Educational corner: Limit cycles in a general predator-prey model
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In each issue we present some short educational text about a subject in mathematical biology. If you think some subject should be treated in the next issue, please let us know. Enjoy!

Introduction

The Rosenzweig-MacArthur model of predator-prey dynamics, combining logistic prey growth with a type II predator functional response, is a classic among models of predatory interactions [2]. Its immortality is assured above all by an occurrence of the so-called *paradox of enrichment*, when enriching the system by supplying more resources on which the prey sustains may jeopardize the very prey and predator existence. Mathematically, this is a consequence of a Hopf bifurcation at which a stable coexistence equilibrium gives way to stable limit cycles of increasing amplitude. The Hopf bifurcation occurs when the vertical predator nullcline and the peak of the humped prey nullcline pass one another. One can find anecdotal mentions that this also happens in some other predator-prey models, but I am aware of no detailed analytical account of this in the literature. Therefore, I offer this text for interested readers, assuming just some elementary knowledge of modelling predator-prey dynamics. I also encourage the readers to try and extend this analysis to some more predator-prey model not covered here.

Let us consider the following predator-prey model:

$$\frac{dN}{dt} = N\,g(N) - f(N)\,P$$
$$\frac{dP}{dt} = e\,f(N)\,P - mP \tag{1}$$

Here N and P stand for prey and predator density, respectively, while e and m represent the consumption efficiency and the per capita mortality rate of the predator, respectively. Moreover, $g(N)$ is the per capita prey growth rate in the absence of predators, and $f(N)$ is the predator functional response (neglecting any interference or facilitation among predators). With $g(N) = r(1 - N/K)$ for some positive parameters r and K, and the Holling type II functional response $f(N) = \lambda N/(1 + h\lambda N)$ for some positive parameters λ and h, the model (1) becomes just the Rosenzweig-MacArthur model of predator-prey dynamics.

In the following, I assume that the functions g and f are continuous and continuously differentiable at any $N \geq 0$. Moreover, for the per capita prey growth rate g I assume that $g(0) > 0$, $g'(N) < 0$ for all $N \geq 0$ and $g(K) = 0$ for some $K > 0$. These assumptions imply that prey growth is logistic-like and that $g(N) < 0$ for all $N > K$. For the predator functional response f I assume that $f(0) = 0$ and $f'(N) > 0$ for all $N \geq 0$, which implies $f(N) > 0$ for all $N > 0$. Moreover, I assume that f is saturating for large N, that is, $\lim_{N \to \infty} f(N) = c < \infty$.

Model equilibria and their stability

There are several equilibria (N, P) of model (1). There are two boundary equilibria that always exist, the *extinction equilibrium* $E_0 = (0, 0)$ and the *prey-only equilibrium* $E_K = (K, 0)$. If any coexistence equilibrium exists it has to lie on the predator nullcline defined by the equation $f(N) = m/e$. This equation has no solution for $m/e \geq c$ yet has a unique solution when $m/e < c$. In the latter case, the predator nullcline is

$$N = N^* = f^{-1}(m/e) > 0 \tag{2}$$

and N^* is the N-coordinate of any potential coexistence equilibrium.

The prey nullcline is defined by the formula

$$P = \frac{N\,g(N)}{f(N)} \tag{3}$$

which is well-defined except possibly at $N = 0$. It follows from the formula (3) that the prey nullcline is positive for $N < K$ and negative for

$N > K$. Therefore, the predator and prey nullclines intersect in the first quadrant and hence a coexistence equilibrium exists if and only if $N^* < K$ or equivalently $ef(K) > m$. Note that this final condition has an obvious biological interpretation: if it holds then the predator population increases when rare if it is introduced into the prey population at its carrying capacity K; otherwise the predator population goes extinct. In any case, if $ef(K) > m$ then

$$P^* = \frac{N^* g(N^*)}{f(N^*)} = \frac{e}{m} N^* g(N^*) > 0 \qquad (4)$$

is the P-coordinate of any potential coexistence equilibrium. Since N^* is unique, so is $P^* = (e/m) N^* g(N^*)$ and hence the coexistence equilibrium (N^*, P^*).

