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COMPETITION AND COOPERATION ON PREDATION: BIFURCATION THEORY OF MUTUALISM

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In this paper, we investigate two predator–prey models which take into consideration hunting cooperation (i.e., mutualism) between two different predators and within one predator species, respectively. Local and global dynamics are obtained for the model systems. By a detailed bifurcation analysis, we investigate the dependence of predation dynamics on mutualism (cooperative predation). From our study, we prove that mutualism may enhance the survival of mutualist predators in a severe condition and break the competitive exclusion principle. We further provide quantitative information about how the cooperative predation (mutualism) may (i) establish multiple stability switches on the positive equilibrium; (ii) generate backward bifurcation on equilibria; (iii) induce supercritical or subcritical Hopf bifurcations; and (iv) establish bi-stability phenomenon between the predator-free equilibrium and a positive equilibrium (or a limit cycle).

Keywords: Predator–Prey Model; Cooperative Predation; Mutualism; Hopf Bifurcation; Global Dynamics.

1. Introduction

Competition, cooperation and predation are three major mechanisms in modeling population biology. A cooperative (respectively, competitive) ordinary differential system generates a monotone forward (respectively, backward) solution flow (see p. 34 in Ref. 1. Especially, for a three dimensional cooperative or competitive system, any compact limit set that contains no equilibrium points should be a limit cycle (see p. 41 in Ref. 1). Predation, however, cannot be modeled by a monotone system and thus may induce more complicated dynamics. Many mathematical models of predation are based on the Lotka–Volterra system which was proposed independently by Lotka in the study of parasite invasion on the host (see p. 88 in Ref. 2, and by Volterra to interpret the fishery data in the Adriatic sea collected before, during, and after the First World War.[3]

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Cooperative hunting plays a significant role in Phylogenetics[4] and is essential for some predators.[5] For instance, the Yellowstone wolves with larger group size have a bigger success rate in capturing their most formidable prey, bison.[6] During the nonbreeding season, Harris' hawks in New Mexico hunt cooperatively to improve capture success.[7] *Dictyostelium discoideum*, a soil amoeba that feeds on bacteria, lives mostly as single cells, but develops social cooperation under starvation conditions.[8,9] A two-dimensional system was proposed in Ref. 10 which includes the Lotka–Volterra model with logistic growth of the prey and hunting cooperation on the predator. This model was further extended in Ref. 11 to incorporate Allee effects in the prey.

Competition arises when two different species of predators hunt on the same prey. By the Gause's law of competitive exclusion principle, only the strongest predator survive after the competition. However, this law fails in some situations. The raven population in Yellowstone became more stable after the reintroduction of wolves.[12] The ravens guide the wolves to the prey by croaking, and as a reward, partake the wolf-acquired carcasses.[13] A recorded observation of intimate relation between the badger and the coyote was made more than 130 years ago.[14] Statistical data indicates that the coyote and the badger hunt the ground squirrel more efficiently than a single coyote.[15] Cooperative predation (mutualism) has also been observed between groupers and giant moray eels in the Red Sea.[16] In Ref. 17, a general three-dimensional population model incorporating both competition and cooperation on predation was proposed and some conditions for coexistence of two different predators via persistence theory in dynamical system. Since the system in Ref. 17 was too general and the predation functions were not specifically given, it was too complicated, if not impossible, to determine the criteria for asymptotic stability of positive equilibria.

The purpose of this paper is to provide a detailed analysis on the existence and asymptotic stability of equilibria for a predator–prey model with competition and cooperation. To achieve this, we simply assume that the predation functions take the mass-action forms. Especially, we will investigate the dependence of model dynamics on the mutualism parameter via bifurcation analysis. We will first propose a three-dimensional predator–prey population model of cooperative hunting between two predator species. Next, we will consider a two-dimensional predator–prey population model of cooperative hunting within one predator species. Mathematically, the second system can be considered as a reduced system of the first one, and thus, more quantitative information (such as the direction of Hopf bifurcation and stability of periodic solutions bifurcated from a Hopf bifurcation point) may be obtained via a detailed analysis. In this paper, we are only interested in the cooperation between predators. For the study of cooperation between preys, we refer to Refs. 18–21 and references therein.

The first predator–prey model with competition and cooperation is given as

$$x'(t) = b - d_0 x(t) - p_1 x(t) y(t) - p_2 x(t) z(t) - 2q x(t) y(t) z(t),$$

$$y'(t) = p_1 x(t)y(t) + qx(t)y(t)z(t) - d_1 y(t),$$

$$z'(t) = p_2 x(t)z(t) + qx(t)y(t)z(t) - d_2 z(t),$$

where $x(t)$ denotes the prey density at time t, and $y(t)$ and $z(t)$ correspond to two different predators which compete for the same prey $x(t)$. The prey has a constant birth rate $b > 0$ and per capita death rate $d_0 > 0$. In the absence of predation, the prey will eventually reach the carrying capacity $K = b/d_0$. It is remarked that our linear birth function for the prey is different from the logistic growth chosen in Refs. 10 and 17 and the one with Allee effect in Ref. 11. The main reason for our choice is to simplify the presentation of the mathematical results and proofs. The predation rate (for the mass-action functional response) and death rate for each predator are positive constants p_i and d_i with $i = 1, 2$. In addition to competition on predation, we assume that these two predators will collaborate on hunting for the prey, and the corresponding functional response is $2qxyz$. For simplicity, we assume that the two predators will divide the hunted prey evenly or have the same chance to catch the prey during collaborative predation. We also assume that there is no loss in the procedure of transferring energy from the prey to the predators. Hence, instead of three parameters, we only need to consider one parameter of mutualism (cooperative predation): q.

To simplify mathematical analysis, we scale the time t by the survival time of the prey and use a standard non-dimensionalization technique to reduce the number of parameters in the model system. To be more specific, we define

$$\tilde{t} = d_0 t, \quad \tilde{x} = \frac{x}{K}, \quad \tilde{y} = \frac{y}{K}, \quad \tilde{z} = \frac{z}{K},$$

where $K = b/d_0$ is the carrying capacity of the prey. Our model system can be transformed to

$$\frac{d\tilde{x}}{d\tilde{t}} = 1 - \tilde{x} - \tilde{p}_1 \tilde{x}\tilde{y} - \tilde{p}_2 \tilde{x}\tilde{z} - 2\tilde{q}\tilde{x}\tilde{y}\tilde{z},$$

$$\frac{d\tilde{y}}{d\tilde{t}} = \tilde{p}_1 \tilde{x}\tilde{y} + \tilde{q}\tilde{x}\tilde{y}\tilde{z} - \tilde{d}_1 \tilde{y},$$

$$\frac{d\tilde{z}}{d\tilde{t}} = \tilde{p}_2 \tilde{x}\tilde{z} + \tilde{q}\tilde{x}\tilde{y}\tilde{z} - \tilde{d}_2 \tilde{z},$$

where

$$\tilde{p}_1 = \frac{p_1 K^2}{b}, \quad \tilde{p}_2 = \frac{p_2 K^2}{b}, \quad \tilde{q} = \frac{qK^3}{b}, \quad \tilde{d}_1 = \frac{d_1}{d_0}, \quad \tilde{d}_2 = \frac{d_2}{d_0}.$$

For convenience, we drop the tilde and rewrite the model system as

$$x'(t) = 1 - x(t) - p_1 x(t)y(t) - p_2 x(t)z(t) - 2qx(t)y(t)z(t), \tag{1.1}$$

$$y'(t) = p_1 x(t)y(t) + qx(t)y(t)z(t) - d_1 y(t), \tag{1.2}$$

$$z'(t) = p_2 x(t)z(t) + qx(t)y(t)z(t) - d_2 z(t), \tag{1.3}$$

where $x(t)$ denotes the ratio of prey density with respect to the carrying capacity. The time t is scaled by the survival time of the prey. Therefore, the birth and death rates for the prey are normalized to be 1.

In the absence of cooperative predation (i.e., $q = 0$), the model dynamics is simple and it can be determined by the basic reproduction numbers for the predators: $R_1 = p_1/d_1$ and $R_2 = p_2/d_2$. The predator-free equilibrium $E_0 = (1,0,0)$ is locally asymptotically stable if and only if both R_1 and R_2 do not exceed the threshold value 1. Moreover, if $R_1 \leq 1$ and $R_2 \leq 1$, we can use the Lyapunov function $V(x,y,z) = x - \ln x + y + z$ to show that E_0 is globally asymptotically stable. If $R_1 > 1$, then E_0 is unstable and the model system possesses another equilibrium $E_1 = (x_1, y_1, 0)$, where $x_1 = 1/R_1$ and $y_1 = 1/d_1 - 1/p_1$. By analyzing the characteristic roots and introducing the Lyapunov function $V(x,y,z) = x - x_1 \ln x + y - y_1 \ln y + z$, one can prove that E_1 is globally asymptotically stable if $R_1 > R_2$ and unstable if $R_1 < R_2$. A similar result holds when $R_2 > 1$. In one word, the Gause's law of competitive exclusion principle holds for the competitive predation model without cooperation. It is thus interesting to ask whether the cooperative predation will violate the competitive exclusion principle. This work aims at exploring the joint impact of competition and cooperation on predation.

The rest of this paper is organized as follows. In Sec. 2, we analyze the equilibria for system (1.1)–(1.3). Local and global analyses of this system are given in Secs. 3 and 4, respectively. In Sec. 5, we focus on a special case when competition is ignored in cooperative predation. This enables us to reduce the number of model parameters and obtain more detailed information about the direction of Hopf bifurcations and stability of periodic solutions. Finally, we give a brief discussion in Sec. 6.

