Competition and Cooperation on Predation: Bifurcation Theory Of Mutualism

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Introduction

We investigate two predator-prey models which take into consideration the cooperation between two different predators and within one predator species, respectively. Local and global dynamics are studied for the model systems. By a detailed bifurcation analysis, we investigate the dependence of predation dynamics on mutualism (cooperative predation).

First Predator-Prey Model with Competition and Co-operation

$$x' = 1 - x - p_1xy - p_2xz - 2qxyz, \quad (1)$$
$$y' = p_1xy + qxyz - d_1y, \quad (2)$$
$$z' = p_2xz + qxyz - d_2z, \quad (3)$$

Where, $x(t)$ is the ratio of prey density with respect to the carrying capacity, $y(t)$ and $z(t)$ is the density of first kind and second kind of predators which compete for the prey $x(t)$. Predation rate and death rate for each predator are p_i and d_i with $i = 1, 2$ respectively . In the absent of cooperative predation i.e. $q = 0$. The Gauss's law of competitive exclusion principle holds.The basic reproduction numbers for the predators: $R_1 = p_1/d_1$ and $R_2 = p_2/d_2$.

Existence and Stability of $E_0, E_1, E_2, E+, E_-$

Consider model (1)-(3) with $R_1 > R_2$. Denote $Q = q/(d_1d_2)$ and let $s_\pm$ is the root of $f(s) = 2s^2 - (Q + R_1 + R_2)s + Q = 0$,
$Q_1 = \frac{R_1(R_1-R_2)}{R_1-1}$,
$Q_\pm = (\sqrt{2} \pm \sqrt{2 - (R_1 + R_2)})^2$ and
$Q_c = \begin{cases} Q_1, & R_2 \geq 3R_1 - 2R_1^2, \\ Q_+, & R_2 \leq 3R_1 - 2R_1^2. \end{cases}$.
Set $x_c = \chi(Q_c)$, $G_c = G(x_c)$ and $\bar{G} = \max_{x\in[0,x_c]} G(x)$, where the functions $\chi(Q) = x_+$ and
$G(x) = 4x - (R_1 + R_2)x^2 - \frac{2-R_1x}{d_2(1-R_1x)} - \frac{2-R_2x}{d_1(1-R_2x)}$.
The predator-free equilibrium $E_0 = (1, 0, 0)$ always exists, and E_0 is locally asymptotically stable if and only if $R_1 \leq 1$.
The competitive-predation equilibrium $E_2 = (x_2, 0, z_2)$ with $x_2 = 1/R_2$ and $z_2 = 1/d_2 - 1/p_2$ exists if and only if $R_2 > 1$, and it is always unstable whenever it exists.
The existence conditions of another competitive-predation equilibrium $E_1 = (x_1, y_1, 0)$ with $x_1 = 1/R_1$ and $y_1 = 1/d_1 - 1/p_1$ and the cooperative-predation equilibria $E_\pm = (x_\pm, y_\pm, z_\pm)$ with $x_\pm = 1/s_\pm$, $y_\pm = (s_\pm - R_2)/(d_1Q)$ and $z_\pm = (s_\pm - R_1)/(d_2Q)$. The stability conditions of E_1 and E_- are given in the following cases.

1. $R_1 \leq 1$. In this case, $Q_c = Q_+$, $x_c = \sqrt{2/Q_+}$, E_1 does not exist, $E_\pm$ exist if and only if $Q \geq Q_+$, and E_- is always unstable whenever it exists.
2. $R_1 > 1$ and $R_2 \leq 3R_1 - 2R_1^2$. In this case, $Q_c = Q_+$, $x_c = \sqrt{2/Q_+}$, E_1 always exists, E_1 is locally asymptotically stable if and only if $Q < Q_1$, E_- exists if and only if $Q \in (Q_+, Q_1)$, E_- is always unstable whenever it exists, and E_+ exits if and only if $Q > Q_+$.
3. $R_1 > 1$ and $R_2 > 3R_1 - 2R_1^2$. In this case, $Q_c = Q_1$, $x_c = 1/R_1$, E_1 always exists, E_1 is locally asymptotically stable if and only if $Q < Q_1$, E_- does not exist, and E_+ exits if and only if $Q > Q_1$.

Existence conditions of positive equilibria.

