

SimBio Virtual Labs®

# EvoBeaker®: Finches and Evolution

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# Finches and Evolution

## Introduction

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In 1835, while traveling with the British Survey ship *HMS Beagle*, Charles Darwin, then 26 years old, visited the Galapagos archipelago. During a five-week stay, Darwin collected a variety of small land birds that he took to be finches, wrens, warblers, and blackbirds. Upon returning home to England, Darwin was gratified to learn, from ornithologist John Gould, that all the birds were new to science. He was surprised, however, to be told that all of them—including the ones Darwin thought were blackbirds, warblers, and wrens—were finches.

The birds have come to be known collectively as Darwin's finches. Biologists now recognize 13 species, plus a 14<sup>th</sup> that lives on Cocos Island. The 14 species are closely related descendants of a small flock of dome-nested finches that flew (or were blown) to the Galapagos between two and three million years ago, probably from the Caribbean (Sato et al. 2001, Burns et al. 2002).

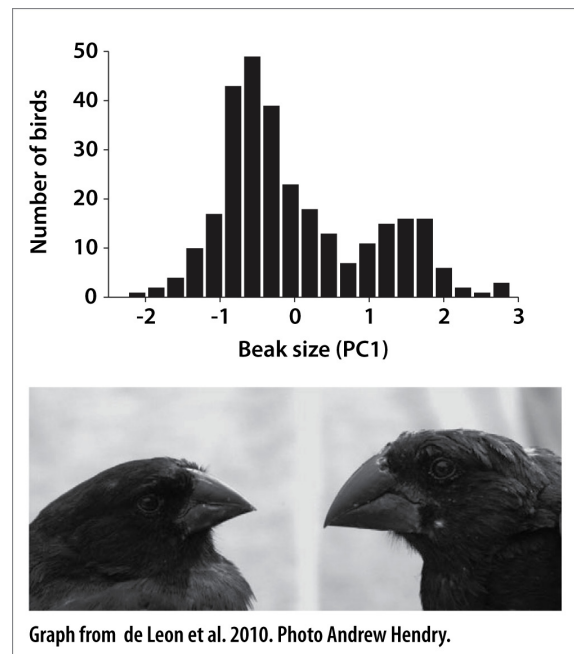
As the early descendants of the original flock spread across the archipelago they began to eat foods that, back in the Caribbean, would have been monopolized by other, more specialized, animals. Gradually, the Galapagos finches evolved into distinct populations, then species, adapted to a diversity of lifestyles. One species eats cactus flowers, another eats leaves, and a third pecks the wings and tails of boobies and drinks their blood. Two use twigs or cactus spines to pry insect larvae from tree bark. Several species spend most of their time on the ground, feeding on seeds.

For several decades Darwin's finches have been a focus of research by evolutionary biologists interested in natural selection, adaptation, divergence, and speciation. Among the reasons the finches make attractive subjects for research on evolution is that they live on oceanic islands. The Galapagos archipelago is a string of volcanoes that rise from the ocean floor 1000 km west of Ecuador. The islands have never been connected to the mainland, making it difficult or impossible for most mainland species to travel there. The islands' biological communities are therefore simpler, with fewer interacting species than on the mainland and differing community composition from island to island. Consequently, the finches, like other island species, often evolve unusual traits. And biologists trying to understand why have a relatively short list of factors to consider. For example, Darwin's finches have few predators. Their main challenges in life are getting enough to eat and finding mates.

Our subject for this lab is a seed-eating species of Darwin’s finch called the medium ground finch (*Geospiza fortis*). Populations occur on over a dozen different islands across the archipelago. The population on Daphne Major Island has been under study since 1973 by Peter Grant, Rosemary Grant and colleagues. Populations on other islands have been studied by Grant and Grant, as well as by Andrew Hendry, Anthony Herrel, Sarah Huber, Luis Fernando de León, and others.

The medium ground finch exhibits on a smaller scale many of the patterns that Darwin’s finches as a group exhibit on a larger scale. Populations of the medium ground finch evolve to adapt to local environmental conditions, resulting both in changes over time within populations and in differences among populations living in different places. And there is evidence that some populations are in the early stages of speciation—that is, of splitting into distinctive lineages with limited interbreeding.