The Jacobian matrix corresponding to the model (1) is

$$J(N,P) =$$
$$\begin{bmatrix} g(N) + N\,g'(N) - P\,f'(N) & -f(N) \\ eP\,f'(N) & ef(N) - m \end{bmatrix}$$
$$(5)$$

Evaluated at the extinction equilibrium $E_0 = (0,0)$, it reduces to

$$J(0,0) = \begin{bmatrix} g(0) & 0 \\ 0 & -m \end{bmatrix} \qquad (6)$$

Since $g(0)$ is positive, E_0 is a saddle point. At the prey-only equilibrium $E_K = (K, 0)$, the Jacobian matrix is

$$J(K,0) = \begin{bmatrix} K\,g'(K) & -f(K) \\ 0 & ef(K) - m \end{bmatrix} \qquad (7)$$

Since $K\,g'(K)$ is negative, E_K is locally asymptotically stable provided that $ef(K) < m$ and unstable if $ef(K) > m$. Note that the latter condition coincides with the existence condition of the coexistence equilibrium. Hence, E_K is locally asymptotically stable if no coexistence equilibrium exists and is unstable once a (unique) coexistence equilibrium exists.

At the coexistence equilibrium (N^*, P^*), the Jacobian matrix corresponding to the model (1)

becomes

$$J(N^*, P^*) =$$
$$\begin{bmatrix} g(N^*) + N^*\,g'(N^*) - P^*\,f'(N^*) & -m/e \\ eP^*\,f'(N^*) & 0 \end{bmatrix}$$
$$(8)$$

Let us now analyse the determinant and trace of this matrix. Since

$$\det J(N^*, P^*) = mP^*\,f'(N^*) > 0 \qquad (9)$$

the product of two eigenvalues of the matrix (8) is positive and this rules out a saddle point. Moreover,

$$\operatorname{tr} J(N^*, P^*) = g(N^*) + N^*\,g'(N^*) - P^*\,f'(N^*) \qquad (10)$$

Let us now play with the right-hand side of equation (10):

$$g(N^*) + N^*\,g'(N^*) - P^*\,f'(N^*)$$
$$= g(N^*) + N^*\,g'(N^*) - N^*\,g(N^*)\frac{f'(N^*)}{f(N^*)}$$
$$= \frac{(g(N^*) + N^*\,g'(N^*))f(N^*) - N^*\,g(N^*)\,f'(N^*)}{f(N^*)}$$
$$= f(N^*)\frac{(g(N^*) + N^*g'(N^*))f(N^*) - N^*g(N^*)f'(N^*)}{(f(N^*))^2}$$
$$= f(N^*)\left[\frac{N\,g(N)}{f(N)}\right]'\Big|_{N=N^*}$$

The expression in square brackets is the prey nullcline, so $[N\,g(N)/f(N)]'|_{N=N^*}$ is the slope of the prey nullcline at $N = N^*$. Moreover, as $f(N^*) > 0$ the trace of the Jacobian matrix at (N^*, P^*) has the same sign as the slope of the prey nullcline at N^*. Since we know the determinant of the Jacobian matrix at (N^*, P^*) is positive, (N^*, P^*) is locally asymptotically stable if $\operatorname{tr} J(N^*, P^*) < 0$. This occurs if and only if the prey nullcline is decreasing at N^*. On the contrary, (N^*, P^*) is unstable if $\operatorname{tr} J(N^*, P^*) > 0$ which occurs if and only if the prey nullcline is increasing at N^*.

Let us now assume that the predator nullcline $N = N^*$ intersects the prey nullcline $P = N\,g(N)/f(N)$ at a local minimum or maximum of the latter. This implies $\operatorname{tr} J(N^*, P^*) = 0$. Since the determinant of the Jacobian matrix

corresponds to the product of its eigenvalues and the trace of the Jacobian matrix corresponds to the sum of its eigenvalues, the eigenvalues have to be purely imaginary with a non-zero imaginary at any local extremum of the prey nullcline. Thanks to continuous changes of eigenvalues with changes of model parameters, the eigenvalues have to be imaginary with a negative real part when $\operatorname{tr} J(N^*, P^*)$ is slightly lower than zero and imaginary with a positive real part when $\operatorname{tr} J(N^*, P^*)$ is slightly higher than zero. Thus, there is a potential for a Hopf bifurcation to occur if the other (rather technical) conditions of the Hopf theorem [2] are met.

