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HOPF BIFURCATION ANALYSIS FOR A PREDATOR-PREY SYSTEM OF HOLLING AND LESLIE TYPE

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Abstract. In this paper we study the Hopf bifurcation for the Holling-Tanner model, a well-known predator-prey model in mathematical ecology. We show that for some parameter ranges, the Hopf bifurcation is subcritical and thus the system may have multiple limit cycles.

1. Introduction

In this paper we shall study the possibilities of multiple limit cycles for the following Holling-Tanner model [4], [5]:

$$\begin{aligned} &\frac{dx}{dt} = rx\left(1-\frac{x}{K}\right) - \frac{mx}{A+x}\,y, \\ &\frac{dy}{dt} = sy\left(1-\frac{hy}{x}\right), \\ &x(0)>0, \quad y(0)>0, \end{aligned} \tag{1.1}$$

where $r, m, s, h, A, K > 0$.

The predator-prey system (1.1) assumes that the prey grows logistically with intrinsic growth rate r and carrying capacity K in the absence of predation. The predator consumes the prey according to Holling type-II functional response and grows logistically with intrinsic rate s and carrying capacity proportional to the population size of the prey. The Holling-Tanner model is an important and interesting model of predator-prey system in both biological and mathematical sense [7], [9]. In [2] we studied the global asymptotic stability when the interior equilibrium (x^*, y^*) is locally asymptotically stable.

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Also in [3] we proved the uniqueness of limit cycles when (x^*, y^*) is an unstable spiral. From these studies we see the possibility that (x^*, y^*) may not be globally asymptotically stable when it is locally asymptotically stable. While in [8] the extensive numerical studies on the system (1.1) showed the equilibrium (x^*, y^*) is either globally asymptotically stable or gives rise to a globally asymptotically stable limit cycle, there can also exist a range of parameters wherein multiple stable states occur. These stable states consist of a focus and a limit cycle, separated from each other in the phase phane by an unstable limit cycle. In this paper we shall apply the Andronov-Hopf Bifurcation Theorem [6] to show that for some parameter range the Hopf bifurcation is subcritical, i.e., there exists a small-amplitude repelling periodic orbit enclosing a stable equilibrium and hence there are multiple limit cycles.

2. Preliminary Results

In this section we summarize some basic results in [2]. First we write the system (1.1) in a nondimensional form. Let

$$\tilde{t} = rt, \quad \tilde{x}(\tilde{t}) = \frac{x(t)}{K}, \quad \tilde{y}(\tilde{t}) = \frac{my(t)}{rK},$$

$$\delta = s/r, \ \beta = \frac{sh}{m}, \quad a = A/K.$$

Then (1.1) takes the form

$$\begin{aligned} \frac{dx}{dt} &= x(1-x) - \frac{x}{a+x}y, \\ \frac{dy}{dt} &= y\left(\delta - \beta\frac{y}{x}\right), \\ x(0) &> 0, \quad y(0) > 0. \end{aligned} \tag{2.1}$$

Obviously from (2.1), there exists a unique positive equilibrium $E^* = (x^*, y^*)$. Let

$$P(x) = 2x^2 + (a + \delta - 1)x + a\delta. \tag{2.2}$$

Lemma 2.1. ([2]) *The equilibrium $E^* = (x^*, y^*)$ of (2.1) is locally asymptotically stable if $P(x^*) > 0$ and E^* is an unstable focus if $P(x^*) < 0$.*

We note from (2.2) that $P(x) \geq 0$ for all $x > 0$ if and only if

$$a + \delta \geq 1 \tag{2.3}$$

or

$$a + \delta < 1 \quad \text{and} \quad (1 - a - \delta)^2 - 8a\delta \le 0. \tag{2.4}$$

If

$$a + \delta < 1 \quad \text{and} \quad (1 - a - \delta)^2 - 8a\delta > 0, \tag{2.5}$$

then $P(x) = 2(x - \alpha_1)(x - \alpha_2)$, where

$$\alpha_1 = \frac{1}{4}\left[1 - a - \delta - \sqrt{(1 - a - \delta)^2 - 8a\delta}\right],$$
$$\alpha_2 = \frac{1}{4}\left[1 - a - \delta + \sqrt{(1 - a - \delta)^2 - 8a\delta}\right],$$
$$0 < \alpha_1 < \alpha_2 < 1.$$

For the case (2.5), the local asymptotic stability of E^* can be reformulated as

$$\alpha_2 < x^* < 1 \tag{2.6}$$

or

$$0 < x^* < \alpha_1 \tag{2.7}$$

and the instability condition for E^* is

$$\alpha_1 < x^* < \alpha_2. \tag{2.8}$$

For fixed a, $\delta > 0$ satisfying (2.5), the conditions (2.6), (2.7), and (2.8) can be expressed explicitly in terms of the parameter β in the following:

$$\beta > \beta_2, \tag{2.6$'$}$$

$$0 < \beta < \beta_1, \tag{2.7$'$}$$

$$\beta_1 < \beta < \beta_2, \tag{2.8$'$}$$

where

$$\beta_i = \frac{\delta\alpha_i}{(1 - \alpha_i)(a + \alpha_i)}, \quad i = 1, 2. \tag{2.9}$$

We summarize the stability results from [2].

Theorem 2.2. ([2])

(i) *Let* (2.3) *or* (2.4) *hold. Then the equilibrium* $E^* = (x^*, y^*)$ *is globally asymptotically stable in the interior of the first quadrant.*

(ii) *Let* (2.5) *and* (2.6) *hold. Then the conclusion of* (*i*) *holds.*

(iii) *Let* (2.5) *hold. For* $\beta > 0$ *sufficiently small,* $x^* = x^*(\beta)$ *is sufficiently close to zero and* (2.7) *holds. Furthermore, the conclusion of* (*i*) *holds for* $\beta > 0$ *sufficiently small.*

(iv) *Let* (2.8) *hold. Then there exists a limit cycle for* (2.1).

We note that in Theorem 2.2 (iv) the existence of a limit cycle follows directly from the Poincaré-Bendixson Theorem. The system (2.1) is persistent [1]. In fact we can construct a compact positively invariant region [5]. So the Poincaré-Bendixson Theorem is applicable.

