MIGRATION AND GENETIC DRIFT AS MECHANISMS OF EVOLUTION
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Introduction

This case study will help you develop an intuition about how migration and genetic drift cause evolution. You will use a software simulation of an evolving population to analyze examples discussed in Chapter 7, and to answer a variety questions concerning changes in the frequencies of alleles. Once you are familiar with the simulation program, you can use it to answer questions of your own. For example, How often does a mildly deleterious allele drift to fixation in populations of different sizes?

To complete the case study you will need the application program AlleleA1. You can download AlleleA1 from the Evolutionary Analysis website. Versions are provided that run under MacOS and Windows. AlleleA1 simulates evolution at a single locus in an ideal population. The locus has 2 alleles: A_1 and A_2. AlleleA1 allows you to enter parameters controlling selection, mutation, migration, drift, and inbreeding. The program then plots a graph showing the frequency of allele A_1 over time. Each generation's frequency is calculated from the previous generation's frequency, according to the equations described in Chapters 6 and 7.

AlleleA1 is easy to use. Small boxes in the lower portion of the AlleleA1 window allow you to enter and change the parameters for the simulation. The tool palette has buttons that allow you to run the simulation, clear the graph, reset all parameters to their default values, print your graph, and quit. More details on using AlleleA1 can be found in the manual, available both as a separate PDF file and online, under the Help menu, while you are running AlleleA1.

Exercises

Hardy-Weinberg equilibrium

1. If you have not used AlleleA1 before, play with it for a bit to see how it works. Then restore all parameters to their default settings. The default settings encompass initial frequencies of 0.5 for both alleles, and the assumptions of no selection, no mutation, no migration, no genetic drift, and random mating. Run the simulation to verify that under these conditions the allele frequencies do not change. Try different values for the starting frequency of allele A_1. Does your experimentation verify that *any* starting frequencies for A_1 and A_2 are in equilibrium so long as there is no selection, no mutation, no migration, and no drift?

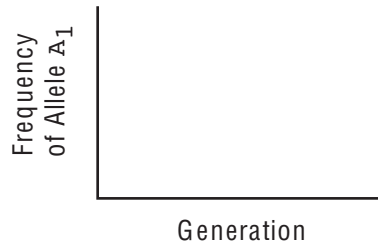## Migration as a mechanism of evolution

2. AlleleA1 uses the one-island model of migration described on pages 234-237 of the text. The simulation tracks the frequency of allele A_1 in an island population. The parameter called *Fraction of migrants each generation* determines the number of individuals that move from the mainland to the island every generation, as a fraction of the island population. For example, setting the parameter to 0.1 means that each generation ten percent of the individuals in the island population are new arrivals from the mainland. The parameter called *Frequency of A_1 in the source pop'n* determines the frequency of allele A_1 on the mainland (and thus among each generation's migrants).

a) Click on the Reset button to restore all parameters to their default values. Predict what will happen when you set the fraction of migrants each generation to 0.01 and the frequency of A_1 in the source population to 0.8. Then set the parameters to these values and run the simulation. If your prediction was not correct, try to explain the difference between what you expected and what actually happened.
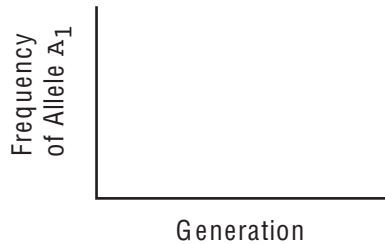
Prediction: What actually happened: Explanation:

b) Leave the frequency of A_1 in the source population at 0.8, and try setting the fraction of migrants each generation to 0.05, then 0.1.

c) Try several different values for the both the fraction of migrants and the frequency of allele A_1 in the source population.

d) Based on your experiences in parts a, b, and c, summarize what migration from the mainland does to the frequency of A_1 on the island. How long does it take for migration to exert its influence? How effective is migration as a mechanism of evolution?

Migration and selection

3. Imagine that allele A_1 is deleterious for individuals living on the island, such that the fitnesses of genotypes A_1A_1, A_1A_2, and A_2A_2 are 0.9, 0.95, and 1.

a) If there is no migration, what is the frequency of A_1 after 500 generations? Why?

b) In accord with what you saw in part a, set the starting frequency of A_1 to 0. Remember that this is the frequency in the island population. Now imagine that although it is deleterious on the island, allele A_1 is *beneficial* on the mainland, such that A_1 is fixed in the source population (that is, its frequency is equal to 1). What is the island frequency of A_1 after 500 generations if the fraction of migrants each generation is 0.0001? 0.001? 0.01? 0.1?