The most intriguing evidence of early-stage speciation is shown by finches at El Garrapatero, on Santa Cruz Island. As can be seen in the graph, birds there come in two types. One type has small beaks, the other large beaks. Graphs showing trait variation typically follow a bell curve. This one, however, has two humps. The technical term for a distribution with two humps is “bimodal.” The two modes in the graph are not fully separated. Some birds fall in between. Still, most finches can be classified as small-beaked or large-beaked. The photo shows one of each. These individuals were captured in the same net at the same time and photographed together.



The distinction between small- versus large-beaked finches is not associated with sex. Both males and females come in both flavors (Hendry et al. 2006). Bimodal distributions that are not associated with sex are unusual. Our ultimate goal in the lab is to understand how this one might have evolved.

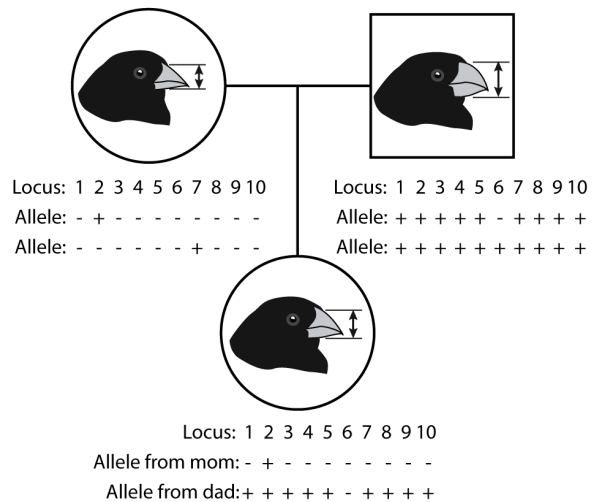
To do so we will build a model, proceeding in steps. We will first construct a virtual finch population in which beak size evolves in response to changes in the kinds of seeds available. We will use the model to explore how a population can evolve to track a fluctuating environment, and how correlations among traits might constrain evolution. Finally, we will see whether, with minimal modifications to the model, our virtual finch population will evolve distinctive subpopulations.

## Exercise 1: Finches and the Weather

- [ 1 ] If you haven't already, start **SimUText**® by double-clicking the program icon on your computer or by selecting it from the Start menu. When the program opens, enter your Log In information and select the **Finches and Evolution** lab from your **My Assignments** window.
- [ 2 ] On the left side of the main window you should see a bird's eye view of an island inhabited by finches. Each finch wears a collar indicating the depth of its beak. Brighter collars mean deeper beaks. To get a closer look at a finch, click on it. An **Information Window** appears, listing the finch's age, beak depth (top-to-bottom, in millimeters), and beak width (right-to-left, in millimeters). Initially we will focus only on beak depth. Dismiss the window by clicking the close button.
- [ 3 ] The **Controls** panel at the bottom left of the screen allows you to run and stop the model. Start the model by clicking on the **GO** button (the one with the triangle on it).
- [ 4 ] You should see the finches flying around as they search for food, seek mates, hatch chicks, and ultimately die. The **phenotype graph** at the upper right shows the variation in beak depth.
- [ 5 ] Pause the model by clicking on the **STOP** button in the **Control Panel** (the one with the square on it).
  - [ 5.1 ] **Judging by eye from the phenotype graph, what is the smallest beak depth present in your population? The largest? What is the current average beak depth?**
- [ 6 ] Click the **RESET** button (the one with an arrow curling back on itself) to get a new population.

In our model, ten genes contribute to beak depth. Each gene has two alleles: one decreases beak depth; the other increases it. The pedigree (right) shows a mating between a shallow-beaked female and a deep-beaked male, producing a medium chick.

Ten loci is an arbitrary number. We chose it because it yields a starting distribution that approximates a bell curve. Among the model finches, as among the finches of El Garrapatero, beak depth runs from a little over 8 mm to just under 15 mm.



Each virtual year the model runs, the female finches try to mate and have babies. Each baby inherits one allele per gene from each parent. Initially, there is no mutation or immigration. Finches tend to stay within a small area but at breeding time may fly over the whole island seeking mates. At present, individuals pick their mates at random.

*Geospiza fortis* eat seeds. Because the plants on the island produce a finite number of seeds, the island supports a finite number of finches. The carrying capacity is currently 500 birds. In the default version of our model, beak depth has no influence on a finch's ability to eat seeds and thus no influence on survival. If the number of finches exceeds the carrying capacity, the model keeps the population in check by increasing the rate at which birds die from accidents and diseases.