Let

$$u = y\ell(x), \quad \ell(x) = \left(\frac{1-x}{x}\right)^{\delta}. \tag{2.10}$$

Then we reduce (2.1) to the following system:

$$\begin{aligned} \frac{dx}{dt} &= x(1-x) - \frac{x}{a+x}\,\frac{u}{\ell(x)}, \\ \frac{du}{dt} &= \frac{u^2\beta}{x\ell(x)(1-x)(a+x)}\left(x + \frac{a}{x^*}\right), (x - x^*), \\ & x(0) > 0, \quad u(0) > 0. \end{aligned} \tag{2.11}$$

Consider the prey-isocline of (2.11):

$$u = h(x) = (1-x)(a+x)\ell(x). \tag{2.12}$$

From [2], if (2.5) holds then it follows that

$$h^{'}(x) = -\frac{\ell(x)}{x}P(x) = -\frac{2\ell(x)}{x}(x-\alpha_1)(x-\alpha_2). \tag{2.13}$$

Thus the prey-isocline $u = h(x)$ has two humps, namely, a local maximum at $x = \alpha_2$ and a local minimum at $x = \alpha_1$. Obviously from (2.12), (2.10), (2.13), we have $h(1) = 0$, $\lim\limits_{x\to 0^+} h(x) = +\infty$ and $h^{'}(x) > 0$ for $\alpha_1 < x < \alpha_2$ and $h^{'}(x) < 0$ for $x \in (0, \alpha_1) \cup (\alpha_2, 1)$. Now we rewrite (2.11) in the following form

$$\begin{aligned} \frac{dx}{dt} &= \varphi(x)\,[h(x) - u] = F(x,u), \\ \frac{du}{dt} &= \psi(x)u^2 = G(x,u), \\ & x(0) > 0, \quad u(0) > 0, \end{aligned} \tag{2.14}$$

where

$$\varphi(x) = \frac{x}{a+x}\,\frac{1}{\ell(x)},$$

$$\psi(x) = \frac{\beta}{xh(x)}(x - x^*)\left(x + \frac{a}{x^*}\right)$$

and $h(x), \ell(x)$ are defined in (2.12), (2.10) respectively.

3. Multiple Limit Cycles

In Section 1 we mentioned that in [8] the numerical studies indicate that for system (1.1) there exists a range of parameters wherein multiple stable states occur. These stable states consist of a stable focus and a stable limit cycle, separated from each other in the phase plane by an unstable limit cycle. In this section we shall justify the phenomena by means of the Andronov-Hopf Bifurcation Theorem.

For the sake of completeness in the following, we state the Andronov-Hopf Bifurcation Theorem [6, p. 224].

Consider a one-parameter family of differential equations

$$(*) \qquad \dot{x} = f(x,\mu) = f_\mu(x)$$

with $x \in \mathbb{R}^2$ satisfying the following assumptions:

(I) The origin is a fixed point for all values μ near $0 : f(0,\mu) = 0$.

(II) The eigenvalues of $Df_\mu(0)$ are $\alpha(\mu) \pm i\beta(\mu)$ with $\alpha(0) = 0$, $\beta(0) = \beta_0 \neq 0$ and $\alpha^{'}(0) \neq 0$, so that the eigenvalues are crossing the imaginary axis.

Suppose there is a change of basis on $\mathbb{R}^2$ such that

$$(**) \qquad x^{'} = A(\mu)x + F(x,\mu)$$

with

$$A(\mu) = \begin{pmatrix} \alpha(\mu) & -\beta(\mu) \\ \beta(\mu) & \alpha(\mu) \end{pmatrix}$$

and

$$F(x,\mu) = \begin{pmatrix} B_2^1(x_1,x_2,\mu) + B_3^1(x_1,x_2,\mu) + O(|x|^4) \\ B_2^2(x_1,x_2,\mu) + B_3^2(x_1,x_2,\mu) + O(|x|^4) \end{pmatrix},$$

where $B_j^k(x_1,x_2,\mu)$ is a homogeneous polynomial of degree j in x_1 and x_2. Let

$$C_3(\theta,\mu) = \cos\theta B_2^1(\cos\theta,\sin\theta,\mu) + \sin\theta B_2^2(\cos\theta,\sin\theta,\mu),$$

$$D_3(\theta,\mu) = -\sin\theta B_2^1(\cos\theta,\sin\theta,\mu) + \cos\theta B_2^2(\cos\theta,\sin\theta,\mu),$$

$$D_4(\theta,\mu) = -\sin\theta B_3^1(\cos\theta,\sin\theta,\mu) + \cos\theta B_3^2(\cos\theta,\sin\theta,\mu).$$

Assume
(III) $K \neq 0$ where

$$K = \frac{1}{2\pi} \int_0^{2\pi} \left(C_4(\theta, 0) - \frac{1}{\beta_0} C_3(\theta, 0) D_3(\theta, 0) \right) d\theta.$$

Andronov-Hopf Bifurcation Theorem. *Make assumptions (I), (II) on the differential equation*

$$x' = f(x, \mu). \tag{$*$}$$

(a) *Then there exists ϵ_0 such that for $0 \leq \epsilon \leq \epsilon_0$, there are (i) differentiable functions $\mu(\epsilon)$ and $T(\epsilon)$ with $T(0) = 2\pi/\beta_0$, $\mu(0) = 0$ and $\mu'(0) = 0$ and (ii) a $T(\epsilon)$-periodic function of t, $x^*(t, \epsilon)$, that is a solution of $(*)$ for the parameter value $\mu = \mu(\epsilon)$ and with initial conditions in polar coordinates given by $r^*(0, \epsilon) = \epsilon$ and $\theta^*(0, \epsilon) = 0$. In fact, for all t, $r^*(t, \epsilon) = \epsilon + 0(\epsilon)$. (Uniqueness) Furthermore, there are $\mu_0 > 0$ and $\delta_0 > 0$ such that any T-periodic solution $x(t)$ of $(*)$ with $|\mu| \leq \mu_0$, $|T - 2\pi/\beta_0| \leq \delta_0$ and $|x(t)| \leq \delta_0$, must be $x^*(t, \mu)$ up to a phase shift, i.e., $x(t + t_0) = x^*(t, \mu)$ where $\mu = \mu(|x(t_0)|)$ and t_0 is chosen so that the polar angle θ is zero for $x(t_0)$, $\theta(t_0) = 0$.*

