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

In this part of the case study we will take the formulation of the mathematical model for the antagonistic interactions between *Daphnia* and its parasite from Case Study 2c on page 484 and simplify it by linearization near one of its equilibrium points. We will then obtain an explicit solution for the frequency of the host and parasite genotypes as functions of time.

The analysis starts with equations

$$\begin{aligned} \frac{dq}{dt} &= s_q q(1 - q)(1 - 2p) \\ \frac{dp}{dt} &= s_p p(1 - p)(2q - 1) \end{aligned} \tag{1}$$

that were obtained in Case Study 2c. 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. In Equations 1, q is the frequency of the type A host and p is the frequency of the type B parasite. The constant s_q represents the reduction in reproductive output of a host due to infection, and s_p is the reduction in reproductive output of a parasite if it is unable to infect a host. In

Case Study 2c we found that $q = \frac{1}{2}$ and $p = \frac{1}{2}$ is an equilibrium of this system of differential equations.

Let's define $\varepsilon_q(t) = q(t) - \frac{1}{2}$ and $\varepsilon_p(t) = p(t) - \frac{1}{2}$ to be the deviations of q and p from these equilibrium values, respectively.

1. Linearize Equations 1 near the equilibrium $q = \frac{1}{2}$, $p = \frac{1}{2}$ to show that ε_q and ε_p satisfy the differential equations

$$\begin{aligned} \frac{d\varepsilon_q}{dt} &= -\frac{s_q}{2}\varepsilon_p \\ \frac{d\varepsilon_p}{dt} &= \frac{s_p}{2}\varepsilon_q \end{aligned} \tag{2}$$

2. Show that the solution to system (2), with initial conditions $\varepsilon_q(0)$ and $\varepsilon_p(0)$, is

$$\varepsilon_q(t) = \varepsilon_q(0)\cos\left(\tfrac{1}{2}\sqrt{s_q s_p}\, t\right) - \varepsilon_p(0)\sqrt{\frac{s_q}{s_p}}\ \sin\left(\tfrac{1}{2}\sqrt{s_q s_p}\, t\right)$$

$$\varepsilon_p(t) = \varepsilon_p(0)\cos\left(\tfrac{1}{2}\sqrt{s_q s_p}\, t\right) + \varepsilon_q(0)\sqrt{\frac{s_p}{s_q}}\ \sin\left(\tfrac{1}{2}\sqrt{s_q s_p}\, t\right)$$

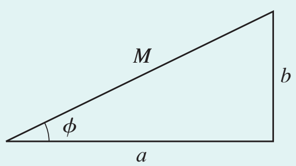

FIGURE 1

3. A useful trigonometric identity is

$$a\cos(ct) + b\sin(ct) = M\cos(ct - \phi)$$

where $M = \sqrt{a^2 + b^2}$ and ϕ is the angle between 0 and 2π whose cosine and sine satisfy the equations $\cos\phi = a/M$ and $\sin\phi = b/M$ (see Figure 1). Note that if $a > 0$ and $b > 0$ (so that we are in the first quadrant), then $\phi = \tan^{-1}(b/a)$. More generally, however, ϕ is *not* given by the principal branch of $\tan^{-1}$. Instead, if $a < 0$ (second or third quadrant), then $\phi = \pi + \tan^{-1}(b/a)$, whereas if $a < 0$ and $b < 0$ (fourth quadrant), then $\phi = 2\pi + \tan^{-1}(b/a)$. Use the identity to show that the solutions in Problem 2 can be written as

$$\begin{aligned} \varepsilon_q(t) &= M_q\cos(ct - \phi_q) \\ \varepsilon_p(t) &= M_p\cos(ct - \phi_p) \end{aligned}$$

where $c = \frac{1}{2}\sqrt{s_q s_p}$,

$$M_q = \sqrt{\varepsilon_q(0)^2 + \varepsilon_p(0)^2\frac{s_q}{s_p}}$$

$$M_p = \sqrt{\varepsilon_p(0)^2 + \varepsilon_q(0)^2\frac{s_p}{s_q}}$$

and ϕ_q and ϕ_p are given by

$$\phi_q = \begin{cases} \tan^{-1}\left(-\dfrac{\varepsilon_p(0)\sqrt{s_q}}{\varepsilon_q(0)\sqrt{s_p}}\right) & \text{if } \varepsilon_q(0) > 0,\ \varepsilon_p(0) < 0 \\ \pi + \tan^{-1}\left(-\dfrac{\varepsilon_p(0)\sqrt{s_q}}{\varepsilon_q(0)\sqrt{s_p}}\right) & \text{if } \varepsilon_q(0) < 0 \\ 2\pi + \tan^{-1}\left(-\dfrac{\varepsilon_p(0)\sqrt{s_q}}{\varepsilon_q(0)\sqrt{s_p}}\right) & \text{if } \varepsilon_q(0) > 0,\ \varepsilon_p(0) > 0 \end{cases}$$

and

$$\phi_q = \begin{cases} \tan^{-1}\left(-\dfrac{\varepsilon_q(0)\sqrt{s_p}}{\varepsilon_p(0)\sqrt{s_q}}\right) & \text{if } \varepsilon_p(0) > 0,\ \varepsilon_q(0) > 0 \\ \pi + \tan^{-1}\left(\dfrac{\varepsilon_q(0)\sqrt{s_p}}{\varepsilon_p(0)\sqrt{s_q}}\right) & \text{if } \varepsilon_p(0) < 0 \\ 2\pi + \tan^{-1}\left(\dfrac{\varepsilon_q(0)\sqrt{s_p}}{\varepsilon_p(0)\sqrt{s_q}}\right) & \text{if } \varepsilon_p(0) > 0,\ \varepsilon_q(0) < 0 \end{cases}$$

Using the definitions of $\varepsilon_q(t)$ and $\varepsilon_p(t)$, we can see that the frequencies $q(t)$ and $p(t)$, as functions of time, are given by the equations

$$\begin{aligned} q(t) &= \tfrac{1}{2} + M_q \cos(ct - \phi_q) \\ p(t) &= \tfrac{1}{2} + M_p \cos(ct - \phi_p) \end{aligned} \tag{3}$$

4. Describe, qualitatively, the predicted behavior of q and p from Equations 3.

5. How do the constants M_q and M_p affect the behavior? How do the constants ϕ_q and ϕ_p affect the behavior? How does the constant c affect the behavior?

6. Use your answers to Problem 5 to explain how the constants s_q and s_p affect the frequency of type A hosts and type B parasites over time. Can you provide a biological explanation for your answer?

The properties of Equations 3, and the predictions that can be obtained from them in terms of experimental data, are explored in Case Study 2a and 2b.