overlooked.

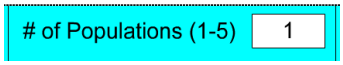
There is a population "0" generated automatically when running simulations that can be treated as a control population. This population appears as a black line. When performing simulations where drift is assumed (a finite population) this population behaves as an infinite population. When simulating infinite populations this may be treated as an additional population. However students may be encouraged to use this population as a control.

A help document is available by clicking on the green button with the question mark. This document provides general information on the function of buttons as well as some of the algorithms used in generating the graphs. Evolutionary theory is not covered.

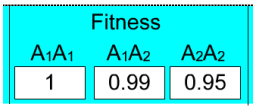


When simulating infinite populations one can vary the initial allele frequency among populations. This provides a way for students to compare the effects allele frequency on the rate of evolution.

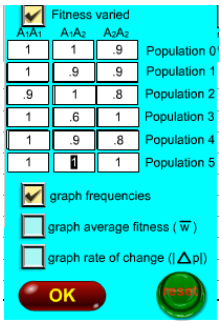
By default, when running simulations with greater than one population the top graph provides data on the frequency of the A_1 allele (p) while the bottom graph reflects the A_2 allele frequency (q). When examining a single population the top graph shows the frequency of both the A_1 and A_2 allele while the bottom graph shows the genotype frequencies, A_1A_1 (p^2), A_1A_2 (2pq) and A_2A_2 (q^2). This feature is particularly useful for helping students understand the persistence of an detrimental recessive allele in the population.



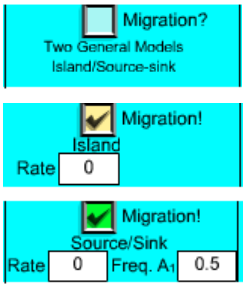
The program designates the two possible alleles as A_1 and A_2 in order to avoid an implied dominance. Students may need to be reminded that here, dominance is in relation to survival and reproduction and not necessarily a physical phenotype. By varying the fitness settings one can set either the A1 or the A2 allele as dominant. On can also demonstrate incomplete dominance by setting the fitness of the heterozygote to an intermediate value between the two homozygotes. Additionally one can simulate either heterosis (heterozygote advantage) by setting the fitness of the heterozygote above either of the homozygotes or negative heterosis by setting the fitness of both homozygotes about the fitness of the heterozygote. Heterosis and negative heterosis is an interesting place to introduce the concept of equilibrium equations (see below); a concept they have probably been exposed to in chemistry in relation to reaction rates.



When dealing with infinite populations it is possible to vary the fitness settings among the various populations. This will allow the user to examine the effects of fitness on both the rate of change in allele frequency and the final outcome of various selection schemes. It is also possible to change the output of the bottom graph from representing the A_2 allele frequency to either indicating change in average fitness ($\overline{w}$) of the population or the rate of chance in allele frequency (Δp).



Web Popgen simulates migration using two different models. The Island model assumes an equal probability of migration among each population. This may best be pictures as an archipelago where each island is equal distance from every other island and emigration is equal to immigration. Students playing with this option with finite populations are quick to realize it is equivalent to increasing the population size. Students will also observe that, under migration, fixation or loss of alleles is temporary as long as there is variation among populations. Migration may also be



discussed as a force that may act in a manor contrary to local adaptation. Wildlife corridors and the sharing of animals among zoological parks may be used to illustrate the importance of migration in maintaining or introducing genetic variation in managed populations.

Mutation rates may be set for A1 → A2 independent of the reverse mutation, A2 → A1. Students should be made aware that mutation rates are generally very very low and that most likely any simulation performed will be an overestimate of mutation rates in natural populations. However, students may experiment with a number of interesting scenarios. Students can predict the equilibrium point:

$$p_{(equ)} = \frac{v}{\mu - v}$$

where $p_{(equ)}$ is the frequency of the A_1 allele at equilibrium, m is the forward mutation rate for A_1 to A_2 and n is the reverse mutation rate from A_2 to A_1.

Without violating the assumptions of HW other than mutation they can vary the forward and reverse mutation rates and observe the equilibrium point as well as the rate of change in allele frequency as that equilibrium point is reached. A web page with the derivation of the equilibrium formula and an additional simulation may be found at http://www.radford.edu/~rsheehy/Gen_flash/Mutation/mutation.html.