(b) *If we also make assumption (III), then not only $\mu'(0) = 0$ but also $\mu''(0) = -2K \neq 0$. Furthermore, the periodic solution is attracting if $K < 0$ and is repelling if $K > 0$.*

In the following, we shall study the Hopf bifurcation of the system (1.1) or equivalently system (2.14) with β as the bifurcation papameter. It is interesting to note that from Theorem 2.2 (iii) the equilibrium (x^*, y^*) of (1.1) or (x^*, u^*) of (2.14) is globally asympototically stable for $\beta > 0$ sufficiently small. We shall restrict our attention to the bifurcation phenomenon as β is near β_1, where β_1 is defined in (2.9). We note that $x^* = x^*(\beta)$ is a function of β and

$$\lim_{\beta \to \beta_1} x^*(\beta) = \alpha_1.$$

Now we return to system (2.14):

$$\begin{aligned} \frac{dx}{dt} &= \varphi(x)[h(x) - u], \\ \frac{du}{dt} &= \psi(x) u^2, \end{aligned} \tag{2.14}$$

where

$$
(3.1)\qquad
\begin{aligned}
&\varphi(x) = \frac{x}{a+x}\,\frac{1}{\ell(x)}, \quad \ell(x) = \left(\frac{1-x}{x}\right)^{\delta},\\
&h(x) = (1-x)(x+a)\ell(x),\\
&\psi(x) = \frac{\beta}{xh(x)}(x-x^*)\left(x+\frac{a}{x^*}\right).
\end{aligned}
$$

Rewrite

$$
(3.2)\qquad
\begin{aligned}
\psi(x) &= \frac{\beta}{h(x)}\frac{(x-x^*)\left(x+\frac{a}{x^*}\right)}{x}\\
&= \frac{\beta}{h(x)}\left[\frac{(1-x^*)(a+x^*)}{x^*} - \frac{(1-x)(a+x)}{x}\right]\\
&= \frac{\beta}{h(x)}\left[\frac{y^*}{x^*} - \frac{(1-x)(a+x)}{x}\right]\\
&= \frac{1}{h(x)}\left[\delta - \beta q(x)\right],
\end{aligned}
$$

where

$$
q(x) = \frac{(1-x)(a+x)}{x}.
$$

Let

$$
(3.3)\qquad
\begin{aligned}
&L(x,\beta) = \exp\left(\int_{x^*}^{x}\frac{\psi(\xi)}{\varphi(\xi)}d\xi\right), \quad \Phi(x,\beta) = \frac{\varphi(x)}{L(x,\beta)},\\
&H(x,\beta) = h(x)L(x,\beta), \quad \Psi(x,\beta) = \psi(x)h(x) = \delta - \beta q(x).
\end{aligned}
$$

From (3.2), (3.3), it is easy to verify that the change of variable $V = uL(x,\beta)$ reduces (2.14) to the following system

$$
(3.4)\qquad
\begin{aligned}
&\frac{dx}{dt} = \Phi(x,\beta)\left[H(x,\beta) - V\right] = F(x,V,\beta),\\
&\frac{dV}{dt} = \Psi(x,\beta)V = G(x,V,\beta),
\end{aligned}
$$

and the unique equilibrium (x^*, V^*) of (3.4) satisfies

$$
(3.5)\qquad H(x^*,\beta) = h(x^*) = V^*, \quad \Psi(x^*,\beta) = \delta - \beta q(x^*) = 0.
$$

We also note that from (3.3), (3.1), we have

$$
(3.6)\qquad H(x,\beta)\Phi(x,\beta) = h(x)\varphi(x) = x(1-x).
$$

Differentiating (3.6) with respect to x three times yields

$$H^{'}(x,\beta)\Phi(x,\beta)+H(x,\beta)\Phi^{'}(x,\beta)=-2x+1,$$

$$H^{''}(x,\beta)\Phi(x,\beta)+2H^{'}(x,\beta)\Phi^{'}(x,\beta)+H(x,\beta)\Phi^{''}(x,\beta)=-2 \tag{3.7}$$

and

$$\begin{aligned}&H^{'''}(x,\beta)\Phi(x,\beta)+3H^{''}(x,\beta)\Phi^{'}(x,\beta)+3H^{'}(x,\beta)\Phi^{''}(x,\beta)\\&+H(x,\beta)\Phi^{'''}(x,\beta)=0.\end{aligned} \tag{3.8}$$

From (3.4), (3.5), (3,7) and (3.8), the Taylor's formulas of $F(x,V,\beta)$ and $G(x,V,\beta)$ about (x^*,V^*) are:

$$\begin{aligned}F(x,V,\beta)=&\Phi(x^*,\beta)H^{'}(x^*,\beta)(x-x^*)-\Phi(x^*,\beta)(V-V^*)\\&+\frac{1}{2!}\left[\left(-2-\Phi^{''}(x^*,\beta)H(x^*,\beta)\right)(x-x^*)^2\right.\\&\left.-2\Phi^{'}(x^*,\beta)(x-x^*)(V-V^*)\right]\\&+\tfrac{1}{3!}\left[-\Phi^{'''}(x^*,\beta)H(x^*,\beta)(x-x^*)^3\right.\\&\left.-3\Phi^{''}(x^*,\beta)(x-x^*)^2(V-V^*)\right]\\&+O\left(|(x-x^*,V-V^*)|^4\right)\end{aligned} \tag{3.9}$$

and

$$\begin{aligned}G(x,V,\beta)=&\Psi^{'}(x^*,\beta)H(x^*,\beta)(x-x^*)\\&+\frac{1}{2!}\left[\Psi^{''}(x^*,\beta)H(x^*,\beta)(x-x^*)^2\right.\\&\left.+2\Psi^{'}(x^*,\beta)(x-x^*)(V-V^*)\right]\\&+\frac{1}{3!}\left[\Psi^{'''}(x^*,\beta)H(x^*,\beta)(x-x^*)^3\right.\\&\left.+3\Psi^{''}(x^*,\beta)(x-x^*)^2(V-V^*)\right]\\&+O\left(|(x-x^*,V-V^*)|^4\right).\end{aligned} \tag{3.10}$$

