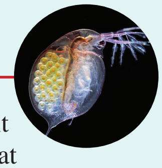
CASE STUDY 2 Hosts, Parasites, and Time-Travel



By definition, a parasite has an antagonistic relationship with the host it infects. For this reason we might expect the host to evolve strategies that resist infection, and the parasite to evolve strategies that subvert this host resistance. The end result might be a never-ending coevolutionary cycle between host and parasite, with neither party gaining the upper hand. Indeed, we might expect the ability of the parasite to infect the host to remain relatively unchanged over time despite the fact that both host and parasite are engaged in cycles of evolutionary conflict beneath this seemingly calm surface.

This is an intriguing idea, but how might it be examined scientifically? Ideally we would like to hold the parasite fixed in time and see if its ability to infect the host declines as the host evolves resistance. Alternatively, we might hold the host fixed in time and see if the parasite's ability to infect the host increases as it evolves ways to subvert the host's current defenses.

Another possibility would be to challenge the host with parasites from its evolutionary past. In this case we might expect the host to have the upper hand, since it will have evolved resistance to these ancestral parasites. Similarly, if we could challenge the host with parasites from its evolutionary future, then we might expect the parasite to have the upper hand, since it will have evolved a means of subverting the current host defenses.

Exactly this sort of "time-travel" experiment has been done using a bacterium as the host and a parasite called a *bacteriophage*.[1] To do so, researchers let the host and parasite coevolve together for several generations. During this time, they periodically took samples of both the host and the parasite and placed the samples in a freezer. After several generations they had a frozen archive of the entire temporal sequence of hosts and parasites. The power of their approach is that the host and parasite could then be resuscitated from this frozen state. This allowed the researchers to resuscitate hosts from one point in time in the sequence and then challenge them with resuscitated parasites from their past, present, and future.

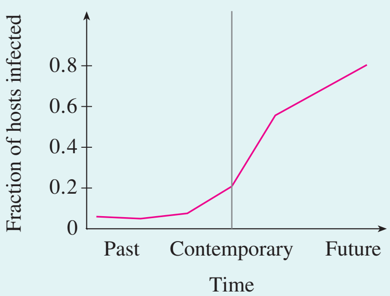


FIGURE 1
Horizontal axis is the time from which the parasite was taken, relative to the host's point in time.

The results of one such experiment are shown in Figure 1. The data show that hosts are indeed better able to resist parasites from their past, but are much more susceptible to infection by those from their future.

This is a compelling experiment but, by its very nature, it was conducted in a highly artificial setting. It would be interesting to somehow explore this idea in a natural host–parasite system. Incredibly, researchers have done exactly that with a species of freshwater crustacean and its parasite.[2]

Daphnia are freshwater crustacea that live in many lakes. They are parasitized by many different microbes, including a species of bacteria called *Pasteuria ramosa*. These two organisms have presumably been coevolving in lakes for many years, and the question is whether or not they too have been undergoing cycles of evolutionary conflict.

Occasionally, both the host and the parasite produce dormant offspring (called propagules) that sink to the bottom of the lake. As a time passes, sediment containing these propagules accumulates at the bottom of the lake. Over many years this sediment builds up, providing a historical record of the host and parasite (see Figure 2). A sediment core can then be taken from the bottom of the lake, giving an archive of the temporal sequence of hosts and parasites over evolutionary time (see Figure 3). And again, as with the first experiment, these propagules can be resuscitated and infection experiments conducted.

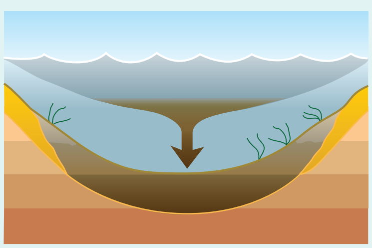


FIGURE 2
Sedimentation

1. A. Buckling et al. 2002, "Antagonistic Coevolution between a Bacterium and a Bacteriophage." *Proceedings of the Royal Society: Series B* 269 (2002): 931–36.