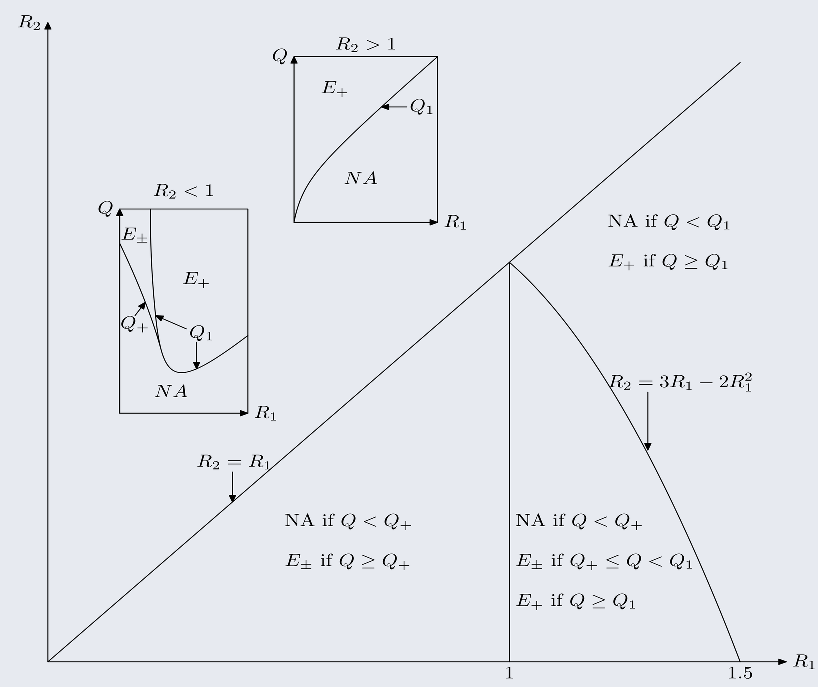


Figure: Existence conditions of positive equilibria.

Stability of E_+

Lemma: Consider an ordinary differential system with a parameter Q. Assume that an equilibrium $E(Q)$ exists for Q in an interval $I \subset \mathbb{R}$ with characteristic polynomial $p(ł, Q) = ł^3 + Q)a_2(Q)ł^2 + (Q)a_1(Q)ł + Q)(Q)a_0(Q)$. Assume that $Q)$, (Q), $a_2(Q)$, $a_1(Q)$ and $a_0(Q)$ are all positive and differentiable functions for $Q \in I$. Define $g(Q) = a_0(Q) - a_1(Q)a_2(Q)$. Then the equilibrium $E(Q)$ is locally asymptotically stable when $g(Q)$ is negative and unstable when $g(Q)$ is positive. If $g(Q)$ has a simple root $Q_h \in I$, then Hopf bifurcation occurs at $Q = Q_h$ with crossing number Sign$[g'(Q_h)]$.

The stability condition of E_+ is given in the following cases.

a. $\bar{G} < 0$. In this case, E_+ is always locally asymptotically stable.
b. $G_c > 0$. In this case, G has a unique root, denoted by x_h, on $(0, x_c)$. E_+ is locally asymptotically stable for $Q \in (Q_h, \infty)$ and unstable for $Q \in (Q_+, Q_h)$, where $Q_h = \phi(x_h)$ is a Hopf bifurcation point.
c. $G_c < 0$ and $\bar{G} > 0$. In this case, G has two roots, $x_{h1} > x_{h2}$, on $(0, x_c)$. E_+ is locally asymptotically stable for $Q \in (Q_+, Q_{h1}) \cup (Q_{h2}, \infty)$ and unstable for $Q \in (Q_{h1}, Q_{h2})$, where $Q_{h1} = \phi(x_{h1})$ and $Q_{h2} = \phi(x_{h2})$ are two Hopf bifurcation points.