Let

$$\bar{x}(t)=x(t)-x^*,\quad \bar{V}(t)=V(t)-V^*.$$

From (3.4), (3.9) and (3.10), we have

$$\frac{d}{dt}\begin{bmatrix}\bar{x}(t)\\ \bar{V}(t)\end{bmatrix} = J^{(0)}(\beta)\begin{bmatrix}\bar{x}(t)\\ \bar{V}(t)\end{bmatrix} + \frac{\bar{x}(t)}{2!}J^{(1)}(\beta)\begin{bmatrix}\bar{x}(t)\\ \bar{V}(t)\end{bmatrix} + \frac{\bar{x}^2(t)}{3!}J^{(2)}(\beta)\begin{bmatrix}\bar{x}(t)\\ \bar{V}(t)\end{bmatrix} + \text{H.O.T.}, \tag{3.11}$$

where

$$J^{(0)}(\beta) = \begin{bmatrix}\Phi(x^*,\beta)H^{'}(x^*,\beta)\ , & -\Phi(x^*,\beta)\\ \Psi^{'}(x^*,\beta)H(x^*,\beta)\ , & 0\end{bmatrix},$$

$$J^{(1)}(\beta) = \begin{bmatrix}-2-\Phi^{''}(x^*,\beta)H(x^*,\beta)\ , & -2\Phi^{'}(x^*,\beta)\\ \Psi^{''}(x^*,\beta)H(x^*,\beta)\ , & 2\Psi^{'}(x^*,\beta)\end{bmatrix}$$

and

$$J^{(2)}(\beta) = \begin{bmatrix}-\Phi^{'''}(x^*,\beta)H(x^*,\beta)\ , & -3\Phi^{''}(x^*,\beta)\\ \Psi^{'''}(x^*,\beta)H(x^*,\beta)\ , & 3\Psi^{''}(x^*,\beta)\end{bmatrix}.$$

From (3.3) and (3.6), it is easy to establish the following lemma whose proof we omit.

Lemma 3.1: (i) $\Psi^{'}(x,\beta) = -\beta q^{'}(x)$, $\Psi^{''}(x,\beta) = -\beta q^{''}(x)$,
$q^{'}(x) = \frac{-(x^2+a)}{x^2} < 0$, $q^{''}(x) = \frac{2a}{x^3} > 0$.
(ii) $\Phi(x,\beta)H^{'}(x,\beta) = \varphi(x)h^{'}(x) + \Psi(x,\beta)$.

Assume $|\beta-\beta_1| \ll 1$ or equivalently $|x^*-\alpha_1| \ll 1$. Let

$$\lambda(\beta) = \frac{1}{2}\Phi(x^*,\beta)H^{'}(x^*,\beta),$$

$$\rho(\beta) = \Phi(x^*,\beta)H(x^*,\beta)\Psi^{'}(x^*,\beta) - \lambda^2(\beta).$$

Then the eigenvalues of the matrix $J^{(0)}(\beta)$ are $\lambda(\beta) \pm \sqrt{\rho(\beta)}i$. Since $x^*(\beta_1) = \alpha_1$, from Lemma 3.1 and (3.6) it follows that $\lambda(\beta_1) = 0$ and

$$\rho(\beta_1) = -\alpha_1(1-\alpha_1)\beta_1 q^{'}(\alpha_1) > 0. \tag{3.12}$$

Hence the eigenvalues of $J^{(0)}(\beta)$ are crossing the imaginary axis as $\beta = \beta_1$. In order to reduce (3.11) to the standard form $(**)$, we introduce

$$M(\beta) = \begin{bmatrix}1 & \dfrac{\lambda(\beta)}{\sqrt{\rho(\beta)}}\\ 0 & \Psi^{'}(x^*,\beta)H(x^*,\beta)/\sqrt{\rho(\beta)}\end{bmatrix}. \tag{3.13}$$

Set

$$\theta(\beta) = \det M(\beta) = \frac{\Psi'(x^*,\beta)H(x^*,\beta)}{\sqrt{\rho(\beta)}} \ . \tag{3.14}$$

Then

$$M^{-1}(\beta) = \begin{bmatrix} 1 & -\frac{\lambda(\beta)}{\theta(\beta)\sqrt{\rho(\beta)}} \\ 0 & \frac{1}{\theta(\beta)} \end{bmatrix}. \tag{3.15}$$

A direct computation gives

$$M^{-1}(\beta)J^{(0)}(\beta)M(\beta) = \begin{bmatrix} m_{11} & m_{12} \\ m_{21} & m_{22} \end{bmatrix},$$

where

$$m_{11} = \Phi(x^*,\beta)H'(x^*,\beta) - \frac{\lambda(\beta)}{\theta(\beta)\sqrt{\rho(\beta)}}\Psi'(x^*,\beta)H(x^*,\beta),$$

$$m_{12} = \frac{\Phi(x^*,\beta)}{\sqrt{\rho(\beta)}}\Big(\lambda(\beta)H'(x^*,\beta) - \Psi'(x^*,\beta)H(x^*,\beta)\Big) - \frac{\lambda^2(\beta)}{\theta(\beta)\rho(\beta)}\Psi'(x^*,\beta)\cdot H(x^*,\beta),$$

$$m_{21} = \frac{\Psi'(x^*,\beta)H(x^*,\beta)}{\theta(\beta)} \ ,$$

$$m_{22} = \frac{\lambda(\beta)}{\sqrt{\rho(\beta)}\theta(\beta)}\Psi'(x^*,\beta)H(x^*,\beta).$$

From (3.14), it follows that

$$m_{11} = 2\lambda(\beta) - \lambda(\beta) = \lambda(\beta),$$

$$m_{12} = \frac{\lambda(\beta)}{\sqrt{\rho(\beta)}}2\lambda(\beta) - \frac{1}{\sqrt{\rho(\beta)}}\left(\rho(\beta) + \lambda^2(\beta)\right) - \frac{\lambda^2(\beta)}{\sqrt{\rho(\beta)}} = -\sqrt{\rho(\beta)},$$

$$m_{21} = \frac{\theta(\beta)\sqrt{\rho(\beta)}}{\theta(\beta)} = \sqrt{\rho(\beta)},$$

$$m_{22} = \frac{\lambda(\beta)}{\sqrt{\rho(\beta)}\theta(\beta)} \cdot \theta(\beta)\sqrt{\rho(\beta)} = \lambda(\beta).$$

Hence we have

$$M^{-1}(\beta)J^{(0)}(\beta)M(\beta) = \begin{bmatrix} \lambda(\beta) \ , & -\sqrt{\rho(\beta)} \\ \sqrt{\rho(\beta)} \ , & \lambda(\beta) \end{bmatrix} \equiv N^{(0)}(\beta). \tag{3.16}$$