In the model's current configuration, our finch population should evolve by genetic drift only—that is, by random change in the frequencies of alleles that contribute to beak depth.

[ 7 ] Click the **GO** button to run the model.

[ 7.1 ] **How much does the composition of the population change from one generation to the next?**

[ 7.2 ] **Does the average beak depth seem to be consistently changing in one direction or the other over time?**

In reality, a finch's beak size often does influence the bird's ability to feed itself and survive. The birds pick up seeds in their beaks and crack them to expose the nutritious tissue inside. Small seeds, such as those of a hairy-leaved plant called *Cacabus*, can be cracked by any finch. All the birds prefer them. Plants such as the weedy *Tribulus*, on the other hand, make large, hard-to-crack seeds that only finches with big beaks can eat. Individuals that can do it eat *Tribulus* as a last resort.

*Geospiza fortis* depend heavily on seasonal rains. The rains induce plants that have been dormant during the long dry season to leaf out, flower, and set seed. Their seeds support the finches for the rest of the year. In rainy years, the plants do well, and there are plenty of small, easy-to-eat seeds for the finches. Birds with smaller beaks survive and reproduce at higher rates, because they can harvest small seeds more efficiently. In dry years, however, the few seeds produced by *Cacabus* are quickly eaten, leaving only the large, hard-shelled *Tribulus* seeds. Now birds with bigger beaks do better.

During especially dry years, such as 1977 on Daphne, finches with small beaks have a really hard time. As the small seeds disappear, it gets harder and harder to find food. Many birds starve or, unable to replace worn out feathers to protect their skin, die of exposure to the equatorial sun. Because the sizes of the available seeds change with the weather, it is sometimes better to have a large beak and other times better to have a small beak.

In the **Parameters** panel at lower right you have slider controls for two parameters related to beak depth. The first, **Best value**, controls the optimal (best) depth a finch could have, given the sizes of seeds currently available. Make sure the slider starts at 14 mm.

The **Selection strength** slider controls how likely a finch is to die if its beak depth is not optimal for the seeds on the island. The higher the selection strength, the more likely a finch with a beak size far from the **Best value** is to die. Probability of death is also influenced by other nearby finches. Within a neighborhood, the finches compete with each other for seeds. Those with beak sizes farther from the best value have a harder time getting seeds and are more likely to die. Finches that starve to death do not pass their genes to the next generation.

[ 8 ]     **RESET** the model. Set the **Selection strength** slider to 0.05.

[ 8.1 ]   **Record the average beak depth in your population:**

[ 9 ]     Now click the **STEP 5** button (third button from left) in the **Controls** panel to run the model for 5 years.

[ 9.1 ]   **Record the average beak depth in your population:**

[ 9.2 ]   **How much has the average beak depth changed?**

[ 10 ]    **RESET** the model. Set the **Selection strength** slider to a value of 0.15 or higher.

[ 10.1 ]   **Record the average beak depth in your population:**

[ 11 ]    Now click the **STEP 5** button in the **Controls** panel to run the model for 5 years.

[ 11.1 ]   **Record the average beak depth in your population:**

[ 11.2 ]   **How much has the average beak depth changed?**

[ 11.3 ]   **Does the strength of selection influence how fast the population evolves?**

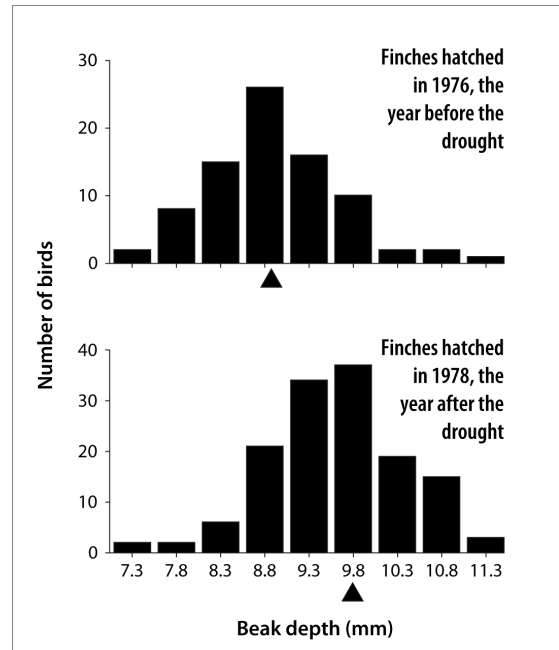
[ 12 ] **RESET** the model. Change the **Best value** for beak depth to a number lower than the current average for your population. Make sure **Selection strength** is still set somewhere above zero.