If students have gone through the drift exercise they will be aware that, in a finite population, the probability of fixation of an allele is the current frequency of that allele in the population. Thus the probability of fixation of a new allele in the diploid population simulated here is 1/(2n). When populations are small, drift may have a powerful influence on the fate of new alleles in the population. Students may set up scenarios to explore a couple of questions: What is the chance that a new mutation resulting in a favorable allele will be lost? Does the dominance level of this allele affect its probability of survival under drift? If so, why?

There are a number of places where students may run into trouble and it helps to be aware of these:

Weaker students are often confused by being allowed to only set the frequency of one allele (the A1 allele). This exercise solidifies the relationship between A_1 and A_2 (p and q) for most of these students.

Students have difficulty envisioning the relationship between allele frequency and genotype frequencies under the various selection regimes. In these situations it is useful to have students run experiments with a single population. With a single population Web PopGen will display the A1 and A2 allele frequencies in the upper graph and the genotype frequencies (p^2, 2pq and q^2) in the lower graph. This is particularly informative for students wrestling with lack of fixation for dominant alleles in an infinite population.

Alleles in this simulation are labeled A1 and A2. Thus there is no implication of dominance. Dominance is determined by the relative fitness of the 3 genotypes. Students often have difficulty with this concept particularly when they are asked to select for the same allele, but treat the allele differently (eg., first select for A1 as a dominant and then select for A1 as a recessive allele).

Once students are comfortable with the basic assumptions of Hardy-Weinberg and the effects of violating those assumptions it becomes easy to move on to more complex problems such as effects of two genes with linkage, inbreeding, and coalescent theory. While not as graphically pleasing, these ideas may be addressed using the program EvolGenius. While not web based, EvolGenius is a java program which should run on most platforms and will allow you to expand the complexity of the questions you can ask your students to address.

Sample Results

Sample results are presented in Figs. 1, 2 and 3.

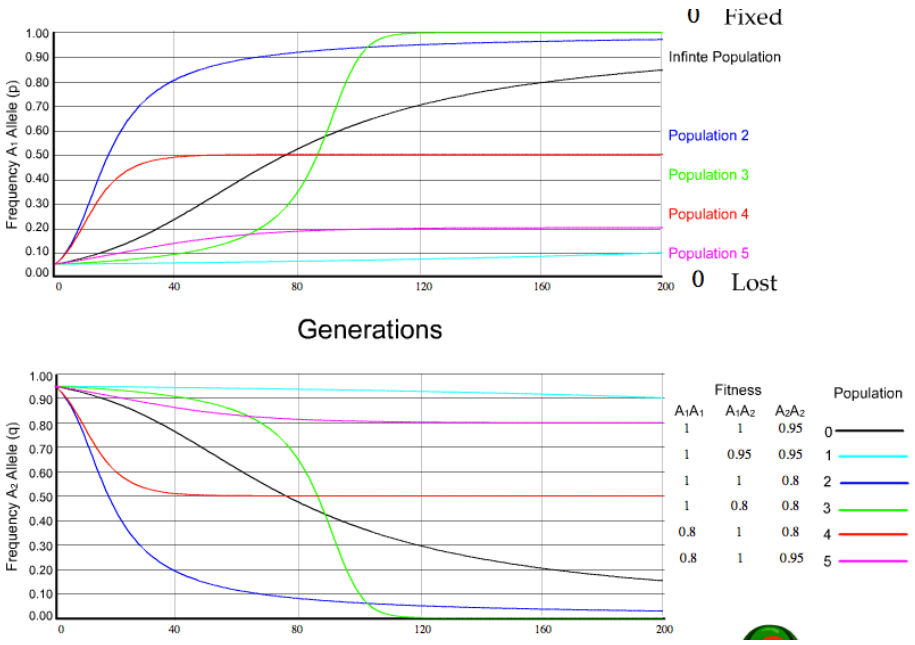


Figure 1. Sample output showing change in A1 (top) and A2 (bottom) allele frequencies under various genotype fitnesses and various levels of dominance. (Infinite population assumed.)