Importantly, these results imply that if the prey nullcline $N\,g(N)/f(N)$ is monotonically decreasing for all $N > 0$ then the coexistence equilibrium (if it exists) is always stable. On the other hand, if $N\,g(N)/f(N)$ initially increases and then decreases with increasing N, or vice versa, then stability of the coexistence equilibrium (if it exists) changes if the model parameters change such that the predator nullcline $N^* = f^{-1}(m/e)$ and the peak of the prey nullcline transverse one another.

Special cases

Linear functional response If $f(N) = \lambda N$ for some $\lambda > 0$, then

$$
\begin{aligned}
\operatorname{tr} J(N^*, P^*) &= \lambda N^* \left[\frac{N\,g(N)}{\lambda N} \right]' \bigg|_{N=N^*} \\
&= N^* g'(N^*) < 0
\end{aligned}
$$

So the coexistence equilibrium (N^*, P^*), if it exists, is always stable.

Exponential prey growth If $g(N) = r > 0$, then

$$
\begin{aligned}
\operatorname{tr} J(N^*, P^*) &= f(N^*) \left[\frac{rN}{f(N)} \right]' \bigg|_{N=N^*} \\
&= r\, \frac{f(N^*) - N^* f'(N^*)}{f(N^*)}
\end{aligned}
$$

Since $f(N^*) > 0$, it is $\operatorname{tr} J(N^*, P^*) < 0$ if and only if $f(N^*) - N^* f'(N^*) < 0$ which is equivalent to

$$
f'(N^*) > \frac{f(N^*)}{N^*}
$$

This is the well-known *Gause's condition of coexistence equilibrium stability* for the predator-prey model with exponential prey growth [1].

Rosenzweig-MacArthur model Assuming logistic prey growth $g(N) = r(1 - N/K)$ for some positive r and K, and a Holling type II functional response $f(N) = \lambda N/(1 + h\lambda N)$ for some positive λ and h, the existence condition $f(K) > m/e$ becomes $e > mh(1 + 1/(h\lambda K))$. Moreover, the prey nullcline

$$
P(N) = \frac{N\,g(N)}{f(N)} = \frac{r}{\lambda}\left(1 - \frac{N}{K}\right)(1 + h\lambda N) \tag{11}
$$

is an equation for inverted parabola with $P(0) = r/\lambda > 0$, which is humped in the first quadrant as soon as

$$
P'(N)\big|_{N=0} > 0 \quad \Leftrightarrow \quad h\lambda K > 1
$$

Otherwise, if $h\lambda K < 1$, $P(N)$ is monotonically decreasing with increasing N in the first quadrant and the coexistence equilibrium (N^*, P^*), if it exists, is therefore stable.

If $h\lambda K > 1$, so the prey nullcline is humped in the first quadrant, the hump occurs at the prey density

$$
N_h = \frac{h\lambda K - 1}{2h\lambda} \tag{12}
$$

As a consequence, an increase in the prey carrying capacity K moves N_h to the right, yet has no effect on the predator nullcline $N^* = m/[\lambda(e - mh)]$ (recall from the above that $f(K) > m/e$ implies $e > mh$). Therefore, if originally $N_h < N^*$ (stability) then by increasing K eventually $N_h > N^*$ and the coexistence equilibrium (N^*, P^*) becomes unstable. Moreover, a Hopf bifurcation occurs at $N^* = N_h$, and a unique stable limit cycle arises. System destabilization via a Hopf bifurcation may occur also due to changes in other model parameters, such as due to decreasing predator mortality rate m; N^* then moves to the left while N_h stays unaffected.