2. Equilibria

It is obvious that the solutions of (1.1)–(1.3) with nonnegative initial conditions are always nonnegative and bounded. In this section, we characterize the existence conditions for (nonnegative) equilibria. By symmetry, we assume that $R_1 > R_2$, where $R_1 = p_1/d_1$ and $R_2 = p_2/d_2$ are the basic reproduction numbers for the two predators. As we shall see later, it is convenient to introduce a new parameter $Q = q/(d_1 d_2)$.

The model system (1.1)–(1.3) always has a predator-free equilibrium $E_0 = (1,0,0)$. If $R_1 > 1$, then a boundary equilibrium $E_1 = (x_1, y_1, 0)$ exists, where $x_1 = 1/R_1$ and $y_1 = 1/d_1 - 1/p_1$. If further $R_2 > 1$, then another boundary equilibrium $E_2 = (x_2, 0, z_2)$ exists, where $x_2 = 1/R_2$ and $z_2 = 1/d_2 - 1/p_2$.

Now, we look for a positive equilibrium $E = (x,y,z)$ with $x > 0$, $y > 0$ and $z > 0$. A simple calculation shows that $x = 1/s$, $y = (s - R_2)/(d_1 Q)$ and $z = (s - R_1)/(d_2 Q)$, where s is a root of

$$f(s) := 2s^2 - (Q + R_1 + R_2)s + Q = 0. \tag{2.1}$$

We call s a feasible root if s is bigger than both 1 and R_1. There are two cases to be considered.

(1) If $R_1 + R_2 \geq 2$, then $R_1 > 1$ and $f(1) \leq 0$. Thus, $f(s)$ has two positive roots

$$s_\pm = \frac{Q + R_1 + R_2 \pm \sqrt{(Q + R_1 + R_2)^2 - 8Q}}{4}. \tag{2.2}$$

Since $s_- \leq 1 \leq s_+$, the smaller root s_- is not feasible. Moreover, s_+ is feasible if and only if $f(R_1) < 0$, or equivalently, $Q > Q_1$, where

$$Q_1 = \frac{R_1(R_1 - R_2)}{R_1 - 1}. \tag{2.3}$$

(2) If $R_1 + R_2 < 2$, then $f(s)$ has two (counting multiplicity) positive roots $s_\pm$ if either $Q \geq Q_+$ or $Q \leq Q_-$, and no root if $Q_- < Q < Q_+$, where

$$Q_\pm = 4 - (R_1 + R_2) \pm \sqrt{16 - 8(R_1 + R_2)} = [\sqrt{2} \pm \sqrt{2 - (R_1 + R_2)}]^2 \tag{2.4}$$

are the solutions of $(Q + R_1 + R_2)^2 = 8Q$. Since $Q_+ Q_- = (R_1 + R_2)^2$, we have $Q_- < R_1 + R_2$. If $Q \leq Q_-$, then $s_+ + s_- = (Q + R_1 + R_2)/2 < R_1 + R_2 < 2$, which together with $f(1) > 0$ implies that both roots $s_\pm$ are not feasible. If $Q \geq Q_+$, then $Q > 4 - (R_1 + R_2)$, which implies that $s_+ + s_- > 2$. Since $f(1) > 0$, we have $s_+ \geq s_- > 1$. To compare $s_\pm$ with R_1, we need to consider the following three subcases.

(a) If $R_1 \leq 1$, then both $s_\pm$ are feasible.
(b) If $R_2 > 3R_1 - 2R_1^2$, then $Q_+ > Q_1$, which implies that $Q > Q_1$; namely, $f(R_1) < 0$. Hence, $f(s)$ has a unique feasible root s_+.
(c) If $R_1 > 1$ and $R_2 \leq 3R_1 - 2R_1^2$, then $Q_+ \leq Q_1$. If $Q \geq Q_1$, then $f(R_1) \leq 0$, and $f(x)$ has exactly one feasible root s_+ except for the critical case $Q = Q_1 = Q_+$ where $s_- = s_+ = R_1$ becomes unfeasible. If $Q_+ < Q < Q_1$, then $s_- > R_1$ and both $s_\pm$ are feasible.

If $s_\pm$ are the feasible solutions of (2.1); namely, $s_\pm$ are bigger than both 1 and R_1, we denote $E_\pm = (x_\pm, y_\pm, z_\pm)$ where $x_\pm = 1/s_\pm$, $y_\pm = (s_\pm - R_2)/(d_1 Q)$ and $z_\pm = (s_\pm - R_1)/(d_2 Q)$. The existence conditions for the positive equilibria $E_\pm$ are illustrated in Fig. 1.

3. Local Analysis

The Jacobian matrix of the system (1.1)–(1.3) for an equilibrium $E = (x, y, z)$ is calculated as

$$J = \begin{pmatrix} -1 - p_1 y - p_2 z - 2qyz & -p_1 x - 2qxz & -p_2 x - 2qxy \\ p_1 y + qyz & p_1 x + qxz - d_1 & qxy \\ p_2 z + qyz & qxz & p_2 x + qxy - d_2 \end{pmatrix}. \tag{3.1}$$

For the predator-free equilibrium $E_0 = (1, 0, 0)$, the three characteristic roots are -1, $p_1 - d_1$ and $p_2 - d_2$. In this section, we still assume that $R_1 > R_2$, where
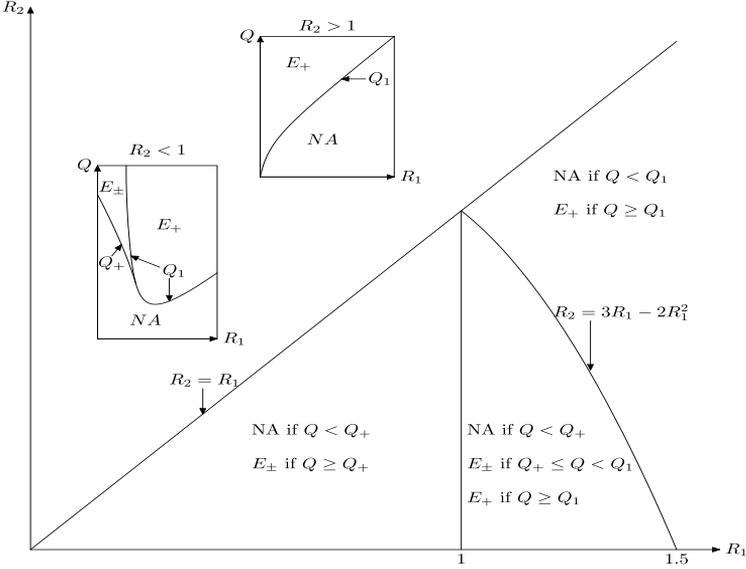
Fig. 1.   Existence conditions of positive equilibria.

$R_1 = p_1/d_1$ and $R_2 = p_2/d_2$. It is readily seen that E_0 is locally asymptotically stable if $R_1 < 1$ and unstable if $R_1 > 1$. For the critical case $R_1 = 1$, we need to make use of the following lemma.

Lemma 3.1. *Let $u(t) = (u_1(t), \ldots, u_n(t))^T$ be a vector-valued function. Consider the ordinary differential system $u'(t) = f(u(t))$ with $f(u) = (f_1(u), \ldots, f_n(u))^T \in C^1(X, X)$, where $X \in \mathbb{R}^n$ is a positive invariant set of the differential system. Let $\bar{u} = (\bar{u}_1, \ldots, \bar{u}_n)^T \in X$ be an equilibrium and denote $f_{ij} = \partial_{u_j} f_i(\bar{u})$. Assume the following conditions are satisfied:*

(1) *$\bar{u}_n = 0$, $f_n(u) = u_n h(u)$ and $h(\bar{u}) = 0$.*
(2) *All eigenvalues of the $(n-1) \times (n-1)$ matrix A with $A_{ij} = f_{ij}$ have negative real parts.*

Denote $h_i = \partial_{u_i} h(\bar{u})$, $\alpha = (h_1, \ldots, h_{n-1})^T$, $\beta = (f_{1n}, \ldots, f_{n-1,n})^T$ and $\lambda_c = h_n - \alpha^T A^{-1} \beta$. Then $\bar{u}$ is locally asymptotically stable if $\lambda_c < 0$ and unstable if $\lambda_c > 0$.