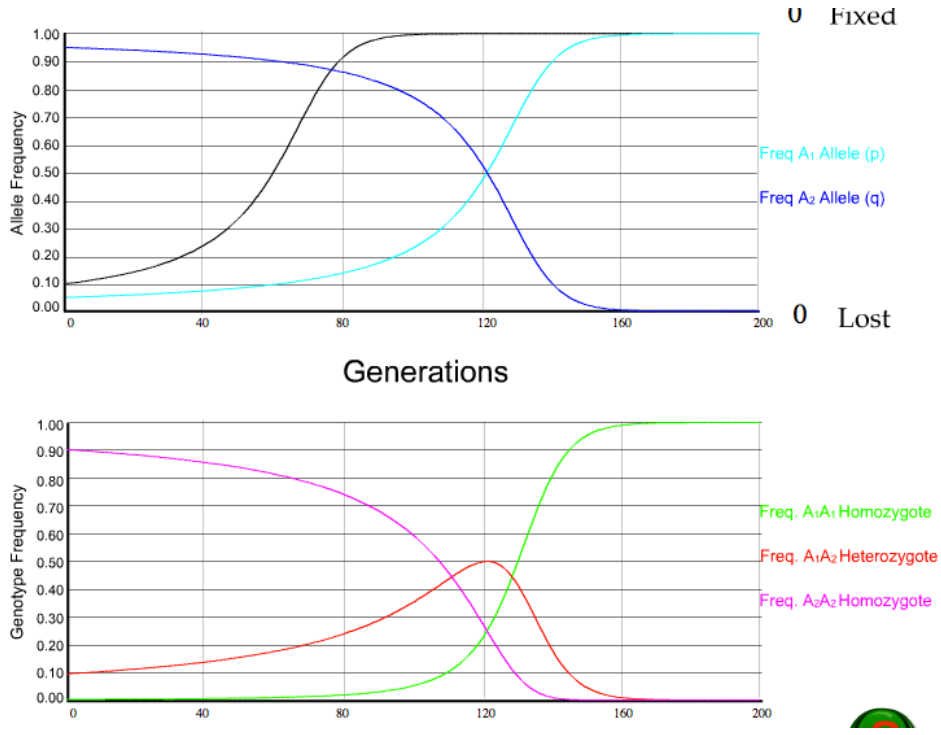


Figure 2. Top graph represents the change in allele frequency of A1 (light blue) and A2 (dark blue) under selection for A1 as a recessive. Bottom graph represents the change in genotype frequencies associated with allele frequency changes (infinite population assumed.)

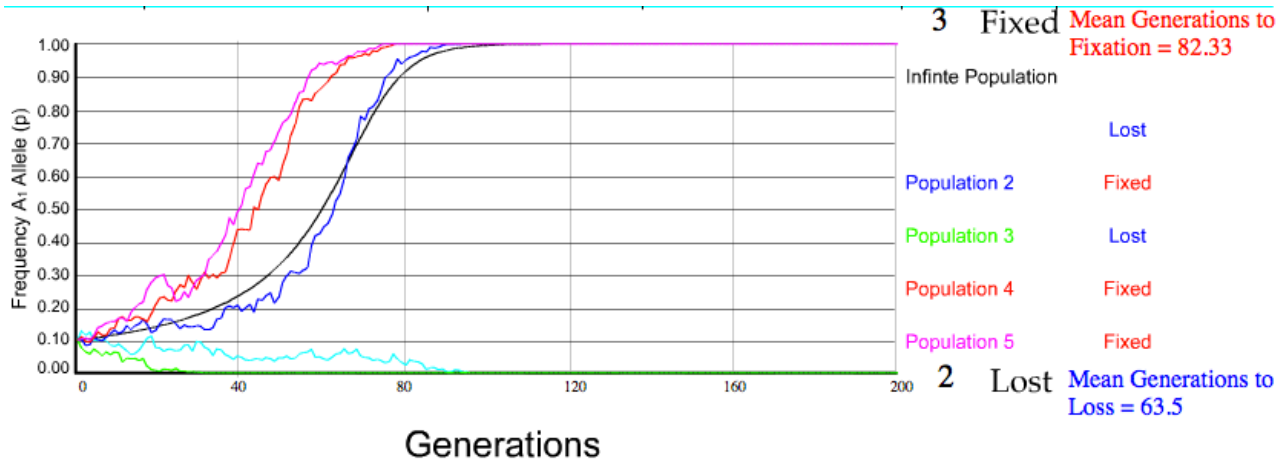


Figure 3. Change in allele frequency in 5 small populations (N=250) with selection for the A1 allele as a recessive. Black line represents an infinite population.