[ 12.1 ] **Predict what will happen when you run the model:**

[ 13 ] Now click the **GO** button to run the model. (You can, if you like, use the **Speed slider** in the **Controls** panel to make the model run faster.)

[ 13.1 ] **Was your prediction correct?**

In 1977, Peter Boag and Laurene Ratcliffe, members of a team led by Peter Grant and Rosemary Grant, witnessed a terrible drought on Daphne Major Island. The resulting shortage of small seeds led to a mass starvation of *Geospiza fortis* in which finches with shallower beaks died at a higher rate than finches with deeper beaks. In 1978, the survivors reproduced, passing their genes—which specified deep beaks—to their offspring. These graphs compare the average adult beak depth of the birds hatched in 1976, before the drought, versus 1978, after the drought. The composition of the population changed across generations. That is, the population evolved.



So far, our model behaves similarly to this real population.

## Exercise 2: Wet and Dry

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- [ 1 ] In the **Select an Exercise** menu, choose **Wet and Dry**. In this exercise, you will impose on the finch population a fluctuating series of rainy and drought years to see how readily it evolves to track the changing environment.
- [ 2 ] Note the buttons labeled **Wet** and **Dry** just below the Island. Click the **Wet** and **Dry** buttons a couple of times to switch back and forth between rainy and drought conditions.
- During wet years the optimal beak depth for finches is 10 mm. During dry years it is 14 mm.
- [ 3 ] **RESET** the model to generate a fresh population of finches.
- [ 3.1 ] **What is the average beak depth in the population?**
- [ 3.2 ] **What is the range of beak depths in the population?**
- [ 3.3 ] **How big is the difference between the largest versus smallest beak?**
- [ 4 ] Click the **Dry** button to impose a drought. Set the **Selection strength** to an intermediate value. Leave the **Mutation rate** at zero. **RUN** the model for 10 years, and then pause it.
- [ 4.1 ] **Now what is the average beak depth in the population?**
- [ 4.2 ] **What is the range of beak depths in the population?**
- [ 4.3 ] **How big is the difference between the largest versus smallest beak?**
- [ 4.4 ] **Describe how the composition of the population has changed:**
- [ 5 ] Click the **Wet** button. **RUN** the model for 10 years, and then pause it.
- [ 5.1 ] **Has the population returned to the original composition that you recorded in Step 3? That is, are average beak depth, range of beak depths, and difference between largest and smallest the same as they were at the start? If not, what do you think has caused the difference?**



- [ 6 ]     **RUN** the model for 10-15 more **wet** years.
- [ 6.1 ]     **Did the population evolve an average beak depth well-adapted for rainy conditions?**
- [ 7 ]     **RESET** the model to get a fresh population. Experiment with different patterns of switching between wet and dry periods (and perhaps different values for **Selection strength**).
- [ 7.1 ]     **Is it possible to drive your finch population to extinction? If yes, describe how:**
- [ 7.2 ]     **Given that our model finch population is capable of rapid evolution in response to a changing environment, explain why you think it, nonetheless, sometimes goes extinct. (If you need a hint, you might look back to Exercise 1, which discusses the genetics behind finch beak size.)**
- [ 8 ]     **RESET** the model. Experiment with how mutations might change the patterns you are seeing. First, allow your population to adapt to wet conditions. Make the environment **WET**. Set **Selection strength** to an intermediate value. At first, leave the **Mutation rate** at zero. Set the model **Speed** (in Controls) to its highest value. Run the simulation for 100 years, and then pause it.
- [ 8.1 ]     **What is the range of beak depths in the population?**
- [ 8.2 ]     **How big is the difference between the largest and smallest beak?**
- [ 9 ]     Now that the population is adapted to wet conditions, look at the effect that mutation, in the absence of selection, has on the distribution of beak depths. Set **Selection strength** to zero. Set the **Mutation rate** to a high value. When the mutation rate is greater than zero, mutations sometimes occur when finches reproduce. As parents pass alleles to offspring, randomly, some large-beak alleles change to small-beak alleles and vice versa. The higher the mutation rate, the more often this happens.
- [ 10 ]    **RUN** the model for another 50 years, and then **STOP** it.