Proof. The Jacobian matrix of the linearized system about $\bar{u}$ is

$$D_u f(\bar{u}) = \begin{pmatrix} A & \beta \\ 0 & 0 \end{pmatrix}$$

$$= \begin{pmatrix} I_{n-1} & -A^{-1}\beta \\ 0 & 1 \end{pmatrix} \begin{pmatrix} A & 0 \\ 0 & 0 \end{pmatrix} \begin{pmatrix} I_{n-1} & A^{-1}\beta \\ 0 & 1 \end{pmatrix},$$

where I_{n-1} is the $(n-1) \times (n-1)$ identity matrix. Let $A^{-1}\beta = (\gamma_1, \ldots, \gamma_{n-1})^T$, and introduce new variables

$$
\begin{pmatrix} z_1 \\ \vdots \\ z_n \end{pmatrix} = \begin{pmatrix} I_{n-1} & A^{-1}\beta \\ 0 & 1 \end{pmatrix} \begin{pmatrix} u_1 - \bar{u}_1 \\ \vdots \\ u_n - \bar{u}_n \end{pmatrix} = \begin{pmatrix} u_1 - \bar{u}_1 + \gamma_1 u_n \\ \vdots \\ u_{n-1} - \bar{u}_{n-1} + \gamma_{n-1} u_n \\ u_n \end{pmatrix}.
$$

It is easily seen that $(0, \ldots, 0)^T$ is an equilibrium of the ordinary differential system for $(z_1, \ldots, z_n)^T$ with Jacobian matrix

$$
\begin{pmatrix} A & 0 \\ 0 & 0 \end{pmatrix}.
$$

According to Sec. 2.1 of Ref. 22, the stability of $\bar{u}$ is determined by the stability of $z_n = 0$ for the following restricted differential equation on the center manifold $z_i = O(z_n^2)$ with $i = 1, \ldots, n-1$,

$$
z_n'(t) = z_n h(\bar{u}_1 - \gamma_1 z_n + O(z_n^2), \ldots, \bar{u}_{n-1} - \gamma_{n-1} z_n + O(z_n^2), z_n) = \lambda_c z_n^2 + O(z_n^3),
$$

where $\lambda_c = -h_1\gamma_1 - \cdots - h_{n-1}\gamma_{n-1} + h_n = h_n - \alpha^T A^{-1}\beta$. If $\lambda_c < 0$, then 0 is locally asymptotically stable for the restricted equation and thus $\bar{u}$ is locally asymptotically stable for the original differential system. If $\lambda_c > 0$, then 0 is unstable for the restricted equation and thus $\bar{u}$ is unstable for the original system. $\qquad\square$

For the critical case $R_1 = 1$, we use the notation in Lemma 3.1 to calculate

$$
\lambda_c = 0 - (p_1 \quad q) \begin{pmatrix} -1 & -p_2 \\ 0 & p_2 - d_2 \end{pmatrix} \begin{pmatrix} -p_1 \\ 0 \end{pmatrix} = -p_1^2 < 0,
$$

which implies that E_0 is locally asymptotically stable.

If $R_1 > 1$, the competitive-exclusion equilibrium $E_1 = (x_1, y_1, 0)$ with $x_1 = 1/R_1$ and $y_1 = 1/d_1 - 1/p_1$ exists. The stability of E_1 is determined by the sign of the characteristic root $\lambda_1 = p_2 x_1 + q x_1 y_1 - d_2$ since the other two characteristic roots always have negative real parts. If $\lambda_1 > 0$, or equivalently, $Q > Q_1$, then E_1 is unstable. If $\lambda_1 < 0$, or equivalently, $Q < Q_1$, then E_1 is locally asymptotically stable. If $\lambda_1 = 0$, or equivalently, $Q = Q_1$, then J has a zero eigenvalue while the other two eigenvalues have negative real parts. Using the notation in Lemma 3.1, we calculate

$$
\lambda_c = -(p_2 + q y_1 \quad q x_1) \begin{pmatrix} -1/x_1 & -p_1 x_1 \\ p_1 y_1 & 0 \end{pmatrix}^{-1} \begin{pmatrix} -p_2 x_1 - 2q x_1 y_1 \\ q x_1 y_1 \end{pmatrix}
$$

$$
= -d_1 d_2 q [2R_2 + (2 - 3x_1)Q]/p_1^2.
$$

Since $Q = Q_1 = R_1(R_1 - R_2)/(R_1 - 1)$, we have $2R_2 + (2 - 3x_1)Q = (R_2 + 2R_1^2 - 3R_1)/(R_1 - 1)$. If $R_2 > 3R_1 - 2R_1^2$, then $\lambda_c < 0$ and E_1 is locally asymptotically stable. If $R_2 < 3R_1 - 2R_1^2$, then $\lambda_c > 0$ and E_1 is unstable.

If $R_2 > 1$, there exists another competitive-exclusion equilibrium $E_2 = (x_2, 0, z_2)$ with $x_2 = 1/R_2$ and $z_2 = 1/d_2 - 1/p_2$. The stability of E_2 is determined by the sign of the characteristic root $\lambda_2 = p_1 x_2 + q x_2 z_2 - d_1$ since the other two characteristic roots always have negative real parts. By symmetry, we only consider the case $R_1 > R_2$. Hence, we have $\lambda_2 > 0$ and E_2 is always unstable whenever it exists.

Now, we analyze the stability of cooperative-predation equilibria $E_\pm = (x_\pm, y_\pm, z_\pm)$. The characteristic polynomials are given by

$$p_\pm(\lambda) = \lambda^3 + \frac{\lambda^2}{x_\pm} + q d_1 d_2 y_\pm z_\pm \left(\frac{2 - R_1 x_\pm}{d_2(1 - R_1 x_\pm)} + \frac{2 - R_2 x_\pm}{d_1(1 - R_2 x_\pm)} - Q x_\pm^2 \right) \lambda$$

$$+ q d_1 d_2 y_\pm z_\pm (2 - Q x_\pm^2). \tag{3.2}$$

Note that $x_+ x_- = 2/Q$. We have $x_+^2 < 2/Q < x_-^2$, which implies that $p_-(0) < 0$ and the characteristic equation $p_-(\lambda) = 0$ has at least one positive root. Thus, E_- is always unstable whenever it exists. To investigate the stability of E_+, we need the following lemma.

Lemma 3.2. *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 $p(\lambda, Q) = \lambda^3 + \alpha(Q) a_2(Q) \lambda^2 + \beta(Q) a_1(Q) \lambda + \alpha(Q) \beta(Q) a_0(Q)$. Assume that $\alpha(Q), \beta(Q), a_2(Q), a_1(Q)$ 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 $\text{Sign}[g'(Q_h)]$.*

Proof. Since the signs of $g(Q)$ and $g'(Q_h)$ do not change if both $a_0(Q)$ and $a_1(Q) a_2(Q)$ are multiplied by the same positive function, we may assume without loss of generality that $\alpha(Q) = \beta(Q) = 1$ for all $Q \in I$. The stability criterion of $E(Q)$ is then a direct application of Routh–Hurwitz criterion.

Assume that $g(Q)$ has a simple root $Q_h \in I$ and set $\omega_h := \sqrt{a_1(Q_h)} = \sqrt{a_0(Q_h)/a_2(Q_h)} > 0$. It is readily seen that $\lambda_{h,\pm} = \pm i \omega_h$ are a pair of imaginary roots of the characteristic equation $p(\lambda, Q_h) = 0$. Since $p(0, Q_h) > 0$, the third characteristic root is negative. By implicit function theorem, there exist two differentiable functions $\lambda_\pm(Q)$ near $Q = Q_h$ such that $p(\lambda_\pm(Q), Q) = 0$ and $\lambda_\pm(Q_h) = \pm i \omega_h$. Furthermore,

$$\lambda'_\pm(Q_h) = -\frac{\partial_Q p(\lambda, Q)}{\partial_\lambda p(\lambda, Q)} \bigg|_{\lambda = \lambda_{h,\pm}, Q = Q_h} = -\frac{a_2'(Q_h) \lambda_{h,\pm}^2 + a_1'(Q_h) \lambda_{h,\pm} + a_0'(Q_h)}{3\lambda_{h,\pm}^2 + 2a_2(Q_h) \lambda_{h,\pm} + a_1(Q_h)}$$

$$= \frac{a_0'(Q_h) - a_1(Q_h) a_2'(Q_h) \pm i \omega_h a_1'(Q_h)}{2\omega_h^2 \mp 2i\omega_h a_2(Q_h)}$$

$$= \frac{\omega_h g'(Q_h) \pm i[\omega_h^2 a_1'(Q_h) + a_2(Q_h) a_0'(Q_h) - a_2(Q_h) a_1(Q_h) a_2'(Q_h)]}{2\omega_h[\omega_h^2 + a_2^2(Q_h)]},$$

which implies that $\text{Sign}[\text{Re }\lambda'_\pm(Q_h)] = \text{Sign}[g'(Q_h)]$. Hence, the crossing number at Q_h is the same as the sign of $g'(Q_h)$. □

Denote

$$Q_c = \begin{cases} Q_1, & R_2 \geq 3R_1 - 2R_1^2, \\ Q_+, & R_2 \leq 3R_1 - 2R_1^2. \end{cases} \tag{3.3}$$

One can prove that E_+ exists if and only if $Q \geq Q_c$; see Fig. 1. Recall that $x_\pm = 1/s_\pm$, where $s_\pm$ are the roots of (2.1). It is easily seen from (2.2) that $x_+ = \chi(Q)$, where

$$\chi(Q) := \frac{4}{Q + R_1 + R_2 + \sqrt{(Q + R_1 + R_2)^2 - 8Q}} \tag{3.4}$$

is a decreasing function of $Q \in [Q_c, \infty)$. Denote $x_c = \chi(Q_c)$. For convenience, we define the inverse function of $\chi(Q)$ as

$$\phi(x) := \frac{2 - (R_1 + R_2)x}{x - x^2}, \quad 0 < x < x_c. \tag{3.5}$$

In view of Lemma 3.2, we obtain from (3.2) and $2/Q > x_+^2$ that the stability of E_+ is determined by the sign of $g(Q) = G(\chi(Q))$, where

$$G(x) = 4x - (R_1 + R_2)x^2 - \frac{2 - R_1 x}{d_2(1 - R_1 x)} - \frac{2 - R_2 x}{d_1(1 - R_2 x)}. \tag{3.6}$$

Note that $G(0) < 0$ and $G''(x) < 0$ for all $x \in [0, x_c]$. Hence, $G(x)$ has a unique maximum $\bar{x}$ on $[0, x_c]$. The signs of $G(x_c)$ and $G(\bar{x})$ determine the zeros and signs of $G(x)$ in $[0, x_c]$, and thus determine the stability of E_+.

We summarize our results in the following theorem with illustrations in Fig. 2.

