



ELSEVIER

Available online at www.sciencedirect.com



Nonlinear Analysis 60 (2005) 1351–1367

**Nonlinear
Analysis**

www.elsevier.com/locate/na

Hopf bifurcation analysis in a delayed Nicholson blowflies equation

Junjie Wei^a, Michael Y. Li^{b,*}

^a*Department of Mathematics, Harbin Institute of Technology, Harbin, Heilongjiang 150001, China*

^b*Department of Mathematical and Statistical Sciences, University of Alberta, Edmonton, Alberta, Canada T6G 2G1*

Received 1 January 2003; accepted 29 April 2003

Abstract

The dynamics of a Nicholson's blowflies equation with a finite delay are investigated. We prove that a sequence of Hopf bifurcations occur at the positive equilibrium as the delay increases. Explicit algorithm for determining the direction of the Hopf bifurcations and the stability of the bifurcating periodic solutions are derived, using the theory of normal form and center manifold. Global existence of periodic solutions are established using a global Hopf bifurcation result of Wu (Trans. Amer. Math. Soc. 350 (1998) 4799), and a Bendixson criterion for higher dimensional ordinary differential equations due to Li and Muldowney (J. Differential Equations 106 (1994) 27).

© 2004 Elsevier Ltd. All rights reserved.

MSC: 34K18 (92D25)

Keywords: Nicholson's blowflies; Delay equations; Hopf bifurcations; Periodic solutions

1. Introduction

The equation

$$N'(t) = -\gamma N(t) + pN(t - \tau)e^{-aN(t-\tau)}, \quad t \geq 0 \quad (1)$$

* Corresponding author. Tel.: +1 7804922032; fax: +1 7804926826.

E-mail address: mli@math.ualberta.ca (M.Y. Li).

was used by Gurney et al. [6] to describe the population dynamics of Nicholson’s blowflies. Here $N(t)$ is the size of the population at time t , p is the maximum per capita daily egg production rate, $1/a$ is the size at which the population reproduces at the maximum rate, γ is the per capita daily adult death rate, and τ is the generation time. Eq. (1) has been extensively studied in the literature. A majority of results on Eq. (1) deal with global attractivity of the positive equilibrium and oscillatory behaviors of solutions (see [13,14,7,15,23,16,19,8,2]). These studies were also carried out on Eq. (1) with time-periodic coefficients (see [28,22]), and on discrete Nicholson’s blowflies equation (see [11,12,24,17,31]). More recent attention was on diffusive Nicholson’s equations and their wave form solutions (see, e.g., [29,25,26,5,4,27]). An earlier result of Kulenovic and Ladas [13] proved, under the assumption $p > \gamma e^2$, that solutions of (1) oscillate about the positive equilibrium $N^* = (1/a) \log(p/\gamma)$ if and only if

$$\gamma \tau e^{a\tau} \left[\log \frac{p}{\gamma} - 1 \right] > \frac{1}{e}. \tag{2}$$

A question of mathematical and biological interest is whether stable and sustained oscillations are possible for Eq. (1). In the present paper, we provide a detailed analysis of this question. Using the delay τ as a parameter, and applying the local and global Hopf bifurcation theory (see e.g. Hale [9] and Wu [30]), we investigate the existence of stable periodic oscillations for Eq. (1). More specifically, we prove under the assumption $p > \gamma e^2$ that, as the delay τ increases, the positive equilibrium N^* loses its stability and a sequence of Hopf bifurcations occur at N^* . Furthermore, using the normal form and center manifold theory, we derive an explicit algorithm and sufficient conditions for the stability of the bifurcating periodic solutions. Existence of periodic solutions for τ far away from the Hopf bifurcation values is also established, using a global Hopf bifurcation result of Wu [30]. A key step in establishing the global extension of the local Hopf branch at $\tau = \tau_0$ is to show that (1) has no nonconstant periodic solutions of period 4. This is accomplished by applying a higher dimensional Bendixson criterion for ordinary differential equations due to Li and Muldowney [18].