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Citing This Article

Sheehy, R. 2015. Exploration and hypothesis testing os population genetics principles through computer simulations. Article 16 in *Tested Studies for Laboratory Teaching,* Volume 36 (K. McMahon, Editor). Proceedings of the 36th Conference of the Association for Biology Laboratory Education (ABLE), http://www.ableweb.org/volumes/vol-36/?art=16

Appendix A
Web Sites for Simulations and Worksheets

Note: Links to these resources are available at: http://www.radford.edu/~rsheehy/Gen_flash/ABLE_Workshop/

WebSites

1) Web PopGen (http://www.radford.edu/~rsheehy/Gen_flash/popgen) is a population genetics simulation program. We will be using this as our primary simulation program.
2) Web PopGen Beta (http://www.radford.edu/~rsheehy/Gen_flash/popgen2).
   Same as above but not validated. May contain a few bugs.
3) Allele and Genotype Frequency Calculations: A practice sheet for calculating allele and genotype frequencies assuming the populations are in Hardy-Weinberg proportions. See Appendix B.
4) http://www.radford.edu/~rsheehy/Gen_flash/Hardy_weinberg/allele_freq_Calculation_Pop.html
4) Mutation Equilibria: A simple model of mutation. http://www.radford.edu/~rsheehy/Gen_flash/Mutation/mutation.html
5) Calculation of Fitness and Selection Coefficient: http://www.radford.edu/~rsheehy/GraphingDemo/fitness1.html
6) EvolGenius (http://www.radford.edu/~rsheehy/Gen_flash/EvolGenius/) is a Java based computer program that simulates micro-evolutionary change within a single population. It is base on an earlier version written in C++ by Rich Kliman. The program follows the evolution of two genes, *Alpha* (*A*) and *Beta* (*B*).
7) Population Genetics Equations: A brief review of the math behind the population genetics we have covered. http://www.radford.edu/~rsheehy/Gen_flash/ABLE_Workshop/Popgen_Equations.pdf

Shared Data

Drift Data Spreadsheet – An example Google Docs data sheet on the effects of population size, allele frequency and fixation rate. (http://tinyurl.com/nbwr9aa)

Appendix B
Worksheet #1: A Worksheet For Students to Practice Calculation of Allele and Genotype Frequencies in Populations that Are in Hardy-Weinberg Proportions

Note: This worksheet is available on the web. Random genotype and allele frequencies are generated providing students with the opportunity to solve unique problems and assess their understanding.
http://www.radford.edu/~rsheehy/Gen_flash/Hardy_weinberg/allele_freq_Calculation_Pop.html

Calculation of Allele and Genotype Frequencies in Populations in Hardy-Weinberg Proportions

Assume that each population is in Hardy-Weinberg proportions. Calculate the missing genotype and/or allele frequencies for each population.

	Freq(MM)	Freq (MN)	Freq(NN)	Freq(M) = p	Freq(N) = q
Population 1	0.005	0.130	0.865		
Population 2				0.48	0.52
Population 3	0.053	0.354			
Population 4					0.55
Population 5			0.578		

Appendix C
Worksheet #2: Worksheet to Prepare Students for Selection Portion of the Lab

Note: The *Calculation of Fitness and Selection Coefficient Worksheet* is available on the web and will generate random problems while walking students through the solution. http://www.radford.edu/~rsheehy/GraphingDemo/fitness1.html

Calculation of Fitness and Selection Coefficient
Survival rate = the overall survival rate is the % of individuals born that survive to reproductive age. But often we can only measure the % that survive over some period of time, e.g. the survival rate of fledglings, the survival rate from one year to the next, or the survival rate through a winter storm.

Reproductive rate = for any given genotype or phenotype, the average number offspring born per individual.

Relative Fitness (w) is the survival and/or reproductive rate of a genotype (or phenotype) relative to the maximum survival and/or reproductive rate of other genotypes in the population.

Calculate the *Relative Fitness (w)* of each genotype by dividing each genotype's survival or reproductive rate by the highest survival or reproductive rate among the 3 genotypes. For example:

If only survival rates differ and reproductive rates are all equal, then the fitnesses are simply equal to each survival rate divided by the highest survival rate.