Fraction of migrants	Ending frequency of A_1
0.0001	
0.001	
0.01	
0.1	

c) In the scenario you investigated in part b, how high does the migration rate have to be for migration to overwhelm selection in controlling the frequency of A_1 on the island? If selection against A_1 on the island were stronger than we assumed in this example, would migration be less likely to overwhelm it?

4. Reread *Empirical research on migration versus selection* on pages 237-239 in the text. Richard King and colleagues studied an example of selection and migration in Lake Erie water snakes that is similar to the scenario you investigated in question 3. On islands in Lake Erie, the allele for banded coloration is deleterious. The allele is fixed on the mainland, however, and migrants move from the mainland to the islands each generation. Box 7.2 on pages 238-239 describes an algebraic analysis by King and Lawson (1995) of the equilibrium in the island population between selection and migration. We can use AlleleA1 to do a similar analysis. Reset all parameters to their default values. Let allele A_1 be the dominant allele for the banded pattern, and A_2 be the recessive allele for the unbanded pattern. Set the starting frequency of A_1 to zero, and the frequency of A_1 in the source population to one.

a) To reflect King and Lawson's best estimates, set the fitnesses of A_1A_1, A_1A_2, and A_2A_2 to 0.84, 0.84, and 1. Set the fraction of migrants each generation to 0.01. What is the frequency of allele A_2 (the allele favored on the islands) after 500 generations?

b) To reflect King and Lawson's high-end estimate (strong selection, little migration) set the fitnesses of A_1A_1, A_1A_2, and A_2A_2 to 0.78, 0.78, and 1, and set the fraction of migrants each generation to 0.003. Now what is the frequency of allele A_2 after 500 generations?

c) Finally, to reflect King and Lawson's low-end estimate (weak selection, much migration) set the fitnesses of A_1A_1, A_1A_2, and A_2A_2 to 0.90, 0.90, and 1, and set the fraction of migrants each generation to 0.024. What is the frequency of allele A_2 after 500 generations?

d) The actual frequency of the unbanded allele in the island population is 0.73. How well did our model perform at predicting this result? Can you think of ways to modify our model to make it more realistic? If so, try them out with AlleleA1.

Genetic drift as a mechanism of evolution

5. We have so far used AlleleA1 to simulate evolution in populations of infinite size. In reality, of course, populations are finite. Is evolution in finite populations different from evolution in infinite populations? Return all parameters to their default settings. Set the number of generations to 15 (use the popup menu to the right of the graph's horizontal axis). Now play with populations of finite size. For example, set the population size to 10 or 20 individuals and run the simulation several times. What happens? Why? Does the same thing happen every time? Why or why not? (For help answering these questions, reread *A Model of Genetic Drift* on pages 240-242.)

6. How much does genetic drift change with population size? Return all parameters to their default settings. Set the number of generations to 100. Set the graph line mode to multiple, and the graph line color to auto. Now investigate the power of genetic drift at different population sizes:

a) Set the population size to 4 and run the simulation several times.

b) Clear the graph. Set the population size to 40 and run the simulation several times.

c) Clear the graph. Set the population size to 400 and run the simulation several times.

d) Compare your results for parts a, b, and c to graphs a, b, and c in Figure 7.15 on page 247. Why are the results different for populations of different sizes?

7. Conservation biologists generally consider genetic diversity to be a good thing. That is, populations are more likely to escape extinction if there are several alleles present for each gene.

a) What does drift do to the genetic diversity in a population as the population nears extinction?

b) Reset all parameters to their default values. Note that the starting frequencies for alleles A_1 and A_2 are 0.5. Roughly how big does the population have to be for the chances to be reasonably good that both alleles will persist for 500 generations?