Introduce

$$z(t) = \begin{bmatrix} z_1(t) \\ z_2(t) \end{bmatrix} = M^{-1}(\beta)\begin{bmatrix} \bar{x}(t) \\ \bar{V}(t) \end{bmatrix}.$$

Then (3.11) takes the form

$$z^{'}(t) = N^{(0)}(\beta)z(t) + \frac{\left(z_1 + \frac{\lambda(\beta)}{\sqrt{\rho(\beta)}}z_2\right)}{2!}N^{(1)}(\beta)z(t) \tag{3.17}$$
$$+\frac{1}{3!}\left(z_1 + \frac{\lambda(\beta)}{\sqrt{\rho(\beta)}}z_2\right)^2 N^{(2)}(\beta)z(t)$$
$$+O\left(|z(t)|^4\right),$$

where

$$N^{(i)}(\beta) = M^{-1}(\beta)J^{(i)}(\beta)M(\beta), \quad i = 1, 2.$$

In order to evaluate the number K in assumption (III), we have to compute $N^{(i)}(\beta_1)$ for $i = 0, 1, 2$.

Lemma 3.2.

(i) $\Psi^{'}(\alpha_1, \beta_1)H(\alpha_1, \beta_1) = -\beta_1 q^{'}(\alpha_1)h(\alpha_1) = -\frac{\delta q^{'}(\alpha_1)}{q(\alpha_1)}h(\alpha_1)$.

(ii) $\Phi(\alpha_1, \beta_1) = \varphi(\alpha_1)$,
$\Phi^{'}(\alpha_1, \beta_1) = \varphi^{'}(\alpha_1)$,
$H^{'}(\alpha_1, \beta_1) = 0$.

(iii) $\Phi(\alpha_1, \beta_1)H^{''}(\alpha_1, \beta_1) = -2 - \varphi^{''}(\alpha_1)h(\alpha_1) - \beta_1 q^{'}(\alpha_1)$.

(iv) $\Phi^{'''}(\alpha_1, \beta_1)H(\alpha_1, \beta_1) = -\left(\varphi(x)h^{'}(x)\right)^{''}\Big|_{x=\alpha_1} + \beta_1 q^{''}(\alpha_1) - \varphi^{'}(\alpha_1)H^{''}(\alpha_1, \beta_1)$.

Proof: When $\beta = \beta_1$, we have $x^*(\beta_1) = \alpha_1$. Since $h^{'}(\alpha_1) = 0$, from (3.2) and (3.3) a direct computation shows

$$\psi(\alpha_1) = 0, \tag{3.18}$$
$$L(\alpha_1, \beta_1) = 1,$$
$$L^{'}(\alpha_1, \beta_1) = \frac{\psi(\alpha_1)}{\varphi(\alpha_1)} = 0.$$

Parts (i) and (ii) follow directly from (3.18), (3.3) and Lemma 3.1 (i).
From (3.7) and (ii) we have

$$\Phi(\alpha_1, \beta_1)H^{''}(\alpha_1, \beta_1) = -2 - \Phi^{''}(\alpha_1, \beta_1)H(\alpha_1, \beta_1). \tag{3.19}$$

Since

$$\Phi^{'}(x, \beta)H(x, \beta) = \left(\Phi(x, \beta)H(x, \beta)\right)^{'} - \Phi(x, \beta)H^{'}(x, \beta) \tag{3.20}$$
$$= \left(\varphi(x)h(x)\right)^{'} - \left(\varphi(x)h^{'}(x) + h(x)\psi(x)\right)$$
$$= \varphi^{'}(x)h(x) - \Psi(x, \beta),$$

we have

$$\Phi^{''}(x,\beta)H(x,\beta)+\Phi^{'}(x,\beta)H^{'}(x,\beta) = \varphi^{''}(x)h(x)+\varphi^{'}(x)h^{'}(x)+\beta q^{'}(x). \tag{3.21}$$

Part (iii) follows directly from (3.19), (3.21) and part (ii).
From (3.6), (3.20) and Lemma 3.1 (i), we have

$$\Big(\Phi^{'}(x,\beta)H(x,\beta)\Big)^{''} = -(h^{'}\varphi)^{''} + \beta q^{''}(x)$$

or

$$\Phi^{'''}H + 2\Phi^{'}H^{'} + \Phi^{'}H^{''} = -(h^{'}\varphi)^{''} + \beta q^{''}. \tag{3.22}$$

Set $\beta = \beta_1$ and $x^* = \alpha_1$ in (3.22). Then from part (i) we complete the proof of part (iv). ∎

In the following we compute the matrices $N^{(i)}(\beta_1),\ i = 0,1,2$. From (3.16) and (3.12), we have

$$N^{(0)}(\beta_1) = \begin{bmatrix} 0 & -\sqrt{\rho(\beta_1)} \\ \sqrt{\rho(\beta_1)}\ , & 0 \end{bmatrix}. \tag{3.23}$$

From (3.13), (3.14) and Lemma 3.2 (i), we have $\theta(\beta_1) > 0$ and

$$M(\beta_1) = \begin{bmatrix} 1\ , & 0 \\ 0\ , & \theta(\beta_1) \end{bmatrix}.$$

A direct computation together with Lemmas 3.1 and 3.2 yields

$$\begin{aligned} N^{(1)}(\beta_1) &= \begin{bmatrix} -2-\Phi^{''}(\alpha_1,\beta_1)H(\alpha_1,\beta_1) & -2\Phi^{'}(\alpha_1,\beta_1)\theta(\beta_1) \\ \theta^{-1}(\beta_1)\Psi^{''}(\alpha_1,\beta_1)H(\alpha_1,\beta_1) & 2\Psi^{'}(\alpha_1,\beta_1) \end{bmatrix} \\ &= \begin{bmatrix} \Phi(\alpha_1,\beta_1)H^{''}(\alpha_1,\beta_1)\ , & -2\varphi^{'}(\alpha_1)\theta(\beta_1) \\ \dfrac{-\beta_1 q^{''}(\alpha_1)h(\alpha_1)}{\theta(\beta_1)}\ , & -2\beta_1 q^{'}(\alpha_1) \end{bmatrix} \\ &\overset{def}{=} \begin{bmatrix} \eta_{11} & \eta_{12} \\ \eta_{21} & \eta_{22} \end{bmatrix} \end{aligned} \tag{3.24}$$

and

$$N^{(2)}(\beta_1) = \begin{bmatrix} -\Phi'''(\alpha_1,\beta_1)H(\alpha_1,\beta_1) & -3\Phi''(\alpha_1,\beta_1)\theta(\beta_1) \\ \dfrac{\Psi'''(\alpha_1,\beta_1)H(\alpha_1,\beta_1)}{\theta(\beta_1)} & -3\beta_1 q''(\alpha_1) \end{bmatrix} \tag{3.25}$$

$$\stackrel{def}{=} \begin{bmatrix} w_{11} & w_{12} \\ w_{21} & w_{22} \end{bmatrix}.$$