Theorem 3.3. *Consider model (1.1)–(1.3) with $R_1 > R_2$, where $R_1 = p_1/d_1$ and $R_2 = p_2/d_2$. Denote $Q = q/(d_1 d_2)$ and let $s_\pm$, Q_1, Q_+ and Q_c be defined as in (2.2)–(2.4) and (3.3), respectively. 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 χ and G are given in (3.4) and (3.6), respectively.*

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 $x_\pm = 1/s_\pm$, $y_\pm = (s_\pm - R_2)/(d_1 Q)$ and $z_\pm = (s_\pm - R_1)/(d_2 Q)$, and 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.*

(a) Case (1a)

(b) Case (1b)

(c) Case (1c)

(d) Case (2a)

(e) Case (2b)

(f) Case (2c)

(g) Case (3a)

(h) Case (3c)
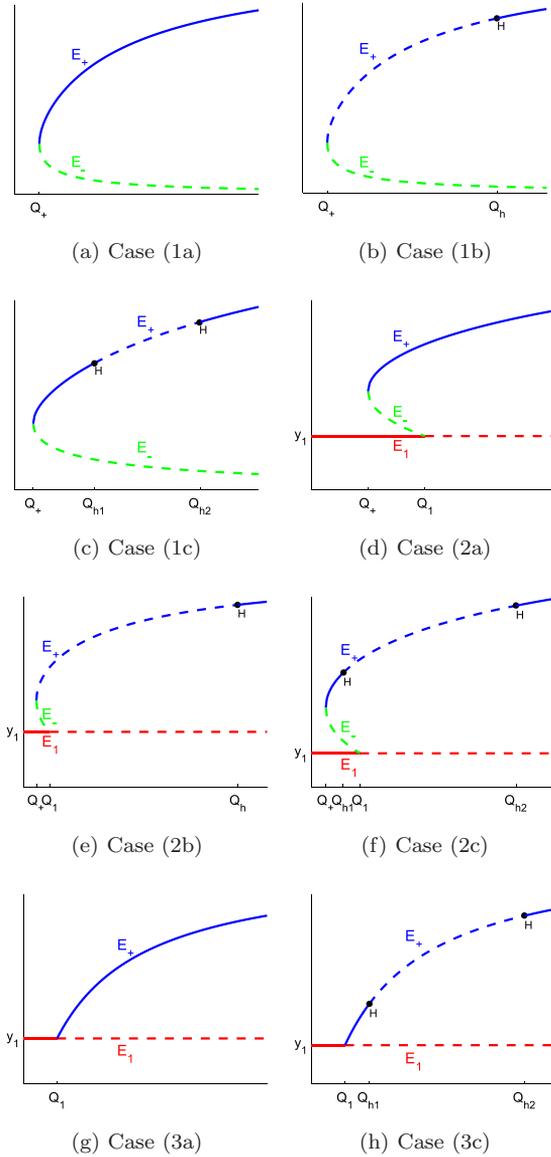
Fig. 2.   (Color online) Existence and stability conditions of equilibria E_1 (red), E_+ (blue), and E_- (green), with projection on $y-Q$ plane. A solid curve indicates that the corresponding equilibrium is locally asymptotically stable, and a dashed curve indicates that the corresponding equilibrium is unstable. A dark dot with a text label "H" indicates the location of a Hopf bifurcation.

(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_+ exists 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_+ exists if and only if $Q > Q_1$.

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.

There are nine possible combinations of the cases (1)–(3) and the cases (a)–(c). For instance, case (1a) means both conditions in case (1) and case (a) are satisfied: $R_1 \leq 1$ and $\bar{G} < 0$. Note that case (3b) is an empty parameter region because $G_c = -\infty$ in case (3) but $G_c > 0$ in case (b).

To determine the direction of Hopf bifurcation and stability of periodic solutions bifurcated from a Hopf bifurcation point, we shall diagonalize the Jacobian (3.1) as $J = PDP^{-1}$ with $D = \text{diag}\{i\omega, -i\omega, -1/x_+\}$ and

$$
P = \begin{pmatrix}
-\omega^2 - q^2 x_+^2 y_+ z_+ & -\omega^2 - q^2 x_+^2 y_+ z_+ & 1/x_+^2 - q^2 x_+^2 y_+ z_+ \\
d_2 q y_+ z_+ + i\omega d_1 y_+/x_+ & d_2 q y_+ z_+ - i\omega d_1 y_+/x_+ & d_2 q y_+ z_+ - d_1 y_+/x_+^2 \\
d_1 q y_+ z_+ + i\omega d_2 z_+/x_+ & d_1 q y_+ z_+ - i\omega d_2 z_+/x_+ & d_1 q y_+ z_+ - d_2 z_+/x_+^2
\end{pmatrix},
$$

where $\pm i\omega$ are a pair of purely imaginary eigenvalues of J at the positive equilibrium $E_+ = (x_+, y_+, z_+)$. Now, we set

$$
\begin{pmatrix} x \\ y \\ z \end{pmatrix} = \begin{pmatrix} x_+ \\ y_+ \\ z_+ \end{pmatrix} + P \begin{pmatrix} \alpha \\ \bar{\alpha} \\ \beta \end{pmatrix}.
$$

It follows that

$$
\alpha' = i\omega\alpha + \frac{\alpha_{200}}{2}\alpha^2 + \alpha_{110}\alpha\bar{\alpha} + \frac{\alpha_{020}}{2}\bar{\alpha}^2 + \alpha_{101}\alpha\beta + \alpha_{011}\bar{\alpha}\beta + \frac{\alpha_{210}}{2}\alpha^2\bar{\alpha} + \cdots,
$$

$$
\bar{\alpha}' = -i\omega\bar{\alpha} + \frac{\bar{\alpha}_{200}}{2}\bar{\alpha}^2 + \bar{\alpha}_{110}\alpha\bar{\alpha} + \frac{\bar{\alpha}_{020}}{2}\alpha^2 + \bar{\alpha}_{101}\bar{\alpha}\beta + \bar{\alpha}_{011}\alpha\beta + \frac{\bar{\alpha}_{210}}{2}\alpha\bar{\alpha}^2 + \cdots,
$$

$$
\beta' = -\frac{1}{x_+}\beta + \frac{\beta_{200}}{2}\alpha^2 + \beta_{110}\alpha\bar{\alpha} + \frac{\beta_{020}}{2}\bar{\alpha}^2 + \cdots,
$$

where the coefficients are given in terms of model parameters, though the explicit formulas are tedious (and thus omitted here). By restricting the above system on

the center manifold $\beta = \frac{\gamma_{20}}{2}\alpha^2 + \gamma_{11}\alpha\bar{\alpha} + \frac{\gamma_{02}}{2}\bar{\alpha}^2 + O(|\alpha|^3)$, we obtain

$$\alpha' = i\omega\alpha + \frac{\alpha_{200}}{2}\alpha^2 + \alpha_{110}\alpha\bar{\alpha} + \frac{\alpha_{020}}{2}\bar{\alpha}^2 + \alpha_{101}\alpha\beta + \alpha_{011}\bar{\alpha}\beta + \frac{\tilde{\alpha}_{210}}{2}\alpha^2\bar{\alpha} + \cdots,$$

where $\tilde{\alpha}_{210} = \alpha_{210} + 2x_+\alpha_{101}\beta_{110} + \alpha_{011}\beta_{200}/(2i\omega + 1/x_+)$. The first Lyapunov coefficient (see (3.20) in Ref. 23) is calculated as $l_1 = \text{Re}(i\alpha_{200}\alpha_{110} + \omega\tilde{\alpha}_{210})/(2\omega^2)$. The Hopf bifurcation is supercritical when $l_1 < 0$ and subcritical when $l_1 > 0$.

4. Global Analysis

In this section, we always assume $R_1 > R_2$. In the absence of cooperative predation ($q = 0$), the global dynamics of competitive predation model is clear: either the predators will be extinct (E_0 is globally asymptotically stable when $R_1 \leq 1$) or one predator dominates the predation (E_1 is globally asymptotically stable when $R_1 > 1$). In this section, we will extend these results to the case when cooperation in predation is weak (i.e., $q > 0$ is small).

Consider the system (1.1)–(1.3). If the initial value $(x(0), y(0), z(0)) \in \mathbb{R}^3_+$, then $x(t) > 0$ and $(y(t), z(t)) \in \mathbb{R}^2_+$ for all $t > 0$. If $y(0) = 0$, then $y(t) = 0$ for all $t \geq 0$. If $y(0) > 0$, then $y(t) > 0$ for all $t \geq 0$. If $z(0) = 0$, then $z(t) = 0$ for all $t \geq 0$. If $z(0) > 0$, then $z(t) > 0$ for all $t \geq 0$. In this section, we always assume that the initial values $x(0)$, $y(0)$ and $z(0)$ are all positive. Consequently, $x(t) > 0$, $y(t) > 0$ and $z(t) > 0$ for all $t \geq 0$. By adding the three equations (1.1)–(1.3), we obtain from comparison principle that the solution is ultimately bounded. Especially, we have

$$\limsup_{t\to\infty} x(t) \leq 1, \quad \limsup_{t\to\infty}[x(t) + y(t) + z(t)] \leq 1/\min\{1, d_1, d_2\}.$$

Lemma 4.1. *Let $(x(t), y(t), z(t))$ be a positive solution of (1.1)–(1.3). If $x(t_0) \leq 1$ for some $t_0 \geq 0$, then $x(t) < 1$ for all $t > t_0$. If $x(t) > 1$ for all $t \geq 0$, then $(x(t), y(t), z(t)) \to (1, 0, 0)$ as $t \to \infty$.*

