EvoDots Tutorial

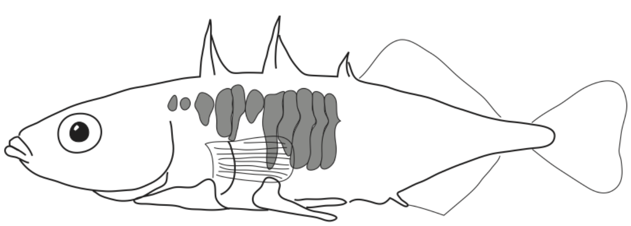
What makes populations evolve?

Threespine sticklebacks are small fish much loved by evolutionary biologists (Bell and Foster 1994):

Threespine sticklebacks live in coastal waters of the Pacific and Atlantic Oceans throughout much of the Northern Hemisphere.They have, in addition, invaded freshwater lakes and streams throughout most of their range. Among the characteristics that make sticklebacks interesting to evolutionary biologists are the striking differences between fish from different populations.

Geographic variation in sticklebacks

Research by D. W. Hagen and L. G. Gilbertson provides an example of variation among stickleback populations. Hagen and Gilberston (1972) caught hundreds of sticklebacks from lakes and streams in Alaska, British Columbia, and Washington State. The researchers counted the bony plates on the sides of each fish. Here's one with eight plates:



Among the populations the biologists sampled were two from the Queen Charlotte Islands in British Columbia.

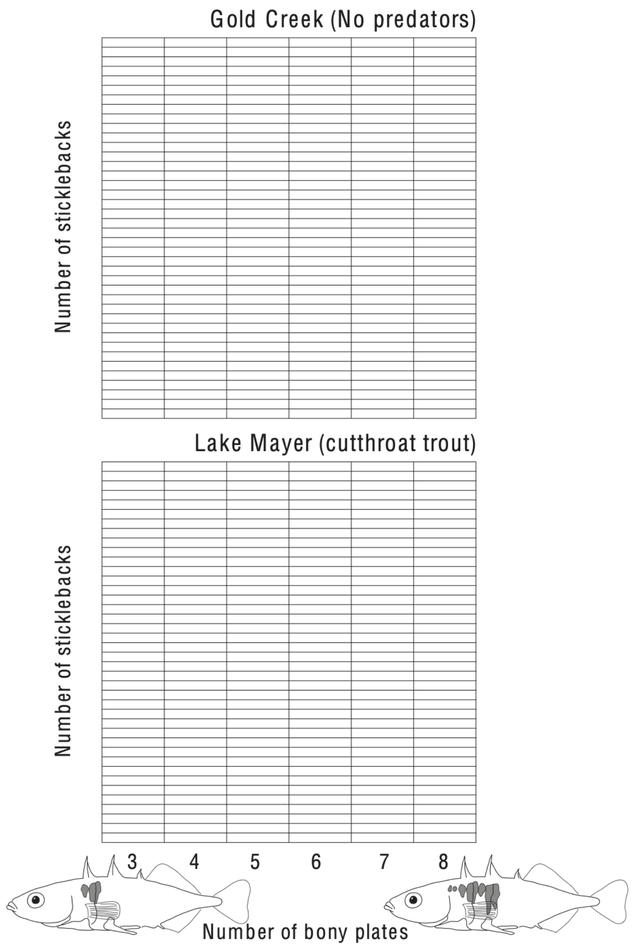
Here are data giving the number of plates on the left side of each of 50 fish from Gold Creek, where sticklebacks have no predators:

6, 5, 4, 4, 4, 4, 5, 4, 5, 6, 6, 5, 6, 4, 5, 6, 5, 4, 4, 5, 5, 4, 5, 3, 5, 5, 4, 5, 6, 5, 4, 4, 4, 5, 7, 5, 4, 5, 5, 3, 4, 5, 5, 5, 4, 4, 6, 4, 5, 3

