Darwin's mechanism of adaptive evolution

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 (Figure 1.1). 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:

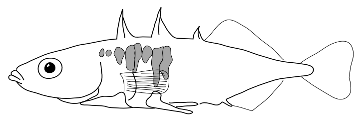


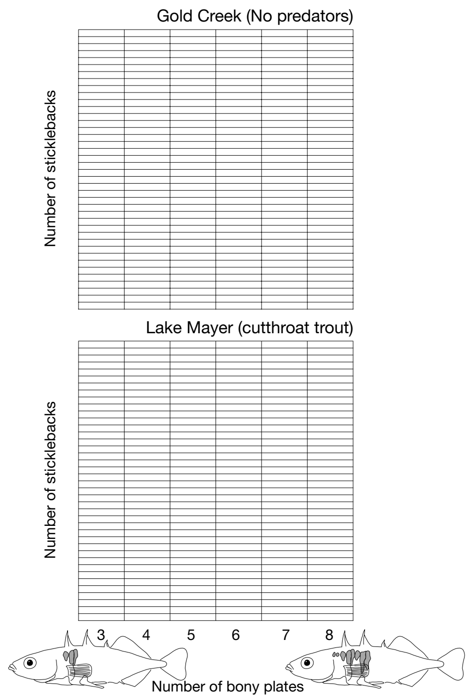
Figure 1.1 **Many threespine sticklbacks have bony plates on their sides.** This fish has eight plates.

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



The stickleback populations from Gold Creek and Lake Meyer are descended from a common ancestral saltwater population. We know this because during the last ice age the Queen Charlotte Islands were covered by glaciers (as was the entire Northwest). 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 pronounced difference between the Gold Creek and Lake Meyer populations must have evolved in the time since colonization. That is, today's sticklebacks are the products of descent with modification from the common ancestral marine population.

How did this descent with modification happen? The mechanism of evolution is the subject of this problem set. 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

To complete this section of the problem set, 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/SoftwareFolder/software.html

There is a version of EvoDots for Windows, and a version for MacOS.

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 prepared for sticklebacks, 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.

1. Predict how the population of dots will evolve in response to predation. 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, 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.

2. 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.

3. 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?

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 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?

7. 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?

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

8. 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?

9. 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?

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

10. 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?

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 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?

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.

12. Are the results of your experiments consistent with Darwin's mechanism of evolution? Explain.

The source of variation among individuals

In all the the simulations you have done so far, your starting population contained individuals of seven different sizes. In later generations, some of the sizes may have disappeared from the population, but no new sizes 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 occassional mutant offpsring will not.

To see the role of mutation in evolution, go to the *Window* menu in EvoDots and select *Mutation's Role.* Click on the *New Population* button. Note that your starting population now contains dots of only four different sizes.

13. Go through a few rounds of selection and reproduction. Try to make the population evolve toward small dots as quickly as you can. Is there a limit to how far you can drive the population? Why?

14. Now note the label at the lower right that says *Size 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 small dots. Can you drive the population further than you could before? Why or why not?

What makes populations evolve?

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

15. 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?

16. Did new sizes appear in the population because the dots needed them in order to survive? If not, where did new sizes come from?

17. 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 in 1968, it had begun to be exposed to predation by trout only recently. We will 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?

Figure 1.2 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.

18. Is there variation in plate count among the sticklebacks?

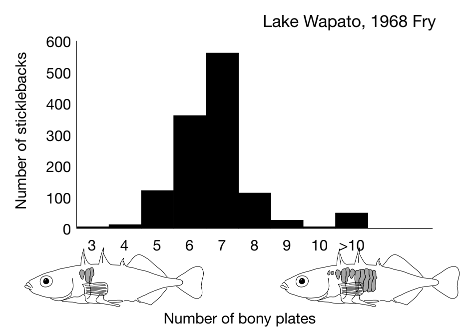
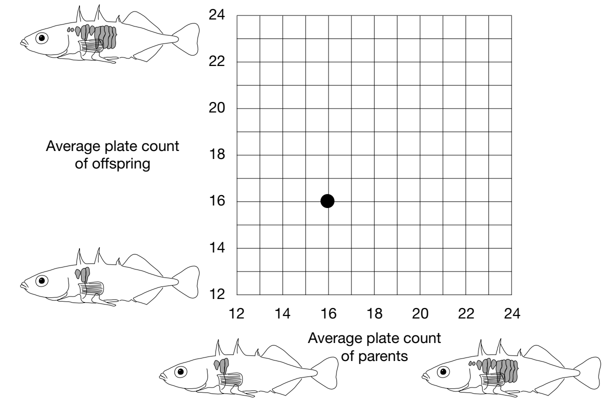