Proof. If $x(t_0) = 1$ for some $t_0 \geq 0$, then $x'(t_0) < 0$, which, together with a contradiction argument, implies $x(t) < 1$ for all $t > t_0$. If $x(t_0) < 1$ for some $t_0 \geq 0$, then we also have $x(t) < 1$ for all $t > t_0$. Now, we assume that $x(t) > 1$ for all $t \geq 0$. It follows from (1.1) that $x'(t) < 0$ for all $t \geq 0$. Since $x(t)$ is bounded below by 1, the limit $x(\infty)$ exists. It then follows from comparison principle that $x(\infty) = 1$. Next, we observe from (1.1) and (1.2) that $x'(t) + y'(t) < 0$, which implies that the limit $\lim_{t\to\infty}[x(t) + y(t)]$ exists and hence $y(\infty)$ exists. We claim $y(\infty) = 0$. Otherwise, there exists $t_1 > 0$ such that $y(t) > y(\infty)/2$ for all $t > t_1$. This together with (1.1) gives $x'(t) < 1 - [1 + p_1 y(\infty)/2]x(t)$ for all $t > t_1$. By comparison principle, the limit $x(\infty)$ is bounded by $1/[1 + p_1 y(\infty)/2] < 1$, a contradiction. Finally, in view of (1.1) and (1.3), we have $x'(t) + z'(t) < 0$, which implies that the limit $\lim_{t\to\infty}[x(t) + z(t)]$ exists and hence $z(\infty)$ exists. A similar argument gives $z(\infty) = 0$. This completes the proof. $\qquad\square$

Now, we consider the case when $R_1 = p_1/d_1 \leq 1$ and intend to show that $E_0 = (1,0,0)$ is globally asymptotically stable for sufficiently small q. On account of Lemma 4.1, we may assume that $x(t) \leq 1$ for all $t \geq 0$. Let $c_0 > 0$ be a constant to be determined later. We construct a Lyapunov function

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

and restrict it on the solution of (1.1)–(1.3). It is easily seen that

$$
\begin{aligned}
\frac{d}{dt} V_0(x(t), y(t), z(t)) &= c_0[-(x-1)^2/x + (p_1 - d_1)y + (p_2 - d_2)z + 2qyz] \\
&\quad - (x-1)^2 - d_1 y^2 - d_2 z^2 - (d_1 + 1)(x-1)y \\
&\quad - (d_2 + 1)(x-1)z - (d_1 + d_2)yz \\
&\leq -(c_0 + 1)(x-1)^2 + (d_1 + 1)(x-1)y - d_1 y^2 \\
&\quad + [2c_0 q - (d_1 + d_2)]yz - d_2 z^2 + [d_2 + 1 + c_0(p_2 - d_2)]z,
\end{aligned}
$$

which is nonpositive provided that

$$
q \leq \frac{d_1 + d_2 + 2\sqrt{d_2[d_1 - \frac{(d_1+1)^2}{4(c_0+1)}]}}{2c_0}, \quad c_0 = \max\left\{\frac{d_2 + 1}{d_2 - p_2}, \frac{(d_1 - 1)^2}{4d_1}\right\}. \tag{4.1}
$$

LaSalle–Lyapunov invariance principle implies that $E_0 = (1,0,0)$ is globally attractive if $R_2 < R_1 \leq 1$ and q satisfies the above inequality. Recall that E_0 is locally asymptotically stable when $R_2 < R_1 \leq 1$. We obtain globally asymptotic stability of E_0 when $q > 0$ is small.

Next, we consider the case when $R_1 > 1$ and prove globally asymptotic stability of $E_1 = (x_1, y_1, 0)$ for sufficiently small q. Given any positive initial condition, we claim that there exists $t_0 \geq 0$ such that $x(t) \leq 1$ for all $t \geq t_0$. Assume to the contrary, it follows from Lemma 4.1 that $(x(t), y(t), z(t)) \to (1,0,0)$ as $t \to \infty$. Especially, there exists $t_1 > 0$ such that $x(t) > (1 + d_1/p_1)/2$ for all $t > t_1$. By (1.2), we have $y'(t) > (p_1 - d_1)y(t)/2$ for all $t > t_1$, which implies $y(t) \to \infty$ as $t \to \infty$, a contradiction. Hence, any trajectory will enter the positively invariant set $B = \{(u_1, u_2, u_3) \in \mathbb{R}_+^3 : 0 \leq u_1 \leq 1\}$ after finite time. Without loss of generality, we may assume $x(t) \leq 1$ for all $t \geq 0$. Now, we define the Lyapunov function

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

where $c_1 > 0$ is a constant to be determined later. Taking derivative of V_1 along the solution with respect to the time gives

$$
\begin{aligned}
\frac{d}{dt} V_1(x(t), y(t), z(t)) &= c_1[-(x - x_1)^2/(x_1 x) + (p_2 x_1 - d_2)z + 2qx_1 yz - qy_1 xz] \\
&\quad - (x - x_1)^2 - d_1(y - y_1)^2 - d_2 z^2 - (d_1 + 1)(x - x_1)(y - y_1) \\
&\quad - (d_2 + 1)(x - x_1)z - (d_1 + d_2)(y - y_1)z
\end{aligned}
$$

$$\leq -(c_1/x_1 + 1)(x - 1)^2 - (d_1 + 1)(x - x_1)(y - y_1) - d_1 y^2$$
$$+ [2c_1 q x_1 - (d_1 + d_2)]yz - d_2 z^2$$
$$+ [c_1(p_2 x_1 - d_2) + (d_2 + 1)x_1 + (d_1 + d_2)y_1]z,$$

which is nonpositive provided that

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

$$c_1 = \max\left\{\frac{(d_2 + 1)x_1 + (d_1 + d_2)y_1}{d_2 - p_2 x_1}, \frac{x_1(d_1 - 1)^2}{4d_1}\right\}. \tag{4.2}$$

LaSalle–Lyapunov invariance principle implies that $E_1 = (x_1, y_1, 0)$ is globally attractive if $R_1 > 1$ and q satisfies the above inequality. It is easily seen that the above inequality implies $Q < Q_1$; namely, E_1 is also locally asymptotically stable. Hence, we obtain globally asymptotic stability of E_1 when $q > 0$ is small.

Summarizing the above arguments gives the following results.

Theorem 4.2. *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 (4.1), then $E_0 = (1, 0, 0)$ is globally asymptotically stable. If $R_1 > 1$ and q satisfies (4.2), then $E_1 = (x_1, y_1, 0)$ is globally asymptotically stable.*

5. A Special Case: Competition-Free and Cooperative Predation

In this section, we consider a special case when $p_1 = p_2 = p$, $d_1 = d_2 = d$ and $y(0) = z(0)$. Biologically, this assumption means that the two predators can be regarded as the same. Mathematically, we can prove by uniqueness of solution that $y(t) = z(t)$ for all $t \geq 0$. Thus, we can reduce the three-dimensional system (1.1)–(1.3) to a planar system

$$x'(t) = 1 - x(t) - 2px(t)y(t) - 2qx(t)[y(t)]^2, \tag{5.1}$$

$$y'(t) = px(t)y(t) + qx(t)[y(t)]^2 - dy(t). \tag{5.2}$$

Note that the growth rate for the prey is linear, while in Ref. 10 a similar model with logistic growth in prey was considered, and in Ref. 11 the growth rate for the prey was a cubic function with Allee effect. The main focus of this section is to determine the direction of Hopf bifurcation and stability of periodic solutions bifurcated from a Hopf bifurcation point. Global dynamics of the above planar system will also be investigated.

A positive equilibrium $E = (x, y)$ of the above system satisfies the equations $1 - x - 2dy = 0$ and $px + qxy - d = 0$. Denote $R = p/d$ and $Q = q/d^2$. By eliminating y, we have

$$Qx^2 - (2R + Q)x + 2 = 0. \tag{5.3}$$

If $R < 1$, then there exist two positive equilibria $E_\pm = (x_\pm, y_\pm)$ if and only if $(2R + Q)^2 > 8Q$ and $2R + Q > 4$; namely, $Q > Q_+$, where

$$Q_+ = 2(1 + \sqrt{1 - R})^2 \qquad (5.4)$$

and

$$x_\pm = \frac{4}{2R + Q \pm \sqrt{(2R + Q)^2 - 8Q}}. \qquad (5.5)$$

If $R > 1$, then there exists a unique positive equilibrium E_+. The Jacobi matrix of the system linearized at a positive equilibrium $E = (x, y)$ is given as

$$J = \begin{pmatrix} -1/x & -2px - 4qxy \\ dy/x & qxy \end{pmatrix}. \qquad (5.6)$$

The determinant of J is

$$\det(J) = -qy + dy(2p + 4qy) = \frac{d^2 y}{x}(2 - Qx^2).$$

Since $x_- x_+ = 2/Q$, we have $Qx_-^2 > 2 > Qx_+^2$. Thus, E_- is always unstable whenever it exists. If $R < 1$ and $Q > Q_+$, we further have $x_+ < \sqrt{2/Q} < \sqrt{2/Q_+} = 1/(1 + \sqrt{1 - R})$. Note that the trace of J is $qxy - 1/x = d - px - 1/x = -(px^2 - dx + 1)/x$. Hence, Hopf bifurcation occurs when $dR - ds + s^2 = 0$ has a root in (s_c, ∞), where

$$s_c = \begin{cases} 1 + \sqrt{1 - R}, & R < 1, \\ R, & R > 1. \end{cases} \qquad (5.7)$$

If $R > 1$, then Hopf bifurcation occurs if and only if $R < d/4$, and in this case, there are two Hopf bifurcation points:

$$Q_{h,\pm} = \frac{2s_{h,\pm}(s_{h,\pm} - R)}{s_{h,\pm} - 1} \quad \text{with } s_{h,\pm} = \frac{d \pm \sqrt{d^2 - 4dR}}{2}. \qquad (5.8)$$

If $R < 1$ and $R \geq d/4$, then there does not exist any Hopf bifurcation. If $R < 1$ and $R < d/4$, then we have one Hopf bifurcation point $Q_{h,+}$ when $R < d(d-2)/(d-1)^2$, two Hopf bifurcation points $Q_{h,\pm}$ when $R > d(d-2)/(d-1)^2$ and $d > 3$, and no Hopf bifurcation point when $R > d(d-2)/(d-1)^2$ and $d < 3$.