The random fixation of alleles

8. You have seen that when genetic drift is the only evolutionary force at work in a population—when there is no selection, no mutation, and no migration—the frequencies of alleles in the population wander between 0 and 1. If we track a particular allele for long enough, its frequency will eventually hit one boundary or the other. That is, sooner or later the allele will drift to loss or fixation. Investigate the effect of an allele's initial frequency on the probability that its ultimate fate will be fixation versus loss.

a) Reset all parameters to their default values, and set the population size to 100. Pick an initial frequency for A_1, and set the starting frequency parameter in AlleleA1 accordingly. Then run the simulation 100 times. Record your results in the grid below. There are 100 squares in the grid. If A_1 drifts to fixation in a particular run, write a 1 in one of the squares on the grid. If A_1 drifts to loss, write a 0 in one of the squares. If a run ends with A_1 still at a frequency between 0 and 1, disregard the run and continue with the experiment. After 100 runs in which A_1 drifted to fixation or loss, count the 1's on your grid to determine the percentage of runs in which A_1 drifted to fixation.

Starting frequency of allele A_1: ____

Final frequencies for 100 runs:

Percentage of runs in which allele A_1 drifted to fixation: ____

b) Repeat the experiment you performed in part a, but use a starting frequency for A_1 that is substantially different from the one you used before. Record your results in the grid below.
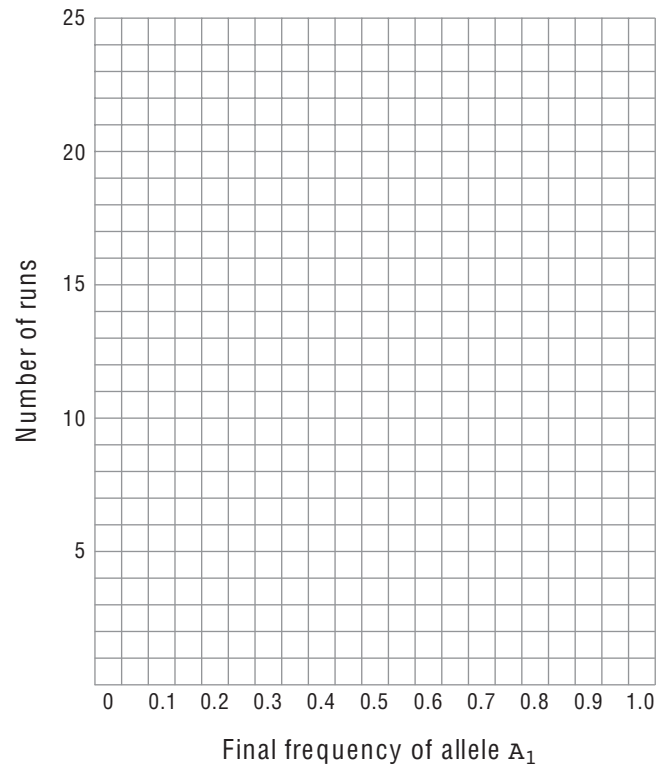
Starting frequency of allele A_1: ____

Final frequencies for 100 runs:

Percentage of runs in which allele A_1 drifted to fixation: ____

c) Based on your experiments in parts a and b, can you use the starting frequency of an allele to predict the probability that the allele will eventually drift to fixation? Compare your conclusion to the analysis in Box 7.3 on page 248.

9. Reread *An Experimental Study on Random Fixation and Loss of Heterozygosity* on pages 249-252. Peter Buri (1956) followed the frequency of the bw^{75} allele for 19 generations in 107 populations of fruit flies. Buri maintained each population at a size of just 16 individuals, which caused the populations to evolve rapidly by genetic drift. Use AlleleA1 to simulate Buri's experiment.

a) Reset all parameters to their default values, then set the population size to 16 and the number of generations to 20. Run the simulation 50 times. After each run, round the final frequency of A_1 to the nearest 0.05, and fill in a box on the grid at right above the resulting value. As the number of runs you have completed grows, stack the filled boxes on top of each other so that they form a histogram, like this:

After completing 50 runs, compare your histogram to the one from generation 19 of Buri's experiment, at the bottom of Figure 7.16 on page 250. How well did your simulated experiment "predict" the results of Buri's actual experiment? Can you explain the difference between the shape of your graph and the shape of Buri's?

Number of runs

25

20

15

10

5

0   0.1   0.2   0.3   0.4   0.5   0.6   0.7   0.8   0.9   1.0

Final frequency of allele A_1

b) Now set the population size to 9, and run the simulation another 50 times. Record your results on the graph at right just as you did in part a. Again compare your histogram to the one from generation 19 of Buri's experiment. Does the shape of your second graph match Buri's more closely than your first graph did?