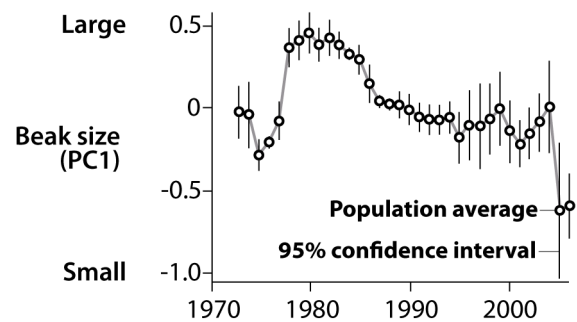
- [ 10.1 ] What is the range of beak depths in the population?
- [ 10.2 ] How big is the difference between the largest versus smallest beak?
- [ 10.3 ] How have these values changed versus the values you recorded before adding mutation (Step 8)?
  
- [ 10.4 ] Given that the population was adapted to wet conditions and is no longer experiencing selection, explain what you think caused the range of variation to change:
  
  
  
  
  
  
  
  
  
  
- [ 10.5 ] If we had left selection at a nonzero value, would it have been as easy to see the effect of mutation? Why or why not?
  
  
  
  
  
  
  
  
  
  
- [ 11 ] **RESET** the model and set the **Mutation rate** to zero. Experiment with different patterns of environmental change and different strengths of selection. Find conditions that are just a little too challenging for the finch population to survive.
  
- [ 11.1 ] Describe the only-slightly-too-challenging conditions you found:
  
  
  
  
  
  
  
  
  
  
- [ 12 ] **RESET** the model and set the **Mutation rate** to a high value. Expose your population to the only-slightly-too-challenging conditions you described in the previous step.

[ 12.1 ] Do mutations allow the population to persist for a longer time than it could without them? Please describe the observations that support your conclusion:

[ 12.2 ] Does the precise value of the mutation rate seem to matter?

[ 12.3 ] Why do you think mutations have the effect they do on the population's capacity to evolve in response to environmental change?

For over 30 years, Peter Grant, Rosemary Grant, and their colleagues have monitored the *Geospiza fortis* population on Daphne Major. The scientists have followed the population through droughts, runs of wet years, changes in the community of plants on the island, and changes in the community of other birds with which the finches compete. This graph tracks a measure of beak size that is a statistical composite of depth, width, and length. Beak size has evolved first in one direction, then the other, as the environment on Daphne has changed.



As you have seen, our model finch population can do the same.

## Exercise 3: Correlated Traits

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Finch beaks are three-dimensional objects, and they vary in more than just depth. When members of Grant and Grant's team catch a finch they also record its beak width and length.

These data allowed Grant and Grant (1995) to make a detailed statistical analysis of the patterns of natural selection on different beak dimensions during the 1977 drought on Daphne Major. As they expected, Grant and Grant found that among birds with the same beak length and beak width, individuals with deeper beaks survived at higher rates. Also as expected, beak length alone had no detectable influence on survival.

A third result came as a surprise. Among individuals with the same beak depth and beak length, individuals with narrower beaks survived at higher rates. This was puzzling, because when they had looked earlier at the raw numbers, the finches that survived the drought had, on average, wider beaks than the birds that died.

[ 1 ] In this exercise, you will use our model to resolve this apparent contradiction. In the **Select an Exercise** menu, choose **Correlated Traits**.

[ 2 ] Although we have ignored it until now, each virtual finch in our model population has a beak width in addition to a beak depth. Like beak depth, beak width is determined by ten genes, each with two alleles. When parents reproduce, they pass to each offspring one of their two gene copies for each locus. Beak widths can vary from 5 mm to 12 mm.

The **Parameters** panel now includes sliders allowing you to set the **Best value** for both beak depth and beak width, and sliders allowing you to adjust the **Selection strength** for each trait. The higher the selection strength for a trait, the more a finch's value for that trait influences its success in local competition for food. For now, leave the **Selection strength** sliders at zero.

