CASE STUDY 2a Hosts, Parasites, and Time-Travel

We are studying a model for the interaction between *Daphnia* and its parasite. Recall that there are two possible host genotypes (A and a) and two possible parasite genotypes (B and b). Parasites of type B can infect only hosts of type A, while parasites of type b can infect only hosts of type a. Here we will take equations that will be obtained in Case Studies 2b and 2d to explore the biological predictions that can be obtained from them.

In Case Study 2d we will derive the functions

(1a) $$q(t) = \tfrac{1}{2} + M_q \cos(ct - \phi_q)$$

(1b) $$p(t) = \tfrac{1}{2} + M_p \cos(ct - \phi_p)$$

where $q(t)$ is the predicted frequency of host genotype A at time t and $p(t)$ is the predicted frequency of parasite genotype B at time t. In these equations ϕ_q, ϕ_p, and c are positive constants, while M_q, M_p are positive constants that are strictly less than $\frac{1}{2}$.

1. Describe, in words, how the genotype frequencies of the host and parasite change over time. Provide an explanation, in biological terms, for these dynamics.
2. How do the constants M_q and M_p affect the pattern of genotype frequencies over time?
3. The constant c is determined by the consequences of infection, in terms of reproduction, for both the host and the parasite. A large difference in reproductive success between infected versus uninfected hosts makes c large. Likewise, a large difference in reproductive success between parasites that are unable to infect a host versus those that are able to infect a host also makes c large. How does c affect the pattern of genotype frequencies over time as predicted by Equations 1? Provide an explanation for this in biological terms.
4. The constants ϕ_q and ϕ_p are referred to as the *phase* of $q(t)$ and $p(t)$, respectively. How do these constants affect the pattern of genotype frequencies over time?
5. As you will see in Equation 3, the difference $\phi^* = \phi_p - \phi_q$ turns out to be important in the coevolution of the host and parasite. What does this difference represent mathematically? Explain why this quantity is a measure of the extent to which the frequency of the parasite genotype lags behind the frequency of the host genotype.

Equations 1 give the genotype frequencies as functions of time. In the *Daphnia*-parasite system described in Case Study 2 on page xlvi, these equations can also be interpreted as giving the dynamics of genotype frequencies as a function of depth in the sediment core shown in Figure 1.

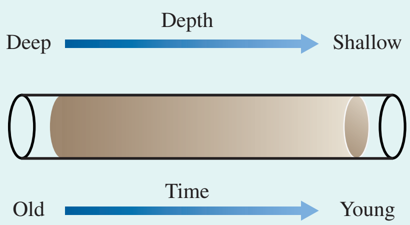

FIGURE 1

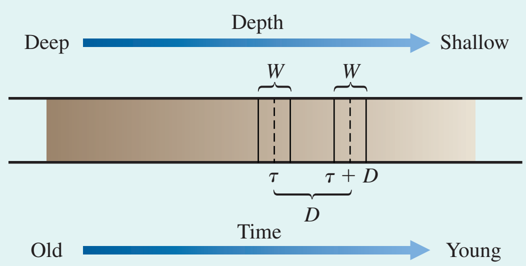

FIGURE 2

In the experiment described in Case Study 2, researchers chose a fixed depth τ and extracted a layer of sediment of width W centered around this depth (see Figure 2). The contents of this layer were mixed completely, and then hosts and parasites were extracted at random from the mixture. Researchers also took deeper and shallower layers (which represent the past and the future for hosts located in the layer at τ) and again completely mixed each layer. The center of these layers was a distance D from the center of the focal layer at τ, with $D < 0$ corresponding to a deeper layer and $D > 0$ a shallower layer (see Figure 2). The researchers then challenged hosts from the layer at τ with parasites from their past (that is, from the layer with $D < 0$), present (the layer at τ), and future (the layer with $D > 0$). For each challenge experiment the fraction of hosts becoming infected was measured.

In Case Study 2b we will show that, when a layer of sediment at location τ with width W is mixed completely, the frequency of type A hosts in this mixture is predicted to be

(2a) $$q_{\text{ave}}(\tau) = \tfrac{1}{2} + M_q \cos(c\tau - \phi_q)\,\frac{2\sin\left(\frac{1}{2}cW\right)}{cW}$$

Likewise, we will show that, when a layer of sediment at location τ with width W is mixed completely, the frequency of type B parasites in this mixture is predicted to be

(2b) $$p_{\text{ave}}(\tau) = \tfrac{1}{2} + M_p \cos(c\tau - \phi_p)\,\frac{2\sin\left(\frac{1}{2}cW\right)}{cW}$$

6. The functions (2a) and (2b) are similar to (1a) and (1b) except that the second terms are multiplied by the quantity $2\sin\left(\frac{1}{2}cW\right)/cW$. Describe how the frequency of the genotypes within a mixed layer depends on the width W of this layer. In particular, what happens as the width of the layer becomes very small (that is, when $W \to 0$)? What happens as the width becomes very large (that is, $W \to \infty$)? Provide a biological interpretation for your answers.

In the experiment introduced in Case Study 2, hosts from depth τ were challenged with parasites from depth $\tau + D$. This was repeated for different depths τ, and the overall fraction of hosts infected was measured. In Case Study 2b we will show that the predicted fraction of hosts infected from such an experiment is

(3) $$F(D) = \tfrac{1}{2} + M_p M_q \cos(cD - \phi^*)\,\frac{4\sin^2\left(\frac{1}{2}cW\right)}{c^2W^2}$$

where $\phi^* = \phi_p - \phi_q$ and $D < 0$ corresponds to parasites from a host's past and $D > 0$ to parasites from a host's future.

7. Sketch the graph of $F(D)$ when $\phi^* = 0$. Be as accurate as possible, showing where the maxima and minima occur as well as where the graph crosses the vertical axis. Construct similar sketches when ϕ^* is small and positive as well as when ϕ^* is small and negative. These plots depict the predicted fraction of infected hosts in the experiment as a function of the relative point in time from which the parasite was taken.

8. Suppose that cD is relatively small, meaning that the layers used in the challenge experiments are close to one another. Use your results from Problem 7 to explain how it is possible to obtain the experimental data like those shown in Figure 3.

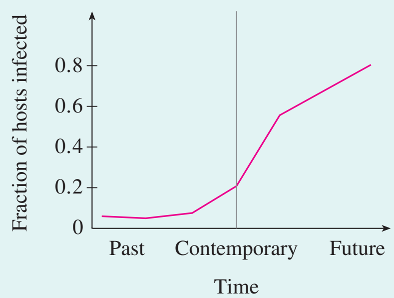

FIGURE 3
Horizontal axis is the time from which the parasite was taken, relative to the host's point in time.

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.

In particular, what is true about the value of ϕ^* in this case? Provide a biological interpretation of your answer.

9. Again suppose that cD is relatively small. Use your results from Problem 7 to explain how it is possible to obtain data like those shown in Figure 4. What is true about the value of ϕ^* in this case? Provide a biological interpretation of your answer.

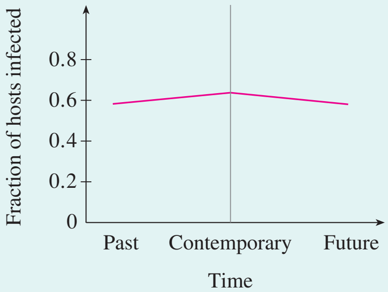

FIGURE 4
Horizontal axis is the time from which the parasite was taken, relative to the host's point in time.

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.