	DD	Dd	dd
Survival rate	10%	10%	20%
Reproductive rate	4	4	4
Relative fitness (w)	10/20 = 0.50	10/20 = 0.50	20/20 = 1.0

If only reproductive rates differ and the survival rates are all equal, then fitnesses are equal to each reproductive rate divided by the highest reproductive rate.

	DD	Dd	dd
Survival rate	10%	10%	10%
Reproductive rate	8	8	4
Relative fitness (w)	8/8 = 1.00	8/8 = 1.00	4/8 = 0.50

If both survival and reproductive rates vary among the genotypes, then divide each survival X reproductive rate by the highest survival X reproductive rate.

	DD	Dd	dd
Survival rate	10%	10%	20%
Reproductive rate	10	8	6
Survival X Reprod.	0.1 X 10 =1.0*	0.1 X 8 = 0.8*	0.20 X 6 = 1.2*
Relative fitness (w)	1.0/1.2 = 0.83	0.8/1.2 = 0.67	1.2/1.2 = 1.0

*On average, every DD born produces 1 viable offspring, while a typical Dd newborn produces 0.8 offspring and dd newborns average 1.2 offspring each.

Interpretation of fitness: w_{dd} = 1.00 means the dd genotype is the most fit, most successful, of the 3 genotypes in that particular environment at that particular time (even though many may be dying young). The fitnesses of the other genotypes are some percentage of that highest fitness. For example, w_{DD} = 0.9 means the DD individuals produce offspring on average at 90% of the rate of individuals with the most successful genotype with w = 1.0.

The selection coefficient is a measure of the relative strength of selection acting against a genotype. Calculate the selection coefficient (s) by subtracting each fitness value from 1.0 (that is, s = 1-w).

Interpretation of selection coefficient: $s_{dd} = 0.0$ means genotype dd is not being selected against. That is, although they are dying, the dd individuals on average are dying at a lower frequency or produce more offspring than the other genotypes in the same population. $s_{DD} = 1.0$ is total selection against the genotype (DD individuals produce no viable offspring.) $s_{DD} = 0.10$ means that in each generation, DD individuals produce offspring on average at 90% of the rate of the dd individuals, or in other words, DD individuals on average have a 10% harder time producing offspring than dd individuals.

Fitness Practice Problems

Calculate the fitnesses and selection coefficients in each of these cases. *Interpret The Meanings of the Numbers.* In some you will have to calculate the survival and/or reproductive rates.

1. DD and Dd individuals have 25% survival rates and dd individuals have a 20% survival rate. They all produce the same number offspring on average.

2. Homozygous dominant and heterozygotes produce 4 offspring per individual on average, while the homozygous recessives produce 8 on average. But all offspring survive at the same rate.

3. Individuals with the dominant phenotype have a 25% survival rate to adulthood, and each produce 4 offspring on average. The recessive phenotypes have a 22% survival rate and produce 8 offspring on average.

4. Homozygotes for the A hemoglobin allele survive at a rate of about 60%, the homozygotes for the S hemoglobin allele at about a rate of 1%, the heterozygotes survive at about a rate of 80%. All produce about the same number of offspring.

5. A population of 1500 corn plants produces 166500 seeds (offspring) of corn. What is the reproductive rate? Give number and units.

6. You plant all of the seeds and find that only 108,225 germinate. What is the average survival rate to that stage of life?

7. You are raising zebrafish. In one generation, 10 adults produce 955 eggs, of which you manage to rear 15 to adulthood. What is the reproductive rate in terms of egg production? What is the survival rate of the young? What is the overall reproductive rate of the original 10 adults? Be sure to give units.

8. In a population of elk 10 males with the largest antlers fathered 200 fawns while the 100 smaller antlered males fathered 220 fawns. What are the reproductive fitnesses and selection coefficients of the 2 types of males?

9. Of the 10 large-antlered elk that mated in the spring, five survived through the following winter to mate again. Of the 100 smaller-antlered males, 70 were still alive the following spring. What are the fitness and selection coefficients of the 2 types of males?

10. What are the overall fitnesses of the large- and small-antlered males in the previous 2 questions if you consider their abilities to survive and reproduce?

11. Make up your own numbers to practice more kinds of scenarios.