[ 3 ] Variation among individuals is now displayed not in a bar graph but in a scatter plot. This is the lower of the two graphs on the right of the screen. Each of the dark dots on the graph represents an individual finch. (These dots may overlap, forming what appear to be bars.) The dot's position along the horizontal axis indicates the finch's beak depth; the dot's position along the vertical axis indicates the finch's beak width. The light-colored dot near the center of the cloud of points represents the population averages for beak depth and beak width.

[ 3.1 ] **Predict what will happen to the population averages over time when you run the model.**

[ 4 ] Click the **GO** button to run the model. You have two ways to keep track of whether and how the population is evolving. First, as the light-colored population average dot on the scatter plot moves around from year to year, it leaves a path tracing its history. Second, the time series graph at the top tracks changes over time in the population average beak depth and width.

[ 4.1 ] **How is the population changing over time?**

[ 4.2 ] **Was the prediction you made in Step 3 correct?**

You should be seeing the population averages move slowly up and down at random as the population evolves by genetic drift.

[ 5 ] **RESET** the model.

[ 5.1 ] **Record the current population averages for beak depth and width:**

[ 6 ] Model the pattern of selection Peter Grant and Rosemary Grant found during the 1977 drought on Daphne Major by setting up an environment in which finches with deeper but narrower beaks are more likely to survive. You can do this by making the **Best value** for beak depth higher than the current population average, and the **Best value** for beak width lower than the current average.

Set the **Selection strength** for beak depth to an intermediate value. Set the **Selection strength** for beak width to a somewhat lower, but nonzero, value.

[ 6.1 ] **Predict what will happen when you run the model:**

[ 7 ] **RUN** the model for at least 100 years. Increase the simulation **Speed** if you wish. If your population goes extinct, **RESET** the model, choose different **Selection strengths** (with stronger selection on depth than on width), and **RUN** the model again.

[ 7.1 ] **Describe what happens to the population averages for beak depth and beak width over time.**

[ 7.2 ] **Was your prediction correct?**

[ 8 ] **RESET** the model, but leave all the parameter values where they are. Examine the beak width versus beak depth scatter plot. Note that there is no association between a finch's beak depth and its beak width. That is, there are birds in the population with deep wide beaks, deep narrow beaks, shallow wide beaks, and shallow narrow beaks.

Move the **Correlation coefficient** slider to a value of about 0.85. This, too, matches the pattern Grant and Grant found for Daphne's *Geospiza fortis*. To see what the correlation coefficient does, **RESET** the model again.

[ 8.1 ] **Once again, examine the scatter plot for beak width versus beak depth. What has changed about the pattern of variation among individuals?**

[ 9 ] As you have discovered, the **Correlation coefficient** in our model determines the association between beak depth and beak width. The correlation coefficient ranges in value from 0 to 1.0. High values mean that depth and width vary together. That is, there are birds with shallow, narrow beaks and birds with deep, wide beaks, but no birds with shallow, wide beaks or deep, narrow beaks.

Precisely why beak depth and beak width are so strongly correlated in finches is unknown. One possible explanation is that there is overlap between the genes that influence growth in both dimensions during development. In other words, it just may not be biologically possible to build a finch with a deep, narrow beak or a shallow, wide one.

[ 9.1 ] **Leave the rest of the parameters where you set them in Step 6. Predict what will happen when you run the model:**

[ 10 ] **RUN** the model for at least 100 years.

[ 10.1 ] **What happened to the population averages for beak depth and beak width?**

[ 10.2 ] **How is this different than when you ran the model in Step 7?**

[ 10.3 ] **Was your prediction correct?**

[ 11 ] If your work in this exercise has not convinced you that a trait can increase in value over time even though, all else being equal, smaller values would lead to higher survival and reproductive success, run a few more experiments. Look for combinations of parameters that will cause the population's average value for a trait to move away from its optimal value. Such combinations should not be too difficult to find.

Our model has provided a plausible explanation, consistent with the data, for why the Daphne Major finch population evolved wider beaks even though narrower beaks were better for survival. Just why narrow beaks provided an advantage during the drought is unclear. One hypothesis favored by finch researchers is that even though bite force increases with both beak depth and beak width, birds with narrower beaks have an easier time executing the special twisting motion required to open *Tribulus* seed pods (see Herrel et al. 2005).