To analyze the direction of Hopf bifurcation and stability of periodic solutions bifurcated from the Hopf bifurcation point, we consider a perturbation about the positive equilibrium $E_+ = (x_+, y_+)$ and obtain an equivalent system

$$\begin{aligned} u' &= 1 - (x_+ + u) - 2p(x_+ + u)(y_+ + v) - 2q(x_+ + u)(y_+ + v)^2 \\ &= -(1 + 2py_+ + 2qy_+^2)u - (2px_+ + 4qx_+y_+)v - 2qx_+v^2 \\ &\quad - (2p + 4qy_+)uv - 2quv^2, \end{aligned}$$

$$v' = p(x_+ + u)(y_+ + v) + q(x_+ + u)(y_+ + v)^2 - d(y_+ + v)$$
$$= (py_+ + qy_+^2)u + (px_+ + 2qx_+y_+ - d)v + qx_+v^2 + (p + 2qy_+)uv + quv^2.$$

In matrix form, we have

$$\begin{pmatrix} u' \\ v' \end{pmatrix} = \begin{pmatrix} -1/x_+ & -2px_+ - 4qx_+y_+ \\ dy_+/x_+ & qx_+y_+ \end{pmatrix} \begin{pmatrix} u \\ v \end{pmatrix}$$
$$+ \begin{pmatrix} -2 \\ 1 \end{pmatrix} [qx_+v^2 + (p + 2qy_+)uv + quv^2]. \qquad (5.9)$$

At the Hopf bifurcation point, we have $2dy_+ = 1 - x_+$, $px_+ + qx_+y_+ - d = 0$, $qx_+y_+ = 1/x_+$ and $\omega^2 = \det(J) = d^2y_+(2 - Qx_+^2)/x_+ = (2d^2y_+ - 1)/x_+$, where $\pm i\omega$ are a pair of purely imaginary characteristic roots for the Jacobi matrix. Let $s = 1/x_+$. Then we have

$$\omega^2 = ds - d - s, \quad p + 2qy_+ = ds + s^2, \quad q = \frac{2ds^3}{s-1}.$$

The Jacobi matrix can be written as

$$J = \begin{pmatrix} -s & -2s - 2d \\ s/2 - 1/2 & s \end{pmatrix} = \begin{pmatrix} 2i\omega - 2s & -2i\omega - 2s \\ s - 1 & s - 1 \end{pmatrix}$$
$$\times \begin{pmatrix} i\omega & 0 \\ 0 & -i\omega \end{pmatrix} \begin{pmatrix} 2i\omega - 2s & -2i\omega - 2s \\ s - 1 & s - 1 \end{pmatrix}^{-1}.$$

Set

$$\begin{pmatrix} u \\ v \end{pmatrix} = \begin{pmatrix} 2i\omega - 2s & -2i\omega - 2s \\ s - 1 & s - 1 \end{pmatrix} \begin{pmatrix} \alpha \\ \bar{\alpha} \end{pmatrix} = \begin{pmatrix} (2i\omega - 2s)\alpha - (2i\omega + 2s)\bar{\alpha} \\ (s - 1)(\alpha + \bar{\alpha}) \end{pmatrix}.$$

It follows that

$$\begin{pmatrix} \alpha' \\ \bar{\alpha}' \end{pmatrix} - \begin{pmatrix} i\omega & 0 \\ 0 & -i\omega \end{pmatrix} \begin{pmatrix} \alpha \\ \bar{\alpha} \end{pmatrix}$$
$$= \begin{pmatrix} 2i\omega - 2s & -2i\omega - 2s \\ s - 1 & s - 1 \end{pmatrix}^{-1} \begin{pmatrix} -2 \\ 1 \end{pmatrix} [qx_+v^2 + (p + 2qy_+)uv + quv^2]$$
$$= \frac{1}{2\omega(s-1)} \begin{pmatrix} \omega - i \\ \omega + i \end{pmatrix} \left[\frac{2ds^2v^2}{s-1} + (ds + s^2)uv + \frac{2ds^3uv^2}{s-1} \right].$$

A simple calculation gives $v^2 = (s-1)^2(\alpha^2 + 2\alpha\bar{\alpha} + \bar{\alpha}^2)$ and

$$\frac{uv}{2(s-1)} = (i\omega - s)\alpha^2 - 2s\alpha\bar{\alpha} - (i\omega + s)\bar{\alpha}^2, \quad \frac{uv^2}{2(s-1)^2} = (i\omega - 3s)\alpha^2\bar{\alpha} + \cdots.$$

Consequently,

$$\alpha' - i\omega\alpha = \frac{\omega - i}{\omega}\left[\frac{ds^2v^2}{(s-1)^2} + \frac{(ds+s^2)uv}{2(s-1)} + \frac{ds^3uv^2}{(s-1)^2}\right]$$

$$= \frac{s(\omega - i)}{\omega}[ds(\alpha^2 + 2\alpha\bar\alpha) + (d+s)(i\omega - s)\alpha^2$$

$$- 2s(d+s)\alpha\bar\alpha + 2ds^2(i\omega - 3s)\alpha^2\bar\alpha + \cdots]$$

$$= \frac{g_{20}}{2}\alpha^2 + g_{11}\alpha\bar\alpha + \frac{g_{02}}{2}\bar\alpha^2 + \frac{g_{21}}{2}\alpha^2\bar\alpha + \cdots,$$

where

$$g_{20} = \frac{2s}{\omega}[\omega(d+s-s^2) + (s^2 + \omega^2 d + \omega^2 s)i], \quad g_{11} = -\frac{2s^3(\omega - i)}{\omega},$$

$$g_{21} = \frac{4ds^3}{\omega}[\omega - 3s\omega + (3s + \omega^2)i].$$

Now, we calculate the first Lyapunov coefficient (see (3.20) of Ref. 23) as

$$l_1 = \frac{1}{2\omega^2}\text{Re}(ig_{11}g_{20} + \omega g_{21}) = \frac{2s^3(s-1)}{\omega^3}[s^2 + s(s+2)d - (2s-1)d^2]$$

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

There are three cases to be considered.

(1) If $d < 3$ and $R < d(d-2)/(d-1)^2$, then there exists one Hopf bifurcation point. Since $d(d-2)/(d-1)^2 < d/(d+1)$, we have $d - (d+1)R > 0$ and $l_1 > 0$. Hence, the Hopf bifurcation is subcritical.

(2) If $d > 3$ and $d(d-2)/(d-1)^2 < R < d/4$, then there exist two Hopf bifurcation points. Since $d(d-2)/(d-1)^2 > d/(d+1)$, we have $d - (d+1)R < 0$ and $l_1 < 0$. Hence, the Hopf bifurcation is supercritical.

(3) If $d > 3$ and $R < d(d-2)/(d-1)^2$, then there exists one Hopf bifurcation point. Assume $l_1 > 0$, then $d - (d+1)R > s(d-3)$, which, together with $s > d/2$, implies that $R < d(5-d)/[2(d+1)]$ and

$$\left[\frac{d-(d+1)R}{d-3}\right]^2 - d\left[\frac{d-(d+1)R}{d-3}\right] + dR > 0,$$

which is equivalent to

$$R < \frac{d(4-d)}{5d - d^2 - 2 + (d-3)\sqrt{d(d-3)}}.$$

Thus, the Hopf bifurcation is subcritical if $R < d(4-d)/[5d - d^2 - 2 + (d-3)\sqrt{d(d-3)}]$ and supercritical if $R > d(4-d)/[5d - d^2 - 2 + (d-3)\sqrt{d(d-3)}]$.

To sum up, we have the following results, with illustration in Fig. 3.

Theorem 5.1. *Let $Q_{h,\pm}$ be defined as in (5.8). If $d < 3$, then there exists no Hopf bifurcation point if $R > d(d-2)/(d-1)^2$, and one subcritical Hopf bifurcation point*
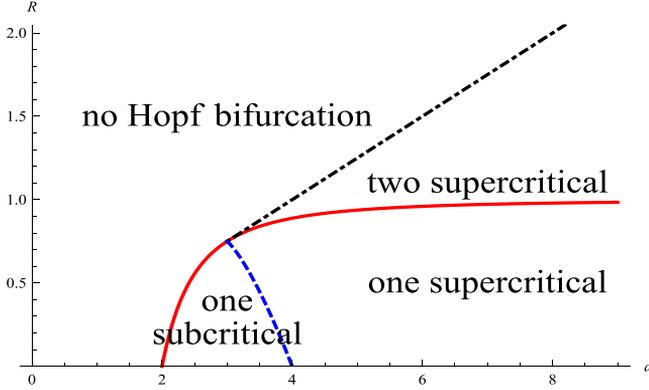
Fig. 3.   (Color online) Existence and property of Hopf bifurcation points in the (d, R) parameter space. The red solid, blue dashed and black dot–dashed curves are $R = d(d-2)/(d-1)^2$, $R = d(4-d)/[5d - d^2 - 2 + (d-3)\sqrt{d(d-3)}]$, and $R = d/4$, respectively.

