Supplementary material to:

Chapter 11: Techniques for Analyzing Models with Periodic Behavior

From:

<u>A Biologist's Guide to Mathematical Modeling in Ecology and Evolution</u>

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Supplementary Material 11.1: A Hopf bifurcation in a predator-prey model

This example provides some practice using Hopf bifurcation theorem. In Chapter 3 (equations 3.16) we introduced a model describing the population dynamics of a single predator species that feeds on a single prey (termed the resource) species. There are many different ways in which the growth rate of the prey and the consumption rate of them by the predator might be modeled (see Table 3.3). Here we assume that the resources dynamics are governed by the logistic equation in the absence of the predator, that there is a saturating (type II) functional response, and that the predator suffers a constant per capita mortality rate (see Table 3.3). Thus we have

$$\begin{aligned} \frac{\mathrm{d}R}{\mathrm{d}t} &= rR\left(1-\frac{R}{K}\right) - P\frac{cR}{a+R} \\ \frac{\mathrm{d}P}{\mathrm{d}t} &= \frac{\varepsilon cR}{a+R}P - dP \end{aligned}, \qquad \text{(S11.1.1)}$$

where R is the density of the resource species and P is the density of the predator species. In this notation r is the per capita rate of increase of the resource when it is rare, K is the resource carrying capacity in the absence of predators, c and a are the parameters of the functional response, ε is the conversion efficiency of consumed prey into new predators, and d is the per capita mortality rate of the predator. We assume that all parameters are positive.

The equilibria of this model were analyzed in Problem 8.5. There are three possible equilibria, given by (i) $\hat{R} = 0$, $\hat{P} = 0$, (ii) $\hat{R} = K$, $\hat{P} = 0$, and (iii) $\hat{R} = \frac{ad}{\varepsilon c - d}$, $\hat{P} = \frac{\varepsilon ar\left(K(\varepsilon c - d) - ad\right)}{K(\varepsilon c - d)^2}$. The third equilibrium is biologically relevant (i.e., $\hat{R} > 0$, $\hat{P} > 0$) only if the numerator of the equilibrium predator density, $K(\varepsilon c - d) - ad$, is positive. (The denominator of the equilibrium resource density, $\varepsilon c - d$, must also be positive, but you can check that this is true provided that $K(\varepsilon c - d) - ad > 0$.)

Problem 8.5 conducts a formal stability analysis of each of these equilibria, but a bit of biological insight reveals how the dynamics will behave. From a biological standpoint we can see that equilibrium (i) will be unstable because, in the absence of the predator, the resource can always increase when rare ($\mathrm{d}R/\mathrm{d}t > 0$ in equation (S11.1.1) when $P = 0$ and R is small). Similarly, at equilibrium (ii), the predator will be able to increase in numbers when rare (and thus this equilibrium will be unstable) provided that $\mathrm{d}P/\mathrm{d}t > 0$ at this equilibrium. From equations (S11.1.1) this requires that $K(\varepsilon c - d) - ad > 0$. Therefore, whenever equilibrium (iii) is biologically relevant (with positive numbers of predator and prey), the equilibrium with the predator absent will be unstable. These considerations suggest that, when $K(\varepsilon c - d) - ad > 0$, the two species will coexist in some fashion. What is not clear is whether the predator and prey coexist at the stable equilibrium (iii) or whether they fluctuate over time in some manner.

Let's start by examining the stability of equilibrium (iii). You can check that, at this equilibrium, the trace and determinant of the Jacobian matrix (Definition 8.2) of equations (S11.1.1) are

$$\begin{aligned} Trace &= \frac{dr\big(K(\varepsilon c - d) - a(\varepsilon c + d)\big)}{\varepsilon c K(\varepsilon c - d)} \\ Det &= \frac{dr\big(K(\varepsilon c - d) - ad\big)}{\varepsilon c K} \end{aligned} . \tag{S11.1.2}$$

The equilibrium of a two-variable model will be locally stable if and only if the trace is negative and the determinant is positive (Recipe 8.2 with Rule P2.25 in Primer 2). The determinant is positive whenever the equilibrium is biologically relevant (i.e., $K(\varepsilon c - d) - ad > 0$). Thus, the trace determines stability, and the equilibrium will be unstable if:

$$K(\varepsilon c - d) - a(\varepsilon c + d) > 0 . \tag{S11.1.3}$$

But what happens when the equilibrium is unstable? Let's use the Hopf bifurcation theorem (Recipe 11.2) to see if periodic behavior results.

First we must choose a bifurcation parameter. We could use any one of the parameters in expression (S11.1.3) but one of the easiest to interpret is the carrying capacity of the resource, K. As the carrying capacity of the resource increases, eventually the equilibrium with both predator and prey loses stability. According to (S11.1.3), the critical value of K where the equilibrium loses stability is $K^* = a\frac{(\varepsilon c + d)}{(\varepsilon c - d)}$. We now need to check the conditions of Recipe 11.2.

The eigenvalues at this equilibrium can be written as $\alpha(K) \pm \sqrt{-1}\,\beta(K)$ with

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$$\begin{aligned} \alpha(K) &= \frac{dr\big(K(\varepsilon c - d) - a(\varepsilon c + d)\big)}{2\varepsilon c K(\varepsilon c - d)} \\ \beta(K) &= \frac{\sqrt{-d^2 r^2\big(K(\varepsilon c - d) - a(d + \varepsilon c)\big)^2 + 4\varepsilon c K dr(\varepsilon c - d)^2\big(K(\varepsilon c - d) - ad\big)}}{2\varepsilon c K(\varepsilon c - d)} \end{aligned} \qquad \text{(S11.1.4a)}$$

From condition (i) of Recipe 11.2, spiraling or periodic behavior around the equilibrium is expected only if the eigenvalues are complex for values of K near the critical value, K^*. This requires that $\beta(K)$ be a real number for such values of K. Near K^*, the first term under the square root sign will be small, while the second term will be positive. Thus, as long as we consider values of K near enough to K^*, $\beta(K)$ will be a real number. Specifically, at K^*, equations (S11.1.4a) become

$$\begin{aligned} \alpha(K^*) &= 0 \\ \beta(K^*) &= \sqrt{\frac{dr(\varepsilon c - d)}{(\varepsilon c + d)}} \end{aligned} \qquad \text{(S11.1.4b)}$$

Because $\varepsilon c - d > 0$ for the equilibrium resource density to be positive at equilibrium (iii), $\beta(K^*)$ is non-zero. Condition (i) of Recipe 11.2 is therefore met.

Proceeding to condition (ii) of Recipe 11.2, we can differentiate $\alpha(K)$ and evaluate it at K^* to obtain

$$\left.\frac{\mathrm{d}\alpha}{\mathrm{d}K}\right|_{K=K^*} = \frac{dr(\varepsilon c - d)}{2a\varepsilon c(\varepsilon c + d)}. \qquad \text{(S11.1.5)}$$

Expression (S11.1.5) is positive under our assumptions, and therefore condition (ii) of Recipe 11.2 is met as well. As a result, we know that, for values of the carrying capacity near the critical value K^*, periodic predator-prey dynamics occur around the coexistence equilibrium point.

Finally, we must assess condition (iii) by carrying out the calculations in the accompanying *Mathematica* notebook. The result predicts a stable limit cycle. As the carrying capacity increases past the critical value, the coexistence equilibrium will lose its stability, resulting in sustained periodic dynamics of predators and prey. In fact, for this model we can also apply the special facts in Box 11.2 to show that the population dynamics must undergo periodic fluctuations in general (see Problem 11.6).