## Exercise 4: Mountains and Valleys

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Recall the puzzling bimodal distribution of beak sizes among *Geospiza fortis* at El Garrapatero on Santa Cruz. In this exercise, we will use our model to start exploring how subpopulations with different beak sizes might evolve. In doing so, we'll also be gaining insight into mechanisms whereby a single species can split into two.

[ 1 ] In the **Select an Exercise** menu, choose **Mountains and Valleys**.

We have given our virtual island a somewhat more complex geography. It now has a wet valley and a dry valley separated by a mountain that our finches may be reluctant to cross.

The left side of the **Parameters** panel has sliders controlling familiar variables. Use these sliders to set up a scenario consistent with what you have learned about the finches and their environment from the models and data in previous exercises:

- The **Best value** for beak depth on the wet side of the island should be small. On the dry side it should be large.
- The **Selection strength** for beak depth should be nonzero but modest.
- The **Best value** for beak width on both sides of the island should be small.
- The **Selection strength** for beak width should be nonzero but weaker than the selection strength for beak depth.
- The **Correlation coefficient** should be high.
- The **Mutation rate** should be nonzero.

As you try to accomplish the goal we are about to pose, try to leave these parameters alone. If you find that you have to change them for the model population to evolve the way you want it to, the parameters to change first are these:

- **The best values for beak width and the selection strength for beak width.** Bite force increases with both beak depth and beak width. The survival advantage afforded by narrow beaks may be particular to environments, like Daphne Major in 1977, in which *Tribulus* is an especially important food for finches. On Santa Cruz, *Tribulus* is much less abundant and thus a much less important food source for finches. It is possible that narrow beaks are not advantageous to the finches that live there (Herrel et al. 2005).
- **The selection strength for beak depth.** In nature, the strength of selection on beak size is highly variable across time and space. This gives you wide latitude in setting this parameter in your model.



[ 2 ] Your goal is this. By using primarily the sliders on the right side of the **Parameters** panel, which control variables new to our model, try to find conditions under which the finch population will evolve a bimodal distribution of beak sizes that persists for at least 100 years. Here are the new variables controlled by the sliders on the right side of the **Parameters** panel:

- **Carrying capacity.** This determines the number of finches the island can support.
- **Mating distance.** As you may have noticed, the finches in our population tend to stay within a small portion of the island over the course of a year. During the breeding season, however, they may fly over the whole island looking for mates. This parameter controls how far finches fly in search of a mate, in kilometers. The highest values cover the whole island, which is about 60 km wide. Smaller values effectively make the finches reluctant to cross the mountain to look for mates on the other side.
- **Mate selectivity.** In at least some populations of *Geospiza fortis* on Santa Cruz, the birds mate assortatively (Huber et al. 2007). That is, big-beaked females pair up with big-beaked males and small-beaked females pair up with small-beaked males. This is because mating song is correlated with beak size, and females are choosy about the songs their mates sing (Huber and Podos 2006). Higher values of this parameter mean females are more likely to mate males with similar-sized beaks.
- **Chicks/parent-year.** This determines the birds' reproductive rates. It is the average number of chicks per parent, per year.
- **Initial frequency of large allele (depth).** Changes in the average beak depth of finches in our model population are due, fundamentally, to changes in the frequencies of the alleles for each of the ten loci that influence the trait. The default value of this parameter is 0.5. This means that when you reset the model, the starting frequency of the large allele at each of the loci is 50%.

[ 3 ] As you try different scenarios, keep in mind that different things can happen in different runs with the same parameter values. You may need to reset the model and run it again several times before you get a clear sense of whether a particular scenario succeeds or fails.

[ 3.1 ] Here is some space to take notes on your experiments:

**[ 3.2 ] Describe at least one biologically reasonable scenario you found that results in the evolution of a stable bimodal distribution.**

**[ 3.3 ] Which parameter(s) from the right side of the panel seem(s) to be most important for the evolution of a bimodal distribution? What evidence supports your answer?**

If you have succeeded in modeling the evolution of a bimodal distribution, you have developed at least one explanation for how partially isolated populations living in different environments can evolve different trait values. This happens frequently in the Galapagos. *Geospiza fortis* populations from different islands, and even from different places on the same island, often have different average beak sizes (see, for example, de León et al. 2010).

We are close to modeling the bimodal distribution at El Garrapatero, but we are not quite there. At El Garrapatero there are no geographic barriers to help keep subpopulations apart. Let us move on to your final challenge.