The paper is organized as follows: in Section 2, we investigate the occurrence of Hopf bifurcations. In Section 3, direction and stability of the Hopf bifurcation are established. Global Hopf bifurcation is established in Section 4.

2. Local Hopf bifurcations

The positive equilibrium $N^* = (1/a) \log(p/\gamma)$ of (1) exists if and only if $a > 0$ and $p > \gamma$. These relations are assumed throughout the paper.

Set $N(t) = N^* + (1/a)x(t)$. Then $x(t)$ satisfies

$$x'(t) = -\gamma x(t) - a\gamma N^* \left[1 - e^{-x(t-\tau)} \right] + \gamma x(t - \tau) e^{-x(t-\tau)}. \tag{3}$$

The linearization of Eq. (3) at $x = 0$ is

$$y'(t) = -\gamma y(t) - \gamma[aN^* - 1]y(t - \tau), \tag{4}$$

whose characteristic equation is

$$\lambda = \gamma - \gamma[aN^* - 1]e^{-\lambda\tau}. \tag{5}$$

For $\tau = 0$, the only root of (5) is $\lambda = -aN^* < 0$, since $p > \gamma$. For $\omega \neq 0$, $i\omega$ is a root of (5) if and only if

$$i\omega = -\gamma - \gamma[aN^* - 1](\cos \omega\tau - i \sin \omega\tau).$$

Separating the real and imaginary parts, we obtain

$$\begin{aligned} \gamma(aN^* - 1) \cos \omega\tau &= -\gamma, \\ \gamma(aN^* - 1) \sin \omega\tau &= \omega, \end{aligned} \tag{6}$$

which lead to

$$\gamma^2(aN^* - 1)^2 = \gamma^2 + \omega^2,$$

namely,

$$\omega = \pm\gamma\sqrt{aN^*(aN^* - 2)}. \tag{7}$$

This is possible if and only if $aN^* > 2$, or equivalently, if $p > \gamma e^2$.

For $p > \gamma e^2$, let

$$\tau_k = \frac{1}{\gamma\sqrt{aN^*(aN^* - 2)}} \left[\sin^{-1} \left(\frac{\sqrt{aN^*(aN^* - 2)}}{aN^* - 1} \right) + 2k\pi \right], \tag{8}$$

$k = 0, 1, 2, \dots$. Set

$$\omega_0 = \gamma\sqrt{aN^*(aN^* - 2)}. \tag{9}$$

Let $\lambda_k = \alpha_k(\tau) + i\omega_k(\tau)$ denote a root of (5) near $\tau = \tau_k$, such that $\alpha_k(\tau_k) = 0$, $\omega_k(\tau_k) = \omega_0$. We have the following result.

Lemma 2.1. $\alpha'_k(\tau_k) > 0$.

Proof. Differentiating both sides of (5) with respect to τ , we obtain

$$\frac{d\lambda}{d\tau} = -\gamma[aN^* - 1]e^{-\lambda\tau} \left[-\lambda - \tau \frac{d\lambda}{d\tau} \right].$$

Therefore

$$\frac{d\lambda}{d\tau} = \frac{\gamma(aN^* - 1)\lambda e^{-\lambda\tau}}{1 - \gamma(aN^* - 1)\tau e^{-\lambda\tau}},$$

and hence

$$\left. \frac{d\lambda}{d\tau} \right|_{\tau=\tau_k} = \frac{\gamma(aN^* - 1)\omega_0 \sin \omega_0 \tau_k + i\gamma(aN^* - 1)\omega_0 \cos \omega_0 \tau_k}{[1 - \gamma(aN^* - 1)\tau_k \cos \omega_0 \tau_k] + i\gamma(aN^* - 1)\tau_k \sin \omega_0 \tau_k}.$$