From $(**)$ and (3.17), (3.24) and (3.25), we have

$$\begin{bmatrix} B_2^1(z_1,z_2) \\ B_2^2(z_1,z_2) \end{bmatrix} = \begin{bmatrix} \frac{1}{2} z_1(\eta_{11}z_1 + \eta_{12}z_2) \\ \frac{1}{2} z_1(\eta_{21}z_1 + \eta_{22}z_2) \end{bmatrix}, \tag{3.26}$$

$$\begin{bmatrix} B_3^1(z_1,z_2) \\ B_3^2(z_1,z_2) \end{bmatrix} = \begin{bmatrix} \frac{z_1^2}{6}(w_{11}z_1 + w_{12}z_2) \\ \frac{z_1^2}{6}(w_{21}z_1 + w_{22}z_2) \end{bmatrix}. \tag{3.27}$$

In order to evaluate the number K in the assumption (III) we need to compute the following functions $C_3(\theta)$, $D_3(\theta)$ and $C_4(\theta)$. From the Andronov-Hopf Bifurcation Theorem, we have

$$C_3(\theta) = \cos\theta B_2^1(\cos\theta,\sin\theta) + \sin\theta B_2^2(\cos\theta,\sin\theta),$$

$$D_3(\theta) = -\sin\theta B_2^1(\cos\theta,\sin\theta) + \cos\theta B_2^2(\cos\theta,\sin\theta),$$

$$C_4(\theta) = \cos\theta B_3^1(\cos\theta,\sin\theta) + \sin\theta B_3^2(\cos\theta,\sin\theta),$$

and

$$K = \frac{1}{2\pi}\int_0^{2\pi} C_4(\theta)d\theta - \frac{1}{\sqrt{\rho(\beta_1)}}\ \frac{1}{2\pi}\int_0^{2\pi} C_3(\theta)D_3(\theta)d\theta. \tag{3.28}$$

From (3.26) and (3.27), a direct computation shows

$$C_4(\theta) = \frac{1}{6}\cos^2\theta\left[w_{11}\cos^2\theta + (w_{12}+w_{21})\cos\theta\sin\theta + w_{22}\sin^2\theta\right],$$

$$\frac{1}{2\pi}\int_0^{2\pi} C_4(\theta)d\theta = \frac{1}{48}(3w_{11}+w_{22}),$$

$$C_3(\theta) = \frac{1}{2}\cos\theta\left[\eta_{11}\cos^2\theta + (\eta_{12}+\eta_{21})\sin\theta\cos\theta + \eta_{22}\sin^2\theta\right], \tag{3.29}$$

$$D_3(\theta) = \frac{1}{2}\cos\theta\left[\eta_{21}\cos^2\theta + (\eta_{22}-\eta_{11})\sin\theta\cos\theta - \eta_{12}\sin^2\theta\right].$$

Compute

$$C_3(\theta)D_3(\theta) = \frac{1}{4}\cos^2\theta\Delta(\theta) = \frac{1}{8}(1+\cos 2\theta)\Delta(\theta), \tag{3.30}$$

where

$$\begin{aligned}
\Delta(\theta) &= [\eta_{11}\cos^2\theta + (\eta_{12}+\eta_{21})\cos\theta\sin\theta + \eta_{22}\sin^2\theta] \\
&\quad \cdot [\eta_{21}\cos^2\theta + (\eta_{22}-\eta_{11})\sin\theta\cos\theta - \eta_{12}\sin^2\theta] \\
&= \frac{1}{4}[\eta_{11}(1+\cos 2\theta) + (\eta_{12}+\eta_{21})\sin 2\theta + \eta_{22}(1-\cos 2\theta)] \\
&\quad \cdot [\eta_{21}(1+\cos 2\theta) + (\eta_{22}-\eta_{11})\sin 2\theta - \eta_{12}(1-\cos 2\theta)] \\
&= \frac{1}{4}[(\eta_{11}+\eta_{22}) + (\eta_{12}+\eta_{21})\sin 2\theta + (\eta_{11}-\eta_{22})\cos 2\theta] \\
&\quad \cdot [(\eta_{21}-\eta_{12}) + (\eta_{22}-\eta_{11})\sin 2\theta + (\eta_{12}+\eta_{21})\cos 2\theta] \\
&= \frac{1}{4}[C_0 + C_1\sin 2\theta + C_2\cos 2\theta + C_3\sin^2 2\theta + C_4\sin 2\theta\cos 2\theta \\
&\quad + C_5\cos^2 2\theta] \\
&= \frac{1}{4}\left[C_0 + C_1\sin 2\theta + C_2\cos 2\theta + C_3\left(\frac{1-\cos 4\theta}{2}\right)\right. \\
&\quad \left. + \frac{C_4}{2}\sin 4\theta + C_5\left(\frac{1+\cos 4\theta}{2}\right)\right]
\end{aligned} \tag{3.31}$$

with

$C_0 = (\eta_{11}+\eta_{22})(\eta_{21}-\eta_{12})$,

$C_3 = -C_5 = (\eta_{12}+\eta_{21})(\eta_{22}-\eta_{11})$,

$C_2 = 2(\eta_{11}\eta_{21}+\eta_{22}\eta_{12})$.