Number of runs

25

20

15

10

5

0   0.1   0.2   0.3   0.4   0.5   0.6   0.7   0.8   0.9   1.0

Final frequency of allele A_1

c) What does it mean to say that although the actual population size in Buri's experiment was 16 individuals, the effective population size was approximately 9? What evidence do you have to support this claim?

Drift and selection

10. Consider the fate of a rare allele in a small population.

a) Reset all parameters to their default values, then set the starting frequency of A_1 to 0.005 and the population size to 100. Run the simulation several times. What usually happens? Why?

b) Now make the rare allele beneficial (and dominant) by setting the fitnesses of genotypes A_1A_1, A_1A_2, and A_2A_2 to 1.1, 1.1, and 1.0. Run the simulation several times. What usually happens? Why?

c) How strong does selection in favor of the rare dominant allele have to be before the allele has a reasonable chance of becoming fixed in the population instead of lost?

d) How strong would selection have to be if the rare allele were recessive instead of dominant?

Drift, mutation, and selection

11. How big must a population be before a mildly advantageous allele will become fixed as rapidly as it would in a population of infinite size? Restore all parameters to their default values. Set the starting frequency of A_1 to zero, and both mutation rates to 0.00001. Make A_1 beneficial by setting the fitnesses of genotypes A_1A_1, A_1A_2, and A_2A_2 to 1.04, 1.02, and 1. Set the number of generations to 1000.

a) Set the graph line color to black, and run the simulation once with the population size set to infinite. How long does it take for allele A_1 to be created by mutation and carried by natural selection to fixation?

b) Now set the graph line mode to multiple, the graph line color to red, and the population size to 10. Run the simulation several times. What typically happens?

c) Set the graph line color to orange and the population size to 100. Run the simulation several times. What typically happens?

d) Set the graph line color to green and the population size to 1000. Run the simulation several times. What typically happens?

e) Finally, set the graph line color to blue and the population size to 10000. Run the simulation two or three times. What typically happens?

f) How large does a population have to be before a mildly advangateous allele will become fixed as rapidly as it would in a population of infinite size? How strongly does the answer depend on the strength of selection and the mutation rate?

Drift, selection, migration, and genetic diversity

12. In question 7, we noted that conservation biologists consider genetic diversity to be a good thing, and found that genetic drift can reduce genetic diversity and potentially hasten the extinction of small populations. We now revisit these issues by investigating a particular scenario in more detail. Imagine that allele A_1 is maintained in a population by heterozygote advantage, with the fitnesses of genotypes A_1A_1, A_1A_2, and A_2A_2 equal to 0.2, 1.0, and 0.8.

a) What is the equilibrium frequency of A_1 in an ideal population? (You can answer this question either by using the formula derived in Box 6.7 on pages 208-209, or by using AlleleA1.)

b) Once the frequency of allele A_1 has reached its equilibrium value, what are the frequencies of the three genotypes? (You can answer this question either by using the Hardy-Weinberg equilibrium principle, or by using AlleleA1.)

c) Once the frequency of allele A_1 has reached its equilibrium value, what is the mean fitness of the population? (To calculate the mean fitness, multiply the fitness of each genotype by its frequency, then sum the results; see Box 6.3 on page 194).

d) Using AlleleA1, first reset all parameters to their default values. Then set the starting frequency of A_1 to 0.2, the fitnesses of A_1A_1, A_1A_2, and A_2A_2 to 0.2, 1.0, and 0.8, and the population size to 20. Run the simulation several times. What usually happens?

e) After A_1 has been lost due to genetic drift, what is the mean fitness of the population? By how much has drift reduced the mean fitness? If this effect were multiplied across several loci, could drift substantially increase the chance that our small population will go extinct? Why or why not?

f) Use AlleleA1 to investigate the effect of introducing a single migrant individual into our small population each generation, where the migrant comes from a large population in which the frequency of A_1 is 0.2. (What value for the *Fraction of migrants each generation* parameter reflects a single individual joining a population of 20?) Could the introduction of migrants maintain enough genetic diversity in the population to ameliorate the effects of genetic drift? Compare the scenario you have investigated in this question to the case of the Florida panther discussed at the beginning and end of Chapter 7.

Literature Cited

Buri, P. 1956. Gene frequency in small populations of mutant *Drosophila*. *Evolution* 10:367–402.

King, R.B., and R. Lawson. 1995. Color-pattern variation in Lake Erie water snakes: The role of gene flow. *Evolution* 49:885–896.