Type III functional response A form commonly used to model the Holling type III func-

tional response is

$$f(N) = \frac{aN^2}{1 + bN^2} \qquad (13)$$

Let us first assume $g(N) = r$ (exponential prey growth), but $f(N) = aN^2$. This gives

$$\operatorname{tr} J(N^*, P^*) = a(N^*)^2 \left[\frac{rN}{aN^2} \right]'\Big|_{N=N^*} = -r < 0$$

So the coexistence equilibrium (N^*, P^*), if it exists, is always stable. Quadratic functional response thus stabilizes predator-prey dynamics.

However, the situation is a bit more complicated when the form (13) is used. The prey nullcline is then

$$P = \frac{r}{aN} \left(1 - \frac{N}{K} \right) (1 + bN^2)$$

and the trace of the Jacobian matrix at the coexistence equilibrium is

$$\operatorname{tr} J(N^*, P^*) = r \left(\frac{2bm}{ae} - 1 - \frac{2bm}{aeK} \sqrt{\frac{m}{ae - bm}} \right)$$

Obviously, this expression is negative for the predator mortality rate m close to zero as well as for m attaining ae/b from the left, but if $m > ae/(2b)$ the trace may go positive. If that is the case, the prey nullcline has both a local minimum and a local maximum in the first quadrant (Fig. 4a). Hence, when increasing m, the coexistence equilibrium is initially stable, then a stable limit cycle emerges in a Hopf bifurcation, but eventually the coexistence equilibrium returns to being stable in another Hopf bifurcation (Fig. 4b).

References

[1] Gause, G.F., Smaragdova, N.P. and Witt, A.A., 1936. Further studies of interaction between predators and prey. *Journal of Animal Ecology*, 5, 1–18.

[2] Kot, M., 2001. *Elements of mathematical ecology.* Cambridge University Press.
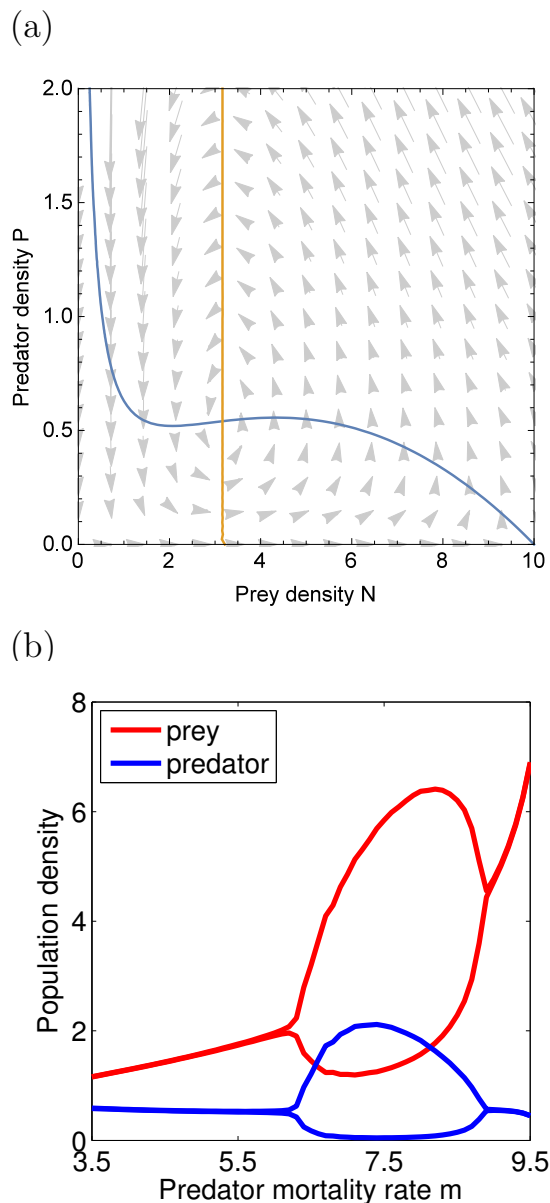
(a)

(b)

Figure 4: Impact of a Holling type III functional response. (a) An example phase portrait with a cubic prey nullcline that has both a local minimum and a local maximum in the first quadrant. (b) A corresponding bifurcation diagram with two Hopf bifurcations. Parameters: $r = 1$, $K = 10$, $l = 2$, $h = 0.2$, $e = 2$, and $m = 8$ in panel (a).