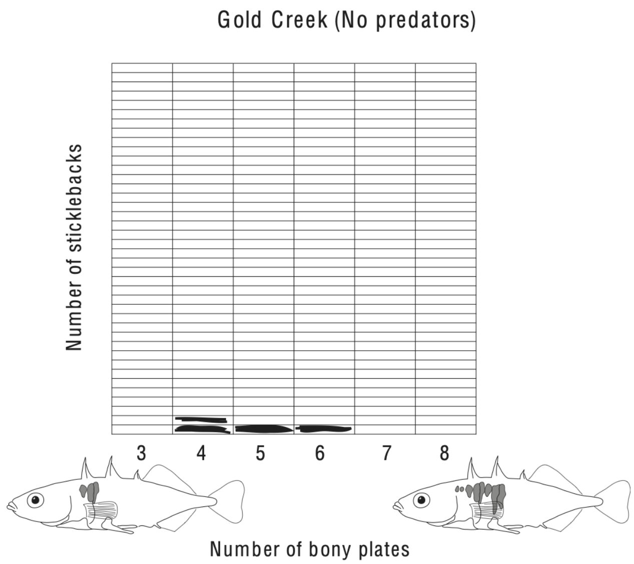
And here are data giving the number of plates on the left side of each of 50 fish from Lake Mayer, where sticklebacks are regularly eaten by cutthroat trout:

6, 5, 7, 7, 7, 7, 7, 7, 6, 7, 7, 8, 7, 7, 7, 7, 7, 6, 6, 7, 7, 7, 7, 7, 7, 7, 7, 6, 6, 7, 7, 7, 6, 7, 6, 7, 7, 8, 6, 6, 7, 7, 7, 7, 7, 7, 7, 7, 7, 7

The easiest way to analyze these data is to plot them on graphs. Here are a pair of grids on which you can plot graphs showing the variation in plate number in the two populations:



Start with the Gold Creek population. For each fish, darken a square on the grid above the number of plates the fish has. When you have more than one fish with the same number of plates, your darkened squares should stack on top of each other. This is what your graph for Gold Creek will look like after you have plotted the data for the first four fish:



Plot the data for all the fish in both populations before reading any further.

Your completed graphs should reveal a pronounced difference between the two populations. The average stickleback from Lake Mayer has more bony plates on its side than does the average stickleback from Gold Creek. This difference is typical of the populations Hagen and Gilbertson examined. Threespined sticklebacks living with predators usually have more bony plates than sticklebacks living without predators.

The stickleback populations from Gold Creek and Lake Meyer are descended from a common ancestral population. We know this because during the last ice age the Queen Charlotte Islands were covered by glaciers. Gold Creek and Lake Meyer didn't exist. When the glaciers retreated and fresh water returned to the Queen Charlottes, threespine sticklebacks that had been living in the ocean colonized the new bodies of water. Thus the difference between the Gold Creek and Lake Meyer populations must have evolved in the time since colonization. That is, today's sticklebacks are the product of descent with modification from the ancestral marine population.

How did this descent with modification happen? The mechanism of evolution is the subject of this assignment. We will do experiments on a model population to explore how evolution works. Then we will return to threespine sticklebacks to see how the model applies to them.

Darwin's mechanism of evolution

EvoDots is a model that lets you explore evolution by natural selection in a population of dots. Follow the link in the previous sentence to open the application in a web browser.

A model of evolution by natural selection When you open the *EvoDots* window, you should see a population of dots and two graphs. Under the population of dots are three buttons. Under the buttons are a pair of tabs. The *Darwin's Theory* tab should be open, with all three checkboxes checked. You can reset the window to its default configuration at any time, by using the *Reset* link at upper right.

Click on the *New Dots* button. This creates a new population of 50 dots, scattered at random across the gray square. Note also that graphs, which are like the ones you just prepared for sticklebacks, show how many dots of each type there are in your population.

You will be a predator on the dots. When you click on the *Start* button, the dots will start to move around. You can then eat the dots by chasing them down and clicking on them. When you kill a dot, it disappears and the *Current* population graph updates.