This implies that

$$\alpha'_k(\tau_k) = \frac{\gamma}{\Delta} (aN^* - 1)\omega_0 \sin \omega_0 \tau_k = \frac{\omega_0^2}{\Delta} > 0,$$

where $\Delta = [1 - \gamma(aN^* - 1)\tau_k \cos \omega_0 \tau_k]^2 + \gamma^2(aN^* - 1)^2 \tau_k^2 \sin^2 \omega_0 \tau_k$, completing the proof. \square

Proposition 2.2. (i) When $\gamma < p \leq \gamma e^2$, all roots of the characteristic equation (5) have negative real parts. (ii) When $p > \gamma e^2$, Eq. (5) has a pair of simple imaginary roots $\pm i\omega_0$ at $\tau = \tau_k$, $k = 0, 1, 2, \dots$. Furthermore, if $\tau \in [0, \tau_0)$, then all roots of Eq. (5) have negative real parts; if $\tau = \tau_0$, then all roots of (5) except $\pm i\omega_0$ have negative real parts; and if $\tau \in (\tau_k, \tau_{k+1})$ for $k = 0, 1, 2, \dots$, Eq. (5) has $2(k + 1)$ roots with positive real parts.

Proof. From the analysis leading to relation (7) we know that, if $p \leq \gamma e^2$, Eq. (5) has no purely imaginary root $i\omega$ with $\omega \neq 0$. Since $\lambda = 0$ is not a solution to (5), we know that, for any τ , (5) has no solutions on the imaginary axis. Applying a result of Ruan and Wei [21, Corollary 2.4], we arrive at the conclusion (i).

If $p > \gamma e^2$, let τ_k be as in (8). From (6) and (7), we know that Eq. (5) has purely imaginary roots $\pm i\omega_0$ if and only if $\tau = \tau_k$ and ω_0 is given in (9). The statements on the number of eigenvalues with positive real parts follow from Lemma 2.1. \square

Spectral properties in Proposition 2.2 immediately lead to stability properties of the zero solution of Eq. (3), and equivalently, of the positive equilibrium $N = N^*$ of Eq. (1).

Theorem 2.3. For Eq. (1), the following hold.

- (i) If $\gamma < p \leq \gamma e^2$, then $N = N^*$ is asymptotically stable.
- (ii) If $p > \gamma e^2$, then $N = N^*$ is asymptotically stable for $\tau \in [0, \tau_0)$ and unstable for $\tau > \tau_0$.
- (iii) For $p > \gamma e^2$, Eq. (1) undergoes a Hopf bifurcation at N^* when $\tau = \tau_k$, for $k = 0, 1, 2, \dots$.

3. Stability and direction of the Hopf bifurcation

In the previous section, we obtained conditions for Hopf bifurcations to occur when $\tau = \tau_k$, $k = 0, 1, 2, \dots$. In this section, we investigate the direction of the Hopf bifurcation when $\tau = \tau_0$, and the stability of the bifurcating periodic solutions, using techniques from normal form and center manifold theory (see e.g. Hassard et al. [10]).

Let $y(t) = x(\tau t)$. Then (3) becomes

$$y'(t) = -\gamma\tau[y(t) + aN^*(1 - e^{-y(t-1)}) - y(t-1)e^{-y(t-1)}]. \tag{10}$$

Correspondingly, the characteristic equation (5) becomes

$$z = -\tau\gamma - \tau\gamma[aN^* - 1]e^{-z}. \tag{11}$$

with $z = \tau\lambda$ for $\tau \neq 0$. From the conclusion (ii) of Proposition 2.2 we know that, if $p > \gamma e^2$ and $\tau = \tau_0$, all roots of (11) except $\pm i\tau_0\omega_0$ have negative real parts. Furthermore, by Lemma 2.1,

$$z(\tau) = \tau\alpha(\tau) + i\tau\omega(\tau)$$

satisfies

$$\left. \frac{d(\tau\alpha(\tau))}{d\tau} \right|_{\tau=\tau_0} = \tau_0\alpha'(\tau_0) > 0.$$