$Q_{h,+}$ if $R < d(d-2)/(d-1)^2$. If $d > 3$, then there exists no Hopf bifurcation point if $R > d/4$, two supercritical Hopf bifurcation points $Q_{h,\pm}$ if $d(d-2)/(d-1)^2 < R < d/4$, one supercritical Hopf bifurcation point $Q_{h,+}$ if $d(4-d)/[5d - d^2 - 2 + (d-3)\sqrt{d(d-3)}] < R < d(d-2)/(d-1)^2$, and one subcritical Hopf bifurcation point $Q_{h,+}$ if $R < d(4-d)/[5d - d^2 - 2 + (d-3)\sqrt{d(d-3)}]$.

The local analysis of equilibria and Hopf bifurcation is summarized in the following theorem and illustrated in Fig. 4.

Theorem 5.2. *Let Q_+ and $Q_{h,\pm}$ be defined as in (5.4) and (5.8), respectively. Denote $E_0 = (1, 0)$ and $E_\pm = (x_\pm, y_\pm)$ with $x_\pm$ given in (5.5) and $y_\pm = (1 - x_\pm)/(2d)$. We divide the first quadrant of (d, R) plane into two regions which contain six subregions.*

(I) *$R \leq 1$. In this region, E_0 is locally asymptotically stable; $E_\pm$ exist if and only if $Q > Q_+$; E_- is always unstable whenever it exists. To describe the locally asymptotic stability of E_+ and the property of Hopf bifurcation, we need to divide this region into four subregions.*

(I.1) *$R > d(d-2)/(d-1)^2$ with $d \leq 3$ or $R > d/4$ with $3 \leq d < 4$. In this subregion, E_+ is always locally asymptotically stable whenever it exists.*

(I.2) *$R < d(d-2)/(d-1)^2$ with $2 < d \leq 3$ or $R < d(4-d)/[5d - d^2 - 2 + (d-3)\sqrt{d(d-3)}]$ with $3 \leq d < 4$. In this subregion, E_+ is locally asymptotically stable when $Q > Q_{h,+}$ and unstable when $Q_+ < Q < Q_{h,+}$. Subcritical Hopf bifurcation occurs at $Q = Q_{h,+}$; namely, unstable periodic solutions appear to right of $Q_{h,+}$.*

(I.3) *$d(4-d)/[5d - d^2 - 2 + (d-3)\sqrt{d(d-3)}] < R < d(d-2)/(d-1)^2$ with $d > 3$. In this subregion, E_+ is locally asymptotically stable when $Q > Q_{h,+}$ and*

(a) Case (I.1)　　　　　(b) Case (I.2)　　　　　(c) Case (I.3)

(d) Case (I.4)　　　　　(e) Case (II.1)　　　　　(f) Case (II.2)
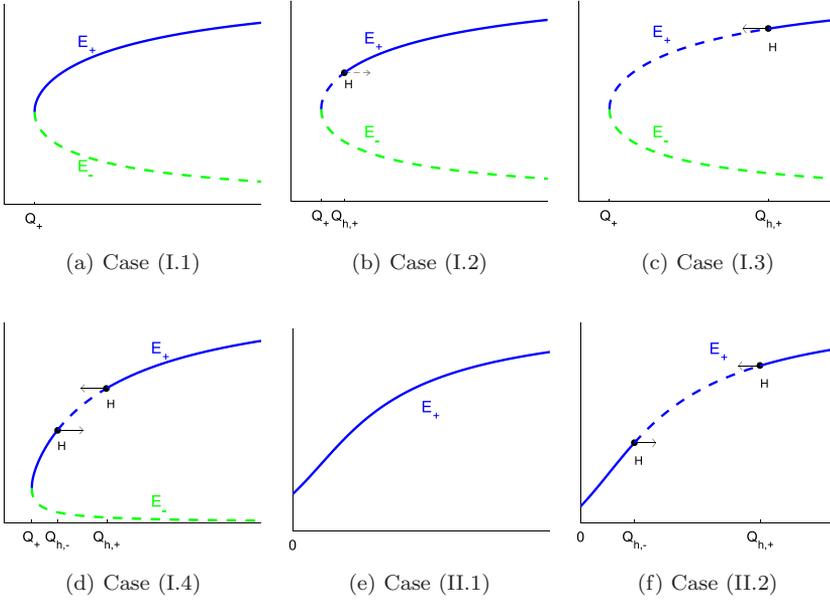
Fig. 4.　(Color online) Existence and stability conditions of equilibria E_+ (blue), and E_- (green), with projection on $y-Q$ plane. A solid curve indicates that the corresponding equilibrium is locally asymptotically stable, and a dashed curve indicates that the corresponding equilibrium is unstable. A dark dot with an arrow and a text label "H" indicates the location and direction of a Hopf bifurcation, where a solid arrow means a supercritical Hopf bifurcation (i.e., periodic solutions are locally asymptotically stable), and a dashed arrow means a subcritical Hopf bifurcation (i.e., periodic solutions are unstable).

　　　　unstable when $Q_+ < Q < Q_{h,+}$. Supercritical Hopf bifurcation occurs at $Q = Q_{h,+}$; namely, stable periodic solutions appear to left of $Q_{h,+}$.

(I.4)　*$d(d-2)/(d-1)^2 < R < 1$ with $d > 3$. In this subregion, E_+ is locally asymptotically stable when $Q \in (Q_+, Q_{h,-}) \cup (Q_{h,+}, \infty)$ and unstable when $Q \in (Q_{h,-}, Q_{h,+})$. Supercritical Hopf bifurcations occur at $Q = Q_{h,\pm}$; namely, stable periodic solutions appear to left of $Q_{h,+}$ and to the right of $Q_{h,-}$.*

(II)　*$R > 1$. In this region, E_0 is always unstable; there exists a unique positive equilibrium E_+. To describe the locally asymptotic stability of E_+ and the property of Hopf bifurcation, we need to divide this region into two subregions.*

(II.1)　*$R > d/4$. In this subregion, E_+ is always locally asymptotically stable.*

(II.2)　*$R < d/4$. In this subregion, E_+ is locally asymptotically stable when $Q \in (0, Q_{h,-}) \cup (Q_{h,+}, \infty)$ and unstable when $Q \in (Q_{h,-}, Q_{h,+})$. Supercritical Hopf bifurcations occur at $Q = Q_{h,\pm}$; namely, stable periodic solutions appear to left of $Q_{h,+}$ and to the right of $Q_{h,-}$.*

We then state the following result on dissipativity and uniform persistence.

Lemma 5.3. *The solution of the system* (5.1)–(5.2) *with positive initial conditions are positive. Furthermore, there exist positive constants $M > 0$ and $\delta > 0$, independent of initial conditions, such that*

$$\limsup_{t\to\infty}[x(t) + 2y(t)] \leq M, \quad \liminf_{t\to\infty} x(t) \geq \delta.$$

If $R > 1$, then there exists $\varepsilon > 0$, independent of initial conditions, such that

$$\liminf_{t\to\infty} y(t) \geq \varepsilon.$$

Proof. The positiveness of solutions is trivial. Since $x'(t)+2y'(t) = 1-x(t)-2dy(t)$, we obtain from comparison principle that $\limsup_{t\to\infty}[x(t) + 2y(t)] \leq M$, where $M = 1/\min\{1, d\} > 0$. Especially, there exists $t_1 > 0$ such that $x(t)+2y(t) < M+1$ for all $t > t_1$. Consequently, it follows from (5.1) that $x'(t) \geq 1-[1+p(M+1)+q(M+1)^2]x(t)$ for $t > t_1$. Comparison principle implies that $\liminf_{t\to\infty} x(t) \geq \delta$, where $\delta = 1/[1+p(M+1)+q(M+1)^2]$. If further, $R > 1$, we denote $X = (0,\infty) \times [0,\infty)$ with interior $X_0 = (0,\infty) \times (0,\infty)$ and boundary $\partial X = (0,\infty) \times \{0\}$. It can be proved by contradiction that the stable set of $E_0 = (1,0)$ does not intersect X_0; otherwise, there exists $t_2 > 0$ such that $x(t) > (1 + d/p)/2$ for all $t > t_2$, and consequently, $y'(t) > [(p - d)/2]y(t)$, but $y(t) \to 0$ as $t \to \infty$, a contradiction. It then follows from the persistence theorem (see Theorem 3.1 in Ref. 24) that $\liminf_{t\to\infty} y(t) \geq \varepsilon$ for some $\varepsilon > 0$ independent of initial conditions. This completes the proof. □

Before presenting the global stability of equilibria for the planar system (5.1)–(5.2), we use Bendixson–Dulac criterion to find sufficient conditions for nonexistence of limit cycles. Let $f = 1 - x - pxy - qxy^2$ and $g = pxy + qxy^2 - dy$. Note that the divergence of $(f, g)^T/(xy^2)$ is

$$-\frac{1}{x^2y^2} - \frac{px - d}{xy^2} = -\frac{px^2 - dx + 1}{x^2y^2} < 0$$

when $d^2 < 4p$. Thus, there exists no periodic solution when $R > d/4$. Also the divergence of $(f, g)^T/y^2$ is

$$-\frac{1 + py + qy^2}{y^2} - \frac{px - d}{y^2} < 0$$

when $d < 1$. Thus, there exists no periodic solution when $d < 1$.