1. Predict how the population of dots will evolve in response to predation. Explain your reasoning.

2. Click the *Start* button, eat 25 dots as fast as you can, then click on the *Stop* button. When you click the *Stop* button. Compare the survivors to the starting population. Has the distribution of dot types changed? How?

3. Now click on the *Reproduce* button. Each of the survivor dots splits to produce two offspring. Note that each mother dot splits to become two daughter dots that are identical in type 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 *Start* 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?

4. Was the prediction you made in Question 1 correct? Why or why not?

5. 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

6. Note that each new population of dots you create contains considerable variation in speed (and color, which is coded to indicate speed). Could the population of dots evolve if there were no variation in the starting population?

7. Test your hypothesis. Next to the label "Speed 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 speed (and color). Go through a few rounds of predation and reproduction. Does the population evolve?

8. Before proceeding, click on the *Variable* check box to make the dots variable again. As we noted above, when the dots reproduce, each mother dot produces two daughters identical in speed to each other and to their mother. In other words, speed is heritable: It is passed from parents to offspring. Could the population of dots evolve if speed were not heritable?

9. Next to the label "Speed 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 *Start* button, and eat 25 dots. Now click on the *Reproduce* button and watch closely what happens. Each mother dot produces two daughter dots whose speed 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 speed is heritable?

10. Before proceeding, click on the *Heritable* check box to make speed heritable again. Until now, when you have eaten dots you have done so selectively. Because faster dots are harder to catch, the faster dots are much more likely to survive than the slower dots. If you were to eat the dots at random, instead of selectively, would the population still evolve?

11. 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 color is variable and heritable). Click on the *Start* 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 square where the dots are moving around 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?

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 versus others, then

the population will **evolve.**

That is, the composition of the population will change across generations. The variations most conducive to survival will become more common, while the variations least conducive to survival will disappear. Evolution by this mechanism is adaptive in the sense that a typical individual among the later generations is better suited to survive in its environment than is a typical individual among the earlier generations.

12. Based on your experimentation with *EvoDots:*
    a. Is evolution by natural selection the only mechanism of evolution?
    b. Is evolution by natural selection the only mechanism of *adaptive* evolution?
    c. Are variation, heritability, and selection required for evolution to be predictably adaptive?
13. After they were born, did the *individual* dots ever change their speed or color?
14. Did the *population* of dots change? If so, describe how. (Try to name at least two properties of the population that changed.)
15. How was it possible for the *population* to change even though the individuals in it did not?
16. 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 the sticklebacks of Lake Wapato

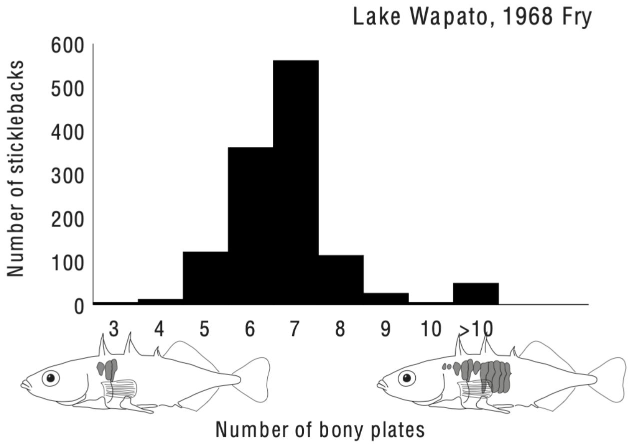
Now that we have had a chance to explore Darwin's theory of evolution by natural selection, we return to threespine sticklebacks. How well does Darwin's theory explain the evolution of differences among populations in the number of bony plates the fish wear on their sides?