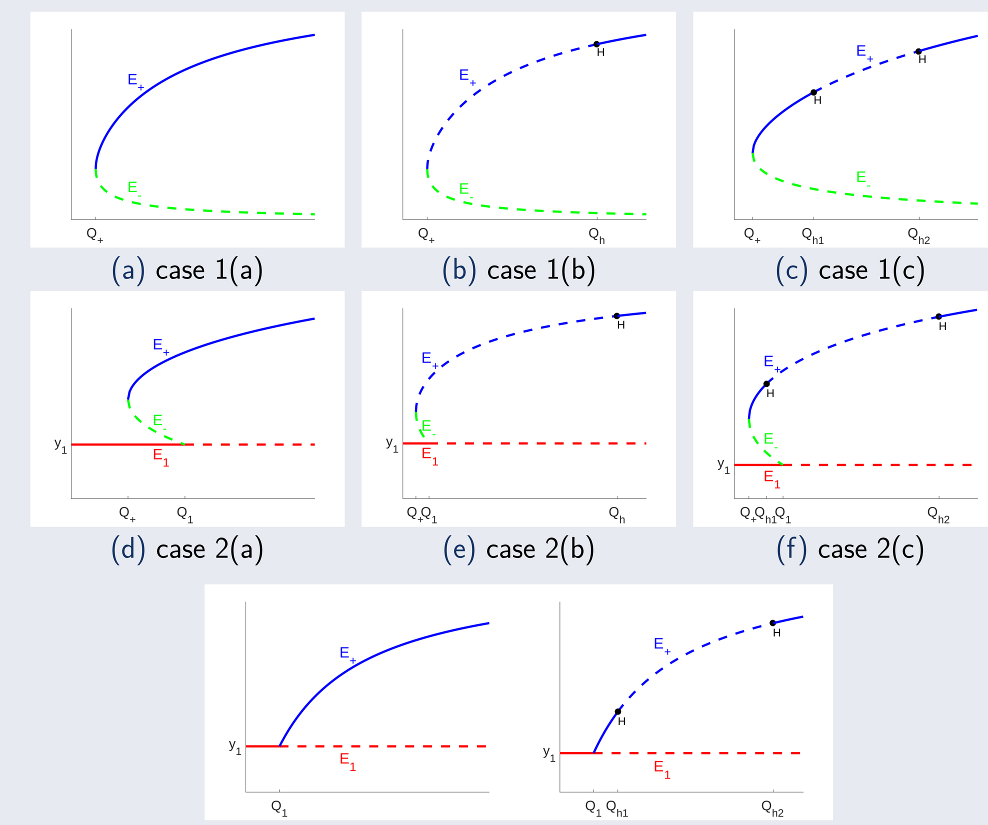
Direction of Hopf bifurcation and stability of periodic solution

Diagonalize the Jacobian matrix of (1)-(3). We calculate the first Lyapunov coefficient l_1. The Hopf bifurcation is supercritical when $l_1 < 0$ and subcritical when $l_1 > 0$ where,

$$l_1 = (i\alpha_{200}\alpha_{110} + \omega\tilde{\alpha}_{210})/(2\omega^2)$$

. $\pm i\omega$ are a pair of purely imaginary eigenvalues of J at the positive equilibrium E_+

Existence and Stability of E_1,E_+ and E_-



(a) case 1(a) (b) case 1(b) (c) case 1(c)
(d) case 2(a) (e) case 2(b) (f) case 2(c)
(g) case 3(a) (h) case 3(c)

Figure: E_1(red),E_+(red) and E_-(green), with projection on y-Q plane

Global Stability of E_0 and E_1

Lyapunov function for the global stability of E_0 :

$$V_0(x, y, z) = c_0(x - \ln x + y + z) + (x + y + z - 1)^2/2$$

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Lyapunov function for the global stability of E_1 :

$$V_1(x, y, z) = c_1(x - x_1 \ln x + y - y_1 \ln y + z) + (x + y + z - x_1 - y_1)^2/2.$$

Theorem: Assume $R_1 > R_2$ and the initial values $(x(0), y(0), z(0))$ are positive. If $R_1 \leq 1$ and q satisfies

$$q \leq \frac{d_1 + d_2 + 2\sqrt{d_2[d_1 - \frac{(d_1+1)^2}{4(c_0+1)}]}}{2c_0}, \quad c_0 = \max\{\frac{d_2+1}{d_2-p_2}, \frac{(d_1-1)^2}{4d_1}\}.$$

, then $E_0 = (1, 0, 0)$ is globally asymptotically stable. If $R_1 > 1$ and q satisfies

$$q \leq \frac{d_1 + d_2 + 2\sqrt{d_2[d_1 - \frac{(d_1+1)^2}{4(c_1/x_1+1)}]}}{2c_1x_1},$$

and, $c_1 = \max\{\frac{(d_2+1)x_1 + (d_1+d_2)y_1}{d_2 - p_2x_1}, \frac{x_1(d_1-1)^2}{4d_1}\}$.

, then $E_1 = (x_1, y_1, 0)$ is globally asymptotically stable.