Theorem 5.4. *Consider the system* (5.1)–(5.2) *with positive initial conditions. The equilibrium $E_0 = (1,0)$ is globally asymptotically stable if $R \leq 1$ and $q < 2(d + \sqrt{d - p})^2$. On the other hand, if $R > 1$, then the unique positive equilibrium $E_+ = (x_+, y_+)$ is globally asymptotically stable when $d < 4R$ or $q < 2/(3x_+^2)$.*

Proof. If $R \leq 1$ and $q < 2(d + \sqrt{d - p})^2$, then E_0 is the unique equilibrium of system (5.1)–(5.2). We introduce a new variable $s = 1/x$ and consider an equivalent

planar system

$$s' = s(-s + 1 + 2py + 2qy^2),$$

$$y' = (y/s)(p + qy - ds).$$

The first quadrant of (y, s) plane can be divided into three regions

$$X_1 := \{(y, s) \in \mathbb{R}_+^2 : s \leq (p + qy)/d\},$$

$$X_2 := \{(y, s) \in \mathbb{R}_+^2 : (p + qy)/d \leq s \leq 1 + 2py + 2qy^2\},$$

$$X_3 := \{(y, s) \in \mathbb{R}_+^2 : s \geq 1 + 2py + 2qy^2\}.$$

Note that $y' \geq 0$ and $s' \geq 0$ in X_1; $y' \leq 0$ and $s' \geq 0$ in X_2; and $y' \leq 0$ and $s' \leq 0$ in X_3. It is readily seen that the regions $X_2 \cup X_3$ and X_3 are positively invariant. Since s and y are ultimately bounded, all trajectories must enter X_3 after finite time and converge to the unique equilibrium E_0 as $t \to \infty$. Thus, E_0 is globally attractive, which together with locally asymptotic stability of E_0 implies that E_0 is globally asymptotically stable.

Next, we consider the case $R > 1$. If $d < 4R$, then the argument preceding this theorem shows that system (5.1)–(5.2) does not possess any periodic solution. Lemma 5.3 implies that this system is uniformly persistent. Thus, it follows from Poincaré–Bendixson theorem that the unique positive equilibrium E_+ is globally asymptotically stable.

Finally, we assume $R > 1$ and $d \geq 4R$. By a similar argument as in the proof of Lemma 4.1, we can show that $x(t) < 1$ for all sufficiently large t. Without loss of generality, we assume $x(t) < 1$ for all $t \geq 0$. Construct a Lyapunov function

$$V(x, y, z) = c_2[x - x_+ \ln x + 2(y - y_+ \ln y)] + (x + 2y - x_+ - 2y_+)^2/2,$$

where $c_2 > 0$ is a constant to be determined later. Taking derivative along the solution gives

$$\frac{d}{dt}V(x(t), y(t), z(t)) = c_2[-(x - x_+)^2/(xx_+) + 2qx_+(y - y_+)^2$$

$$- 2qy_+(x - x_+)(y - y_+)] - (x - x_+)^2$$

$$- 2(1 + d)(x - x_+)(y - y_+) - 4d(y - y_+)^2$$

$$\leq -(1 + c_2/x_+)(x - x_+)^2 - 2(1 + d + c_2qx_+)(x - x_+)(y - y_+)$$

$$- (4d - 2c_2qx_+)(y - y_+)^2,$$

which is nonpositive provided

$$4d - 2c_2qx_+ \geq \frac{(1 + d + c_2qx_+)^2}{1 + c_2/x_+}.$$

Choose $c_2 = 3x_+(d-1)/4$. Then the above inequality is satisfied when $q \leq 2/(3x_+^2)$. Lasalle–Lyapunov invariance principle implies that E_+ is globally asymptotically stable. The proof is completed. $\square$

6. Discussion

In both models (with or without competition), we observe that cooperative pre-dation (mutualism) may increase the survival probability of predators in a severe environment where non-cooperative predation is not sufficient to battle with the natural death. Competitive exclusion principle may not hold when cooperation plays a dominant role. Moreover, cooperative predation (mutualism) may destabi-lize 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.

In the parameter region where only one Hopf bifurcation point exists (cf. Figs. 2(b), 2(e), 4(b) and 4(c)), the global Hopf branch should be unbounded. Since the solution is ultimately bounded, either the period or the bifurcation parameter is unbounded. Numerical simulation seems to suggest the former; namely, a hete-roclinic cycle is connected to the Hopf point by the global Hopf branch. When two Hopf bifurcation points exist (cf. Figs. 2(c), 2(f), 2(h), 4(d) and 4(f)), it is possi-ble that the global Hopf branch is bounded and connects these two Hopf points. However, numerical exploration indicates another possibility that each Hopf point is connected to a heteroclinic cycle; see Fig. 5. It is conjectured that global Hopf branches for system (5.1)–(5.2) are bounded in region II.2 (Fig. 4(f)) and unbounded in region I.4 (Fig. 4(d)).

Since the model in Ref. 17 is more general than our model (1.1)–(1.3), it is worthwhile to compare their main results with ours. Even though the linear growth rate of prey in our model differs from the logistic growth in their model, the persis-tence results and mathematical arguments in Ref. 17 can be easily extended to our

(a) Bounded hopf branch.   (b) Unbounded hopf branches.
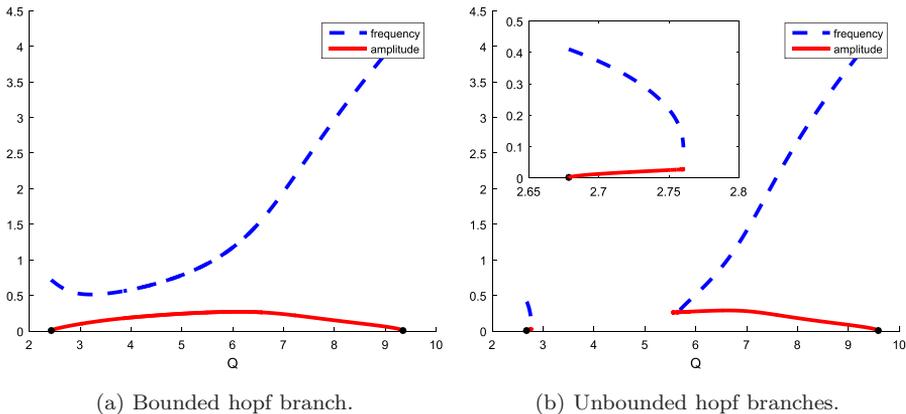
Fig. 5.   (Color online) Global Hopf branches for system (5.1)–(5.2). The red solid and blue dashed curves give the amplitudes ($\max y(t) - \min y(t)$) and frequencies of periodic solutions. The param-eters are chosen as $d = 6$ and $R = 1.02$ in the left panel, and $d = 6$ and $R = 0.98$ in the right panel. The Hopf points (black dots) are $Q_{h,-} = 2.43$ and $Q_{h,+} = 9.34$ (left); and $Q_{h,-} = 2.68$ and $Q_{h,+} = 9.58$ (right).

model. The facultative case considered in Sec. 4 of Ref. 17 is equivalent to the case $R_1 > R_2 > 1$, and their main result was uniform persistence of the system under the condition $Q > Q_1$. The facultative-obligate case considered in Sec. 5 of Ref. 17 is equivalent to the case $R_1 > 1 > R_2$ and their main result was persistence of the system under the condition $Q > Q_1$. For both cases, our study complimented these persistence results, in the sense that, we provided stability analysis of all equilibria and conducted local Hopf bifurcation analysis. The obligate case considered in Sec. 6 of Ref. 17 is equivalent to the case $1 > R_1 > R_2$ and it was remarked that "the criteria for asymptotic stability" of the positive equilibrium were "complicated". In this paper, thanks to the specific forms of predation functions, we were able to provide quantitative criteria for asymptotic stability of all equilibria. For our second model with only one predator species, we further calculated the direction of Hopf bifurcation and derived explicit necessary and sufficient conditions for the stability of periodic solutions bifurcated from Hopf bifurcation points.

Note that periodic solution does not exist when mutualism (cooperative predation) is weak (due to globally asymptotic stability of the equilibrium). Based on numerical simulations, we conjecture that periodic solution cannot exist when the cooperative predation is sufficiently strong. Had this been justified, any unbounded Hopf branch would be connected by a heteroclinic cycle. For the three-dimension system (1.1)–(1.3), it is conjectured that the positive equilibrium E_+ is globally asymptotically stable when E_- does not exist (i.e., $R_1 > 1$) and Q is sufficiently large.

Finally, we mention that the model (1.1)–(1.3) is a simplified version of the general system when energy loss during predation is taken into consideration:

$$x'(t) = b - d_0 x(t) - p_1 x(t)y(t) - p_2 x(t)z(t) - q_0 x(t)y(t)z(t),$$
$$y'(t) = \alpha_1 p_1 x(t)y(t) + q_1 x(t)y(t)z(t) - d_1 y(t),$$
$$z'(t) = \alpha_2 p_2 x(t)z(t) + q_2 x(t)y(t)z(t) - d_2 z(t),$$

where $\alpha_1, \alpha_2 \in (0, 1]$ account for the transmission rate of energy during predation, and $q_1 + q_2 \leq q_0$. By introducing the dimensionless scale $\tilde{t} = d_0 t$, $x = \tilde{x}b/d_0$, $y = \tilde{y}\alpha_1 b/d_0$ and $z = \tilde{z}\alpha_2 b/d_0$, we may assume without loss of generality that $b = d_0 = \alpha_1 = \alpha_2 = 1$. However, there are still three parameters q_0, q_1, q_2 to characterize the cooperative predation. In our analysis, we have assumed $q_1 = q_2 = q_0/2 = q$ so that only one parameter of cooperative predation is left. Biologically, this assumption indicates that the energy loss during predation is negligible. A more detailed analysis is needed if the energy transmission rates (in terms of q_1/q_0 and q_2/q_0) are taken values other than $1/2$. We leave this problem for further investigation. Another generalization is to replace the linear growth function of prey by a more general function to account for the logistic growth[10,17] or Allee effect.[11] It is expected that the model dynamics would be more complicated and we will consider this problem in a forthcoming paper.

Acknowledgment

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