We will focus on a study, by Hagen and Gilbertson (1973), of the evolution of plate number in a particular stickleback population. This population is in Lake Wapato, Washington. When Hagen and Gilbertson conducted their study in 1968 and 1969, the Lake Wapato stickleback population was young. Lake Wapato had been poisoned with rotenone, by State authorities, in 1957. The poisoning killed all the fish in the lake. Shortly after the poisoning, Lake Wapato was recolonized by sticklebacks from Lake Chelan.

Starting in 1965, the State Fisheries department began stocking Lake Wapato with about 50,000 trout fry each year. Thus, when Hagen and Gilbertson began to monitor the Lake Wapato stickleback population, it had begun to be exposed to predation by trout only recently.

We will now consider, point-by-point, how well Darwin's theory applies to the Lake Wapato population.

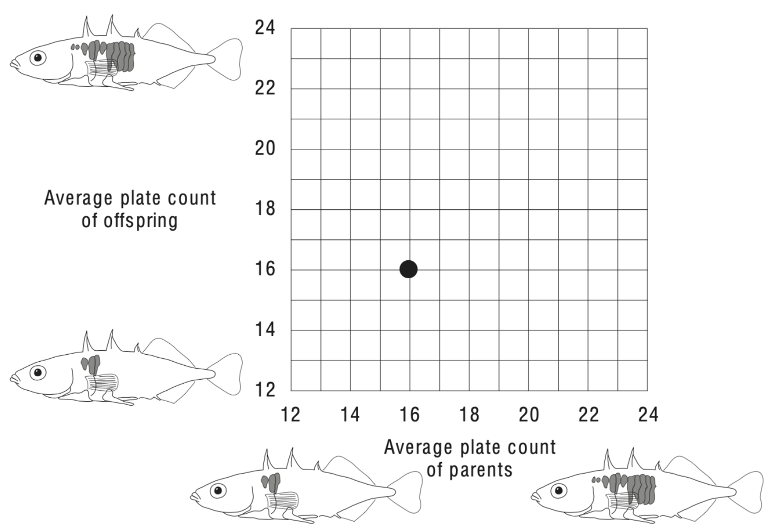
Was there variation in plate number among the sticklebacks in Lake Wapato? This graph shows the distribution of plate counts among the sticklebacks that hatched in Lake Wapato in 1968, the first year of Hagen and Gilbertson's study:



Is there variation in plate count among the sticklebacks?

Is the variation in plate count among Lake Wapato sticklebacks heritable? When we ask whether plate count is heritable, we are asking whether the differences among individuals are due to differences in the genes they have inherited from their parents. Hagen (1973) assessed the heritability of plate count in the Lake Wapato sticklebacks by collecting adults from the lake, mating them in his lab, then rearing the eggs and fry under uniform conditions. The table at left gives Hagen's data for 20 families. The numbers represent the average plate count for the parents in each family, and the average plate count for the offspring. (Plate count here is the sum of the plates on both sides of the body.)

Family	Average of parents	Average of offspring
1	16	16
2	14	14
3	21.5	19.5
4	14	14
5	13	13
6	13	13.5
7	20	19.5
8	12	12
9	13	13.5
10	20.5	20.5
11	21.5	19.5
12	18	17
13	14.5	14
14	24	21
15	21	20.5
16	21	20.5
17	12	12.5
18	21	19.5
19	13.5	13.5
20	12.5	13



