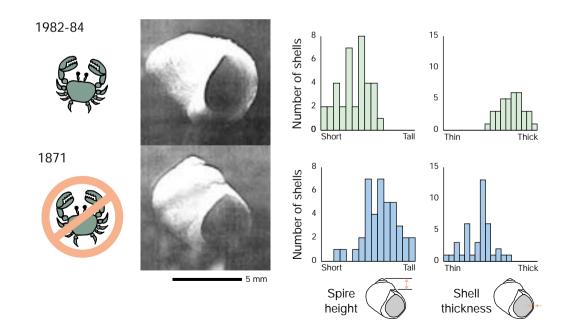
What makes populations evolve?

The flat periwinkle is a small (~ 1 cm long) marine snail that lives in the intertidal zone in New England. Among this snail's predators is the European green crab. As it's name suggests, the European green crab is not native to North America. It is an invasive species that reached the East Coast from Europe early in the 19th century. Prior 1900, the green crab did not occur north of Cape Cod, Massachusetts. After the turn of the century, however, the crab expanded its range northward, and is now found as far north as Nova Scotia. The crab's range expansion exposed periwinkle populations north of Cape Cod to a new agent of natural selection.



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Biologist Robin Seeley investigated whether flat periwinkle populations evolved in response to predation by green crabs. Seeley found, in a museum, samples of pre-1900 periwinkle shells collected at Appledore Island, north of Cape Cod. She compared these old shells to shells she collected herself at the same place. Seeley measured the spire height and thickness of each shell. Seeley's data are depicted in the graphs below. As the graphs-and the photos- show, the crab population on Appledore island in the early 1980s was, indeed, dramatically different than it was in 1871. The snails had, on average, shells that were both thicker and flatter than those of their ancestors.



How did this change, this descent with modification, happen? The mechanism of evolution is the subject of this tutorial. We will do experiments on a model population to explore how evolution works. Then we will return to Seeley's flat periwinkles to see how the model applies to them.

A model of evolution by natural selection

To complete this tutorial, you will need the software application EvoDots. You can download EvoDots from Jon Herron's website at the following URL:

http://faculty.washington.edu/~herronjc/

Click on Software, then on EvoDots. There are versions of EvoDots for Windows, Mac OS Classic, and Mac OS X. Download the appropriate version to your computer and launch it.

EvoDots lets you explore evolution by simulating natural selection in a population of dots. The EvoDots window contains three white areas, three buttons, and three check boxes. Look to make sure that all three check boxes are checked. Under the *File* menu, select *Options*. Click to select size as the characteristic in which the dots vary, then click *Okay*. Now click on the *New Population* button. This creates a new population of 50 dots, scattered at random across the white area on the left. Note also that the white area on the upper right now contains a graph, like the ones you just looked at for snails, showing how many dots of each color (and size) there are in your population. In the EvoDots simulation, you will be a predator on the dots. You will eat the dots by chasing them and clicking on them with the mouse. Before proceeding, jot down a prediction about how the population of dots will evolve in response to predation, and explain your reasoning.

Now click on the *Run* button and try to kill a few dots. To play your role correctly, you must act like a hungry predator. Don't just wait for the dots to come to you. Go after them! When you click on a dot successfully, it first turns red, then disappears. Eat 25 dots as fast as you can (note the display that tells you how many dots are left), then click on the *Stop* button.

When you click the *Stop* button, the dots stop moving and the white area on the lower right displays a histogram showing the distribution of colors among the survivors. Compare the survivors to the staring population. Has the distribution of colors changed? How?

Now click on the *Reproduce* button. Each of the survivor dots splits into two daughter dots. Note that each mother dot splits to become two daughter dots that are identical in color and size to each other and to their mother (who now no longer exists). This is analogous to the asexual reproduction of organisms like bacteria and paramecia.

Click on the *Run* button again, and eat 25 more dots as fast as you can. Again, compare the survivors to the starting population. Has the distribution of colors changed again? How? Was the prediction you made above correct? Why or why not?

Continue for a few more rounds of reproduction and predation. How many generations does it take for your population of dots to reach a point at which it can no longer evolve?

The requirements for evolution by natural selection

Now that you have a feel for how EvoDots works, we will start modifying the biology of our model population to explore the requirements for evolution by natural selection.

Variation

Note that each new population of dots you create contains considerable variation in size (and color, which is coded to indicate size). Do you think the population of dots would evolve if there were no variation in the starting population? Write down a prediction, and explain your reasoning.

Now test your hypothesis. Next to the label *Size of dots is:* click on the checkbox labeled *Variable*. There should no longer be a check in the box. Now create a new population. All the dots are the same size (and color). Go through a few rounds of predation and reproduction. Does the population evolve? Was your prediction correct?

Before proceeding, click on the *Variable* check box to make the dots variable again.

Inheritance

As we noted above, when the dots reproduce, each mother dot produces two daughters identical in size to each other and to their mother. In other words, size is heritable: It is passed from parents to offspring. Do you think the population of dots would evolve if size were not heritable? Write down a prediction, and explain your reasoning.