From (3.30) and (3.31) we have

$$\int_0^{2\pi} C_3(\theta)D_3(\theta)d\theta = \frac{1}{8}\int_0^{2\pi}\Delta(\theta)d\theta + \frac{1}{8}\int_0^{2\pi}\cos 2\theta\Delta(\theta)d\theta, \tag{3.32}$$

$$\int_0^{2\pi}\Delta(\theta)d\theta = \frac{C_0}{4}\cdot 2\pi = \frac{\pi}{2}(\eta_{11}+\eta_{22})(\eta_{21}-\eta_{12}), \tag{3.33}$$

$$\begin{aligned}
\int_0^{2\pi}\cos 2\theta\Delta(\theta)d\theta &= \int_0^{2\pi}\frac{C_2}{4}\cos^2 2\theta d\theta \\
&= \frac{C_2}{8}\cdot 2\pi = \frac{\pi}{2}(\eta_{11}\eta_{21}+\eta_{22}\eta_{12}).
\end{aligned} \tag{3.34}$$

From (3.28)–(3.30) and (3.32)–(3.34), it follows that

$$K = \frac{1}{48}(3w_{11} + w_{22}) - \frac{1}{32}\ \frac{1}{\sqrt{\rho(\beta_1)}}[\eta_{11}(2\eta_{21} - \eta_{12}) + \eta_{22}\eta_{21}]. \tag{3.35}$$

By the definitions of $w_{ij}, \eta_{ij}, i, j = 1, 2$, in (3.24) and (3.25), it follows that

$$\begin{aligned} K \;=\; & -\frac{1}{16}\Big\{ \Big[\Phi^{'''}(\alpha_1,\beta_1)H(\alpha_1,\beta_1) + \beta_1 q^{''}(\alpha_1)\Big] \\ & + \frac{1}{\sqrt{\rho(\beta_1)}}\Big[\Phi(\alpha_1,\beta_1)H^{''}(\alpha_1,\beta_1)\cdot\left(\frac{-\beta_1 q^{''}(\alpha_1)h(\alpha_1)}{\theta(\beta_1)}\right) \\ & + \Phi(\alpha_1,\beta_1)H^{''}(\alpha_1,\beta_1)\varphi^{'}(\alpha_1)\theta(\beta_1) \\ & + \beta_1^2 q^{'}(\alpha_1)\ \left(\frac{q^{''}(\alpha_1)h(\alpha_1)}{\theta(\beta_1)}\right)\Big]\Big\}. \end{aligned} \tag{3.36}$$

From (3.14) and Lemma 3.2 (i), we have

$$\frac{{\beta_1}^2 q^{'}(\alpha_1)q^{''}(\alpha_1)h(\alpha_1)}{\sqrt{\rho(\beta_1)}\theta(\beta_1)} = -\beta_1 q^{''}(\alpha_1). \tag{3.37}$$

From (3.12) and (3.14) we have

$$\frac{\Phi(\alpha_1,\beta_1)H^{''}(\alpha_1,\beta_1)\varphi^{'}(\alpha_1)\theta(\beta_1)}{\sqrt{\rho(\beta_1)}} = H^{''}(\alpha_1,\beta_1)\varphi^{'}(\alpha_1). \tag{3.38}$$

From (3.14) and Lemma 3.2 (i) we have

$$\begin{aligned} & -\frac{\Phi(\alpha_1,\beta_1)H^{''}(\alpha_1,\beta_1)\beta_1 q^{''}(\alpha_1)h(\alpha_1)}{\sqrt{\rho(\beta_1)}\theta(\beta_1)} \\ & = \Phi(\alpha_1,\beta_1)H^{''}(\alpha_1,\beta_1)\frac{q^{''}(\alpha_1)}{q^{'}(\alpha_1)}. \end{aligned} \tag{3.39}$$

From (3.36), (3.37), (3.38), (3.39) and Lemma 3.2 (ii), (iii), it follows that

$$\begin{aligned} -16K \;=\; & \Phi^{'''}(\alpha_1,\beta_1)H(\alpha_1,\beta_1) + \varphi^{'}(\alpha_1)H^{''}(\alpha_1,\beta_1) \\ & + \Phi(\alpha_1,\beta_1)H^{''}(\alpha_1,\beta_1)\frac{q^{''}(\alpha_1)}{q^{'}(\alpha_1)} \\ =\; & -\Big(\varphi(x)h^{'}(x)\Big)^{''}\Big|_{x=\alpha_1} + \beta_1 q^{''}(\alpha_1) \\ & + \Big(-2 - \varphi^{''}(\alpha_1)h(\alpha_1) - \beta_1 q^{'}(\alpha_1)\Big)\,\frac{q^{''}(\alpha_1)}{q^{'}(\alpha_1)} \end{aligned}$$

$$= -\left[h^{'''}\varphi + 2\varphi^{'}h^{''} + \varphi^{''}h^{'}\right]\Big|_{x=\alpha_1} + \left(-2 - \varphi^{''}(\alpha_1)h(\alpha_1)\right)\frac{q^{''}(\alpha_1)}{q^{'}(\alpha_1)} .$$

Since $(\varphi h)^{''} = -2$ and $h^{'}(\alpha_1) = 0$, it follows that $-2 - \varphi^{''}(\alpha_1)h(\alpha_1) = \varphi(\alpha_1)h^{''}(\alpha_1)$. Hence

$$16K = h^{'''}(\alpha_1)\varphi(\alpha_1) + 2\varphi^{'}(\alpha_1)h^{''}(\alpha_1) - \varphi(\alpha_1)h^{''}(\alpha_1)\frac{q^{''}(\alpha_1)}{q^{'}(\alpha_1)} . \tag{3.40}$$

Now we are in a position to derive a criterion determining $K > 0$ and $K < 0$. From (3.1) and (2.13), we have

$$\varphi(x) = \frac{x}{\ell(x)}\,\frac{1}{a+x}, \quad h^{'}(x) = -\frac{\ell(x)}{x}P(x),$$

where

$$P(x) = 2(x-\alpha_1)(x-\alpha_2),\ \ell(x) = \left(\frac{1-x}{x}\right)^{\delta} .$$