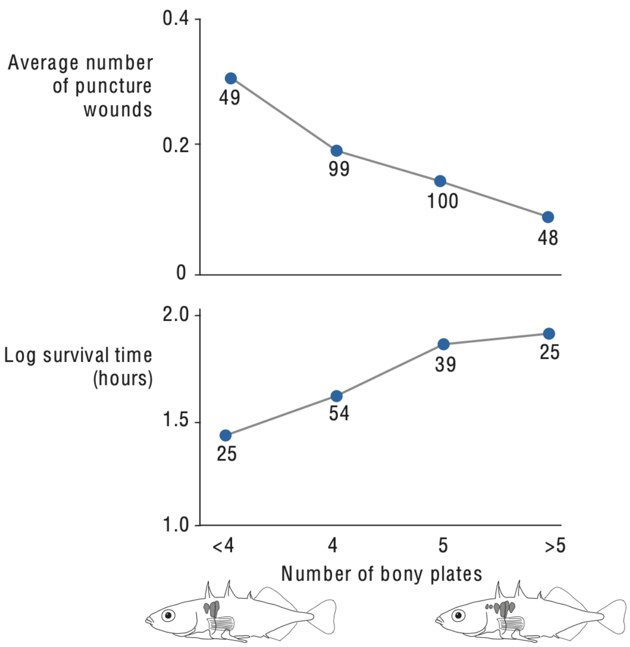
If the differences among the sticklebacks in Lake Wapato are due to differences in genes, then offspring should resemble their parents. The simplest way to see whether they do is to graph Hagen's data on a scatterplot. Here is a grid for doing so. Each family is represented by a dot. The position of the dot on the horizontal axis gives the average plate count for the parents. The position of the dot on the vertical axis gives the average plate count for the offspring. The dot for family 1 is already on the grid. Add the dots for the rest of the families. If offspring resemble their parents, then the dots should fall roughly on a diagonal line running from lower left to upper right.

Because all the offspring grew up in the same environment, any variation among them must be due to differences in the genes they inherited from their parents.

Can we conclude that plate count is heritable in the Lake Wapato stickleback population?

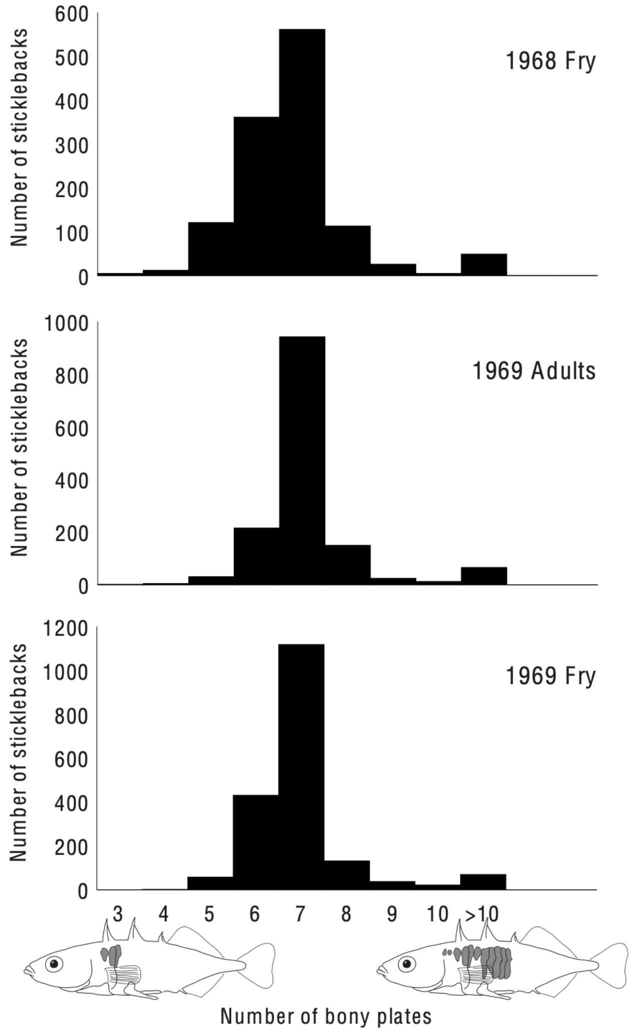
Do some kinds of sticklebacks survive and reproduce at higher rates than others? Hagen and Gilbertson examined the stomach contents of trout caught by fishermen in Lake Wapato. Many of these trout stomachs contained sticklebacks. When Hagen and Gilbertson compared the average number of bony plates on sticklebacks in trout stomachs to the average on sticklebacks caught swimming in the lake, they found that trout show a small, but real tendany to eat sticklebacks with fewer bony plates. This suggests that bony plates provide some protection against trout attacks, and that sticklebacks with more bony plates are more likely to survive to reproduce.