2. E. Decaestecker et al., "Host-Parasite 'Red Queen' Dynamics Archived in Pond Sediment." *Nature* 450 (2007): 870–73.

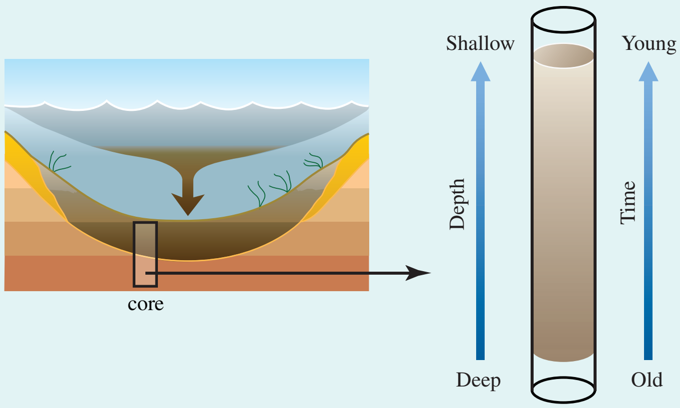


FIGURE 3

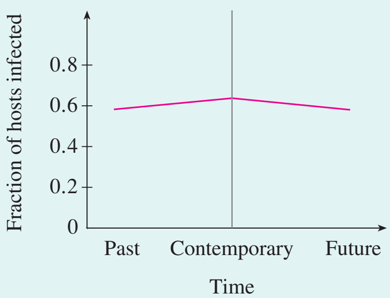


FIGURE 4
Horizontal axis is the time from which the parasite was taken, relative to the host's point in time.

Source: Adapted from S. Gandon et al., "Host-Parasite Coevolution and Patterns of Adaptation across Time and Space," *Journal of Evolutionary Biology* 21 (2008): 1861–66.

The results of the second experiment are shown in Figure 4: The pattern is quite different from that in Figure 1, with hosts being able to resist parasites from their past and their future, more than those taken from a contemporary point in time.

How can we understand these different patterns? Is it possible that this *Daphnia*–parasite system is also undergoing the same dynamic as the bacteriophage system, but that the different pattern seen in this experiment is simply due to differences in conditions? More generally, what pattern would we expect to see in the *Daphnia* experiment under different conditions if such coevolutionary conflict is actually occurring? To answer these questions we need a more quantitative approach. This is where mathematical modeling comes into play.

Models begin by simplifying reality (recall that a model is "a lie that makes us realize truth"). Thus, let's begin by supposing that there are only two possible host genotypes (A and a) and two possible parasite genotypes (B and b). Suppose that parasites of type B can infect only hosts of type A, while parasites of type b can infect only hosts of type a. Although we know reality is likely more complicated than this, these simplifying assumptions capture the essential features of an antagonistic interaction between a host and its parasite.

Under these assumptions we might expect parasites of type B to flourish when hosts of type A are common. But this will then give an advantage to hosts of type a, since they are resistant to type B parasites. As a result, type a hosts will then increase in frequency. Eventually, however, this will favor the spread of type b parasites, which then sets the stage for the return of type A hosts. At this point we might expect the cycle to repeat.

In this case study you will construct and analyze a model of this process. As is common in modeling, the order in which different mathematical tools are used by scientists is not always the same as the order in which they are best learned. For example, when scientists worked on this question they first used techniques from Chapter 7 and then Chapter 10 to formulate the model. They then used techniques from Chapter 6 and then Chapter 2 to draw important biological conclusions.[3] To fit with our learning objectives, however, this case study is developed the other way around. Following Chapter 2, in Case Study 2a, we will use given functions to draw biological conclusions about host–parasite coevolution. Following Chapter 6, in Case Study 2b, we will then begin to fill in the gaps by deriving these functions from the output of a model. Following Chapter 7, in Case Study 2c, we will then formulate this model explicitly, and following Chapter 10, in Case Study 2d, we will derive the output of the model that is used in Case Study 2b.

3. S. Gandon et al., "Host–Parasite Coevolution and Patterns of Adaptation across Time and Space," *Journal of Evolutionary Biology* 21 (2008): 1861–66.