Figure 1.2 **The distribution of plate counts among Lake Wapato sticklback fry hatched in 1968.**

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



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. Because all the offspring grew up in the same environment, any variation among them must be due to either random chance or differences in the genes they inherited from their parents. The table at the top of this page 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.)

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. There is grid at the top of this page that will allow you to do 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.

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

Did some kinds of sticklebacks survive and reproduce at higher rates than others?

20. Do you think the number of plates a stickleback has on its sides will affect its chances of surviving to reproduce? Why or why not?

21. Design an experiment to test your prediction. Describe the results you'll get if your hypothesis is correct, and the results you get if it is incorrect.

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.

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 (Figure 1.3).

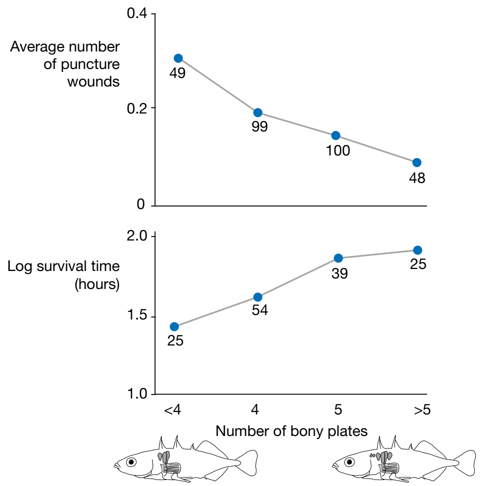


Figure 1.3 **Bony plates help protect sticklebacks against predators.**

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 in Figure 1.4 (top and center).

22. Can we conclude that sticklebacks with fewer bony plates are less likely to survive to reproduce? Are the data you've seen consistent your hypothesis in question 20? Why or why not?

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; 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.

Figure 1.4 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.

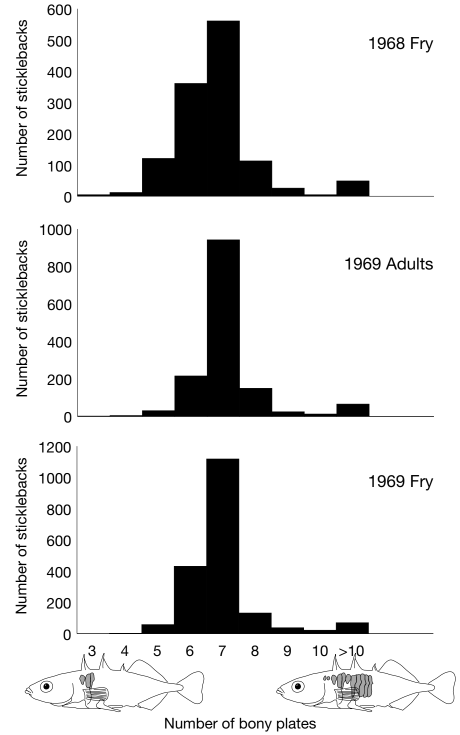


Figure 1.4 **Evolution by natural selection in the Lake Wapato stickleback population.** The top graph shows the variation in bony plate count among the fish hatched in 1968. The center graph shows the variation among the individuals who survived to reproduce in 1969. The survivors had slightly more plates, on average, than the hatchlings. When the survivors reproduced in 1969, they passed their higher plate counts to their offspring. The bottom graph shows that the 1969 fry have, like their parents, slightly more plates, on average, than the 1968 hatchlings. (Source: Drawn from data in Table 3 of Hagen and Gilbertson 1973.)

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.

23. Look back at the graphs you drew on the first page. Why do the sticklebacks in Lake Mayer have more bony plates, on average, than the stickleback in Gold Creek?

Literature Cited

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