Set $\tau = \tau_0 + \mu$, $\mu \in \mathbb{R}$. Then $\mu = 0$ is a Hopf bifurcation value for Eq. (10). Rewrite Eq. (10) as

$$\begin{aligned} y'(t) = & -(\tau_0 + \mu)\gamma[y(t) + (aN^* - 1)y(t - 1)] \\ & + (\tau_0 + \mu)\gamma \left[\frac{a(N^* - 2)}{2} y^2(t - 1) - \frac{(aN^* - 3)}{6} y^3(t - 1) \right] \\ & + O(y^4). \end{aligned} \tag{12}$$

For $\psi \in \mathcal{C} = C([-1, 0], \mathbb{R})$, let

$$L_\mu\psi := -(\tau_0 + \mu)\gamma[\psi(0) + (aN^* - 1)\psi(-1)],$$

and

$$\begin{aligned} f(\mu, \psi) := & (\tau_0 + \mu)\gamma \left[\frac{a(N^* - 2)}{2} \psi^2(-1) - \frac{(aN^* - 3)}{6} \psi^3(-1) \right] \\ & + O(\psi^4(-1)). \end{aligned} \tag{13}$$

By the Riesz Representation Theorem, there exists a function $\eta(\theta, \mu)$ of bounded variation for $\theta \in [-1, 0]$, such that

$$L_\mu\psi = \int_{-1}^0 d\eta(\theta, \mu)\psi(\theta), \quad \text{for } \psi \in \mathcal{C}. \tag{14}$$

In fact, we can choose

$$\eta(\theta, \mu) = -(\tau_0 + \mu)\gamma\delta(\theta) + (\tau_0 + \mu)\gamma(aN^* - 1)\delta(\theta + 1). \tag{15}$$

For $\psi \in \mathcal{C}$, define

$$A(\mu)\psi := \begin{cases} d\psi(\theta)/d\theta, & \theta \in [-1, 0), \\ \int_{-1}^0 d\eta(t, \mu)\psi(t), & \theta = 0, \end{cases} \tag{16}$$

and

$$R(\mu) := \begin{cases} 0, & \theta \in [-1, 0), \\ f(\mu, \psi), & \theta = 0. \end{cases} \tag{17}$$

Then we can rewrite (12) as

$$y'_t = A(\mu)y_t + R(\mu)y_t, \tag{18}$$

where $y_t(\theta) = y(t + \theta)$ for $\theta \in [-1, 0]$. For $\phi \in C^1[0, 1]$, define

$$A^* \phi(s) := \begin{cases} d\phi(s)/ds, & s \in (0, 1], \\ \int_{-1}^0 d\eta(t, 0)\phi(-t), & \theta = 0. \end{cases}$$

For $\psi, \phi \in C[-1, 0]$, define a bilinear form

$$\langle \phi, \psi \rangle = \bar{\phi}(0)\psi(0) - \int_{-1}^0 \int_{\xi=0}^{\theta} \bar{\phi}(\xi - \theta) d\eta(\theta)\psi(\xi) d\xi, \tag{19}$$

where $\eta(\theta) = \eta(\theta, 0)$. Then A^* and $A(0)$ are adjoint operators. By the discussion at the beginning of this section, we know that $\pm i\omega_0\tau_0$ are eigenvalues of $A(0)$. Thus, they are also eigenvalues of A^* .