Test your hypothesis. Next to the label *Size of dots is:* click on the checkbox labeled *Heritable*. There should no longer be a check in the box. Create a new (variable) population, click on the *Run* button, and eat 25 dots. Now click on the *Reproduce* button and watch closely what happens. Each mother dot produces two daughter dots whose size is chosen at random. They may or may not be identical to each other or their mother. Go through a few rounds of predation and reproduction. Does the population of dots evolve? If so, does it evolve the same way it does when size is heritable? Was your prediction correct?

Before proceeding, click on the *Heritable* check box to make size heritable again.

Selection

Until now, when you have eaten dots you have done so selectively. Because smaller dots are harder to catch, the smaller dots are much more likely to survive than the larger dots. If you were to eat the dots at random, instead of selectively, do you think the population would still evolve? Write down a prediction and explain your reasoning.

Test your hypothesis. Next to the label *Survival is:* click on the checkbox labeled *Selective*. There should no longer be a check in the box. Create a new population (in which size is variable and heritable). Click on the *Run* button and eat 25 dots. Notice that when you click the mouse button, you kill not the dot you are pointing at, but a dot selected at random. (In fact, clicking anywhere inside the EvoDots window will kill a randomly selected dot.) Go through a few rounds of random predation and reproduction. Does the population of dots evolve? If so, does it evolve in the same way it does when survival is selective? Was your prediction correct?

Darwin's theory of evolution by natural selection

Charles Darwin identified natural selection as the mechanism of adaptive evolution. Darwin's theory of evolution by natural selection works as follows:

If a population contains variation, and

if the variation is at least partly heritable, and

if some variants survive to reproduce at higher rates than others,

then the population will evolve.

That is, the composition of the population will change across generations. The traits most conducive to survival will become more common, while the traits least conducive to survival will disappear. Are the results of your experiments consistent with Darwin's mechanism of evolution?

Reflect on your experiments with EvoDots and consider the following issues:

- 1. After they were born, did the individuals dots ever change their size or color? If the *individuals* didn't change, how was it possible for the *population* to change?
- 2. What role did the predators play in causing the population of dots to evolve? Did they create a need for the dots to change? Or did they simply determine which dots survived to reproduce and which didn't?

Evolution by natural selection in flat periwinkles

Robin Seeley hypothesized that the flat periwinkles of Appledore Island evolved by Darwin's mechanism. When the green crabs arrived, they started eating the thin-shelled snails. This left only the thick shelled ones to reproduce. And when the thick-shelled survivors reproduced, they had thick-shelled offspring. The end result is that the composition of the population changed. Thin-shelled snails became rare, and thickshelled snails became common.

Seeley performed two experiments to test her hypothesis. In the lab, Seeley offered each of 8 crabs a thin-shelled snail. All 8 crabs quickly crushed and ate their snails. It took them an average of 42 seconds. Seeley offered each of another 8 crabs a thick-shelled snail. Only one of these crabs was able to crush and eat its snail within 8 minutes. During that time many of the other 7 crabs gave up trying.

In the field, Seeley drilled small holes in the shells of a number of snails, and used fishing line to tether the snails to seaweeds in the intertidal zone. She then returned every few days to see which snails survived. This method allowed Seeley to distinguish between snails that were killed by crabs, part of whose crushed shells remained tied to their tethers, from the few snails that broke free of their tethers or died in their shells. She tethered the snails in pairs, with each pair including one thin-shelled snail and one thick-shelled snail. Seeley tethered 15 pairs at Timber Cove, where crabs appear to be absent; 15 pairs at Sipp Bay, where crabs are present but rare; and 15 pairs of snails at Gleason Point, where crabs are common. She checked on the snails after 6, 9, and 16 days. The results appear in the graphs on the next page. Blue circles represent snails with thin shells; red circles represent snails with thick shells.

What is the pattern in the data from Seeley's field experiment? What does this pattern suggest about whether and why crabs cause snail populations to evolve?

Review the requirements for evolution by natural selection. Have you seen documentation that the flat periwinkles of Appledore island vary in the thickness of their shells? Have you seen documentation that shell thickness is heritable? Have you seen documentation that snails with thick shells are more likely to survive than snails with thin shells?

You may feel that Seeley has missed something in her efforts to show that the periwinkle population evolved by natural selection imposed by predatory crabs. Your challenge now is to design an experiment that would supply the missing information. What would you with the snails? What data would you collect? What graphs would you plot from your data? What would the graphs look like if the snail population fits Darwin's theory? What would they look like if it doesn't? For one biologist's follow-up experiment, see the paper by Geoffrey Trussell listed in the bibliography.

Bibliography

Seeley, Robin Hadlock. 1986. Intense natural selection caused a rapid morphological transition in a living marine snail. *Proceedings of the National Academy of Sciences, USA* 83: 6897-6901.

Trussell, Geoffrey C. 1996. Phenotypic plasticity in an intertidal snail: The role of a common crab predator. *Evolution* 50: 448-454.