Then a direct computation yields

$$2\varphi^{'}(\alpha_1)h^{''}(\alpha_1) = 2\frac{P^{'}(\alpha_1)}{(a+\alpha_1)^2} - 2\frac{\ell(\alpha_1)}{\alpha_1}\ P^{'}(\alpha_1)\ \frac{1}{a+\alpha_1}\cdot\left(\frac{x}{\ell(x)}\right)^{'}\Big|_{x=\alpha_1},$$

$$\varphi(\alpha_1)h^{'''}(\alpha_1) = \frac{-2}{a+\alpha_1} + 2\frac{1}{a+\alpha_1}\ \frac{\ell(\alpha_1)}{\alpha_1}\ P^{'}(\alpha_1)\ \left(\frac{x}{\ell(x)}\right)^{'}\Big|_{x=\alpha_1},$$

$$\varphi(\alpha_1)h^{''}(\alpha_1)\frac{q^{''}(\alpha_1)}{q^{'}(\alpha_1)} = \frac{1}{a+\alpha_1}\ P^{'}(\alpha_1)\ \frac{a}{\alpha_1(a+\alpha_1^2)} .$$

Then $K > 0$ iff

$$P^{'}(\alpha_1)\left(\alpha_1^3 - a^2\right) > \alpha_1(a+\alpha_1)\left(a+\alpha_1^2\right)$$

or

$$2(\alpha_1-\alpha_2)\left(\alpha_1^3 - a^2\right) > \alpha_1(a+\alpha_1)\left(a+\alpha_1^2\right) . \tag{3.41}$$

From (2.5), for fixed $0 < a < 1$, we have

$$0 < \delta < \delta^*(a) = 1 + 3a - \sqrt{8a(1+a)} .$$

Claim: *For fixed* $a, 0 < a < 1$, *there exists a unique* $\hat{\delta} = \hat{\delta}(a), 0 < \hat{\delta} < \delta^*(a)$, *such that* $g(\hat{\delta}) = 0$, *where*

$$\begin{aligned} g(\delta) &= 2\left(\alpha_1(\delta) - \alpha_2(\delta)\right)\left(\alpha_1^3(\delta) - a^2\right) \\ &\quad -\alpha_1(\delta)\left(a + \alpha_1(\delta)\right)\left(a + \alpha_1^2(\delta)\right), \quad 0 < \delta < \delta^*(a). \end{aligned}$$

We note that with a fixed a, $0 < a < 1$,

$$\alpha_1 = \alpha_1(\delta) = \frac{1}{4}\left[1 - a - \delta - \sqrt{(1 - a - \delta)^2 - 8a\delta}\right],$$

$$\alpha_2 = \alpha_2(\delta) = \frac{1}{4}\left[1 - a - \delta + \sqrt{(1 - a - \delta)^2 - 8a\delta}\right].$$

Since α_1, α_2 are roots of $P(x) = 0$, where $P(x)$ is defined in (2.2) as

$$P(x) = 2x^2 + (a + \delta - 1)x + a\delta,$$

we have

$$\alpha_1(\delta) + \alpha_2(\delta) = \frac{(1 - a - \delta)}{2}\ .$$

Differentiating both sides of $P(\alpha_1(\delta)) = 0$ and $P(\alpha_2(\delta)) = 0$ with respect to δ yields

$$\alpha_1'(\delta) = \frac{(a + \alpha_1(\delta))}{2\left(\alpha_2(\delta) - \alpha_1(\delta)\right)} > 0$$

and

$$\alpha_2'(\delta) = \frac{-\left(a + \alpha_2(\delta)\right)}{2\left(\alpha_2(\delta) - \alpha_1(\delta)\right)} < 0.$$

Since $\lim_{\delta\to 0} \alpha_1(\delta) = 0$ and $\lim_{\delta\to 0} \alpha_2(a) = \frac{1-a}{2}$, it follows that

$$g(0+) = a^2(1 - a) > 0.$$

On the other hand, $\lim_{\delta\to\delta^*(a)}(\alpha_1(\delta) - \alpha_2(\delta)) = 0$ implies $g(\delta^*(a)-) < 0$. Hence for fixed a, $0 < a < 1$, there exists $\hat{\delta}$, $0 < \hat{\delta} < \delta^*(a)$, such that $g(\hat{\delta}) = 0$. For the uniqueness of $\hat{\delta}$, it suffices to show that if $g(\hat{\delta}) = 0$ then $g'(\hat{\delta}) < 0$. A direct computation shows

$$\begin{aligned} g'(\delta) &= 6\left(\alpha_1(\delta) - \alpha_2(\delta)\right)\alpha_1^2(\delta)\alpha_1'(\delta) \\ &\quad +2\left(\alpha_1'(\delta) - \alpha_2'(\delta)\right)\left(\alpha_1^3(\delta) - a^2\right) \\ &\quad -\alpha_1'(\delta)(a + \alpha_1(\delta))\left(a + \alpha_1^2(\delta)\right) \\ &\quad -\alpha_1(\delta)\alpha_1'(\delta)\left[a + 2a\alpha_1(\delta) + 3\alpha_1^2(\delta)\right]. \end{aligned}$$

If $g(\hat{\delta}) = 0$ then $\alpha_1^3(\hat{\delta}) - a^2 < 0$. It is easy to verify that $g'(\hat{\delta}) < 0$. Thus we complete the proof of the claim. ■

Summarizing the above results, from the Andronov-Hopf Bifurcation Theorem, we have

Theorem 3.3.

(i) *$K > 0$ for $0 < a < 1$ and $0 < \delta < \hat{\delta}(a)$. The periodic solution of Hopf bifurcation of* (3.1) *is repelling with $\beta(\varepsilon) < \beta_1, |\varepsilon| \le \varepsilon_0, \varepsilon \ne 0$, i.e., the Hopf bifurcation is subcritical.*

(ii) *$K < 0$ for $0 < a < 1$ and $\hat{\delta}(a) < \delta < \delta^*(a)$. The periodic solution of Hopf bifurcation of* (3.1) *is attracting with $\beta(\varepsilon) > \beta_1, |\varepsilon| \le \varepsilon_0, \varepsilon \ne 0$, i.e. the Hopf bifurcation is supercritical.*

Now we are in a position to discuss the possibility of multiple limit cycles. When the parameters a, δ satisfy $0 < a < 1, 0 < \delta < \hat{\delta}(a)$, we have $K > 0$. Then for $\beta < \beta_1$, β near β_1, there exists a small-amplitude repelling periodic orbit enclosing a stable equilibrium (x^*, u^*). Since the solution of (2.14) is positively invariant in a compact region away from the x and u axes (see [5, p. 76]), obviously we have another limit cycle solution $\Gamma_{\beta,\delta}$ with large amplitude. This explains the phenomenon of outbreaking in [8] obtained by numerical simulations.

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