T. E. Reimchen (1992) examined the adaptive significance of bony plates in more detail. Reimchen caught a large number of sticklebacks and inspected them for injuries caused by predator attacks. Reimchen found that fish with more bony plates had fewer puncture wounds, and survived longer after being injured, than fish with fewer bony plates:



Finally, Hagen and Gilbertson were able to compare directly the distribution of plate counts among the sticklebacks hatched in Lake Wapato in 1968 versus the distribution among the individuals that survived to reproduce. The sticklebacks in Lake Wapato live only one year. Thus all the adults present in the lake just prior to the breeding season in 1969 were survivors from the 1968 hatch.

The distributions for the sticklebacks hatched in 1968, and the individuals who survived to breed in 1969, appear here (top and center):



As we would expect based on the evidence that bony plates give some protection against trout attacks, the survivors had slightly more bony plates, on average, than the hatchlings.

Can we conclude that sticklebacks with more bony plates have, on average, higher lifetime reproductive success?

Did the stickleback population evolve? The data we have examined show that the Lake Wapato stickleback population satisfies all three assumptions of Darwin's theory of evolution by Natural Selection. There is variation among individuals in plate number; this variation is passed genetically from parents to offspring; more individuals are born than survive to reproduce; survival is selective in that individuals with more bony plates are more likely to survive. If Darwin's theory is correct, then the composition of the population should change from one generation to the next.

It does. The figure above includes, at the bottom, a graph showing the distribution of plate counts among the sticklebacks that hatched in the spring of 1969. These are the offspring of the survivors from the hatch of 1968. Like their parents, the 1969 fry have, on average, slightly more bony plates than the 1969 fry did. The stickleback population evolved by a small but measurable amount between the generations of 1968 and 1969.

Literature Cited

- Bell, M. A., and S. A. Foster, eds. 1994. The Evolutionary Biology of the Threespine Stickleback. Oxford University Press.
- Hagen, D. W. 1973. Inheritance of numbers of lateral plates and gill rakers in Gasterosteus aculeatus. Heredity 30: 303-312.
- Hagen, D. W., and L. G. Gilberston. 1972. Geographic variation and environmental selection in Gasterosteus aculeatus L. in the Pacific Northwest, Amercia. Evolution 26: 32-51.
- Hagen, D. W., and L. G. Gilberston. 1973. Selective predatio and the intensity of selection acting upon the lateral plates of threespine sticklebacks. Heredity 30: 273-287.
- Reimchen, T. E. 1992. Injuries on stickleback from attacks by a toothed predator (Oncorhynchus) and implications for the evolution of lateral plates. Evolution 46: 1224-1230.

Extra

If your group finishes early, spend some time exploring the source of variation in *EvoDots:*

In all the the simulations you have done so far, your starting population contained individuals of seven different speeds. In later generations, some of the speeds may have disappeared from the population, but no new speeds appeared. In real populations, where do new variations come from? The answer is mutations. For our present purposes, a mutation is an error that occurs during reproduction. That is, while most offspring may resemble their parents, an occasional mutant offspring will not.

To see the role of mutation in evolution, go to the *Mutation's Role* tab in *EvoDots* and select. Click on the *New Dots* button. Note that your starting population now contains dots of only three different speeds

- Go through a few rounds of selection and reproduction. Try to make the population evolve toward fast dots as quickly as you can. Is there a limit to how far you can drive the population? Why?
- Now note the label at the lower right that says "Speed of dots is variable and heritable." Click the box next to the label *with mutation.* The box should now be checked. Make a new population, and go through a few rounds of selection and reproduction. After each round of reproduction, examine the dots carefully. Can you spot the mutants? Try, again, to make the population evolve toward fast dots. Can you drive the population further than you could before? Why or why not?