## Exercise 5: Large and Small Seeds

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- [ 1 ] El Garrapatero does not have geographic barriers separating distinctive habitats, but it does have an environment that imposes disruptive selection on its *Geospiza fortis* population. At least during droughts, finches with small beaks and finches with large beaks survive at higher rates than finches with medium beaks (Hendry et al. 2009). This pattern of selection appears to result from a food supply consisting of small, soft seeds and large, hard seeds, with relatively few choices in between (Hendry et al. 2006).

In the **Select an Exercise** menu, choose **Large and Small Seeds**.

- [ 2 ] The **Best value** sliders in the **Parameters** panel now control optimal beak dimensions, not for finches living on different parts of the island, but for finches trying to eat small, soft seeds versus large, hard seeds. When the **Selection strength** parameters are set to nonzero values, the birds face local competition for food. Any given individual's beak will be closer to either the best value for eating small seeds or the best value for eating large seeds. The more neighbors it has with beaks even closer to the nearest optimum, the less chance the individual has of surviving.

The rest of the parameters are familiar from earlier exercises.

- [ 3 ] Your challenge is once again to find a biologically reasonable scenario in which the finch population evolves a bimodal distribution that persists for at least 100 years. Try, in particular, to find a scenario in which the **Mating distance** parameter is 50 or higher.

[ 3.1 ] Here is some space for notes:

**[ 3.2 ] Describe at least one scenario you found that results in the evolution of a stable bimodal distribution.**

**[ 3.3 ] Which parameter(s) from the right side of the panel seem to be most important for the evolution of a bimodal distribution? What evidence supports your answer?**

If you have succeeded in modeling the evolution of a bimodal distribution, you have developed at least one explanation for how a single population can evolve two distinctive phenotypes. The biologists who study the finches at El Garrapatero entertain three hypotheses for how the bimodal distribution arose, and are undecided about which one is correct (de León et al. 2010):

- The two modes might have diverged at different locations, as in our Mountains and Valleys exercise, and then come back into contact.
- One of the modes might have arisen as a result of hybridization with another species of Darwin's finch.
- The two modes might have evolved in place by the mechanism you have modeled—that is, disruptive selection due to different-sized seeds and assortative mating based on beak size.

The biologists have genetic data that lead them to be skeptical of the first hypothesis, but they cannot rule it out. The second hypothesis is at least plausible, given hybridizations that have been observed on other islands. De León and colleagues (2010) prefer the third explanation, in part because beak size appears to be precisely the kind of “magic trait” that can lead to divergence in place. A magic trait is a single characteristic that influences both survival and mate choice.

The distinctive and still-changing *Geospiza fortis* populations in the Galapagos provide evidence of incipient ecological speciation. Ecological speciation, thought to be an important process in the diversification of life, is the divergence of lineages as they adapt to different environments or resources, ultimately resulting in reproductive isolation. The finches of El Garrapatero furthermore appear to show that, under the right conditions, ecological speciation can begin in the absence of physical separation between subpopulations. The fact that our model replicates all of these processes suggests that it has captured essential features of the mechanism of evolution.

## Graded Questions

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- [ 1 ] Use the **SELECT AN EXERCISE** menu to launch "**Graded Questions**".
- [ 2 ] Enter your answers for each of the questions and click the **SUBMIT ALL** button. **NOTE:** You must answer all of the questions before you click the **SUBMIT ALL** button.

## References

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Further reading:

**For a Pulitzer Prize-winning book, written by a reporter, about Darwin's finches and the research on them by Peter Grant, Rosemary Grant, and their team, see:**

Weiner, J. 1994. *The Beak of the finch*. Knopf, NY.

**For books by Rosemary Grant and Peter Grant themselves, see:**

Grant, B. R. and P. R. Grant. 1989. *Evolutionary dynamics of a natural population: The large cactus finch of the Galapagos*. University of Chicago Press, Chicago.

Grant, P. R. 1999. *Ecology and evolution of Darwin's finches*, 2nd ed. Princeton University Press, Princeton.

Grant, P. R. and B. R. Grant. 2008. *How and why species multiply: The radiation of Darwin's finches*. Princeton University Press, Princeton.

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Sato, A., H. Tichy et al. 2001. On the origin of Darwin's finches. *Molecular Biology and Evolution* 18: 299–311.