Special Case

Biologically, we assume that the two predators can be regarded as the same. Thus, we can reduce the three-dimensional system (1)-(3) to a planar system

$$x'(t) = 1 - x(t) - 2px(t)y(t) - 2qx(t)[y(t)]^2, \quad (4)$$
$$y'(t) = px(t)y(t) + qx(t)[y(t)]^2 - dy(t). \quad (5)$$

Diagonalize the Jacobian matrix of (4)-(5). We calculate the first Lyapunov coefficient l_1. The Hopf bifurcation is supercritical when $l_1 < 0$ and subcritical when $l_1 > 0$ where,

$$l_1 = \frac{2ds^3(s-1)}{3}[s(3-d) + d - dR - R]$$

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Existence and property of Hopf bifurcation points

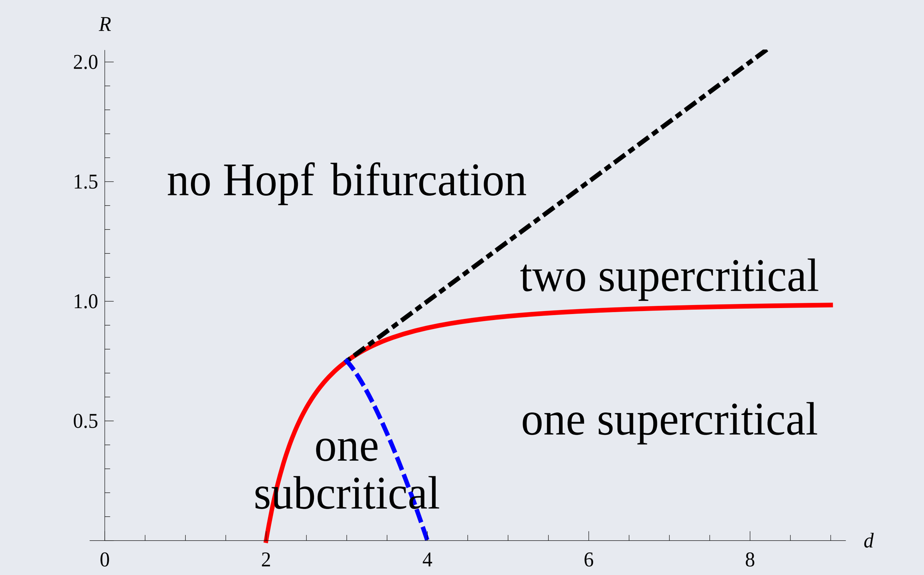
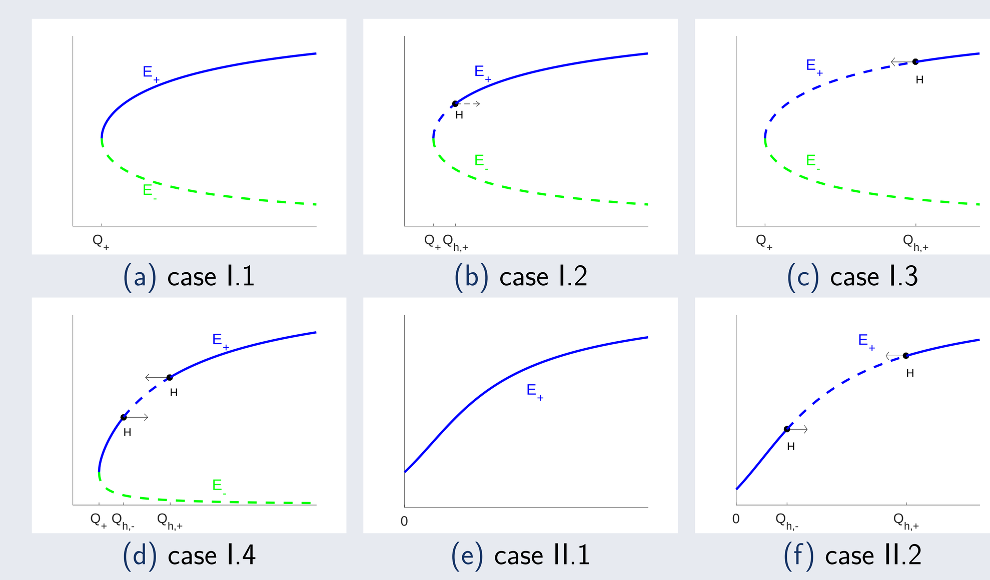


Figure: Existence and property of Hopf bifurcation points in the (d, R) parameter space. The red solid, blue dashed and black dotdashed curves are $R = d(d-2)/(d-1)^2$, $R = d(4-d)/[5d - d^2 - 2 + (d-3)\sqrt{d(d-3)}$, and $R = d/4$, respectively.

Existence and Stability of E_+ and E_-



(a) case I.1 (b) case I.2 (c) case I.3
(d) case I.4 (e) case II.1 (f) case II.2

Figure: E_+(blue) and E_-(green), with projection on y-Q plane

Conclusion

1. In both models cooperative predation may increase the survival probability of predators in the severe environment when non cooperative predation is not efficient to battle with the natural death.
2. Cooperative predation may destabilize a positive equilibrium and induce a Hopf bifurcation.Depending on the model parameters, the limit cycles bifurcated from the Hopf points may or may not be stable.

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