It can be verified that $q(\theta) = e^{i\omega_0\tau_0\theta}$ is an eigenvector of $A(0)$ with respect to the eigenvalue $i\omega_0\tau_0$, and $q^*(s) = De^{i\omega_0\tau_0s}$ is an eigenvector of A^* with respect to the eigenvalue $-i\omega_0\tau_0$. Furthermore,

$$\langle q^*, q \rangle = 1, \quad \langle q^*, \bar{q} \rangle = 0,$$

where

$$D = \frac{1}{1 + \tau_0\gamma - i\omega_0\tau_0}. \tag{20}$$

Using the same notations as in Hassard et al. [10]; we first compute the center manifold C_0 at $\mu = 0$. Let y_t be the solution of Eq. (12) when $\mu = 0$. Define

$$z(t) = \langle q^*, y_t \rangle, \quad W(t, \theta) = y_t(\theta) - 2 \operatorname{Re}\{z(t)q(\theta)\}.$$

On the center manifold C_0 we have

$$W(t, z) = W(z(t), \bar{z}(t), \theta),$$

where

$$W(z, \bar{z}, \theta) = W_{20}(\theta) \frac{z^2}{2} + W_{11}(\theta)z\bar{z} + W_{02}(\theta) \frac{\bar{z}^2}{2} + W_{30}(\theta) \frac{z^3}{6} + \dots,$$

z and \bar{z} are local coordinates for the center manifold C_0 in the direction of q^* and \bar{q}^* . Note that W is real if y_t is real. We consider only real solutions. For a solution $y_t \in C_0$ of (12), since $\mu = 0$, we have

$$\begin{aligned} z'(t) &= i\omega_0\tau_0z + q^*(\theta)f(W + 2 \operatorname{Re}\{z(t)q(\theta)\}) \\ &= i\omega_0\tau_0z + \bar{q}^*(0)f(W(z, \bar{z}, 0) + 2 \operatorname{Re}\{z(t)q(0)\}) \\ &:= i\omega_0\tau_0z + \bar{q}^*(0)f_0(z, \bar{z}). \end{aligned}$$

We rewrite this equation as

$$z'(t) = i\omega_0\tau_0z + g(z, \bar{z}) \tag{21}$$

with

$$g(z, \bar{z}) = \bar{q}^*(0) f_0(z, \bar{z}) = g_{20} \frac{z^2}{2} + g_{11} z \bar{z} + g_{02} \frac{\bar{z}^2}{2} + g_{21} \frac{z^2 \bar{z}}{2} + \dots \tag{22}$$

By (18) and (21), we have

$$\begin{aligned} W' &= u'_t - z'q - \bar{z}'\bar{q} \\ &= \begin{cases} AW - 2\operatorname{Re}\{\bar{q}^*(0) f_0 q(\theta)\}, & \theta \in [-1, 0) \\ AW - 2\operatorname{Re}\{\bar{q}^*(0) f_0 q(0) + f_0\}, & \theta = 0 \end{cases} \\ &:= AW + H(z, \bar{z}, \theta), \end{aligned}$$

where

$$H(z, \bar{z}, \theta) = H_{20}(\theta) \frac{z^2}{2} + H_{11} z \bar{z} + H_{02}(\theta) \frac{\bar{z}^2}{2} + \dots \tag{23}$$

Expanding the above series and comparing the corresponding coefficients, we obtain

$$\begin{aligned} (A - 2i\omega_0 \tau_0) W_{20}(\theta) &= H_{20}(\theta), \\ AW_{11}(\theta) &= -H_{11}(\theta), \\ (A - 2i\omega_0 \tau_0) W_{02}(\theta) &= -H_{02}(\theta), \\ \dots & \end{aligned} \tag{24}$$

Note that $y_t = W(t, \theta) + zq(\theta) + \bar{z}\bar{q}(\theta)$ and $q(\theta) = e^{i\omega_0 \tau_0 \theta}$. We get

$$y(t - 1) = ze^{-i\omega_0 \tau_0} + \bar{z}e^{i\omega_0 \tau_0} + W_{20}(-1) \frac{z^2}{2} + W_{11}(-1) z \bar{z} + W_{02}(-1) \frac{\bar{z}^2}{2} + \dots$$

Therefore,

$$\begin{aligned} f_0 &= \tau_0 \gamma \left[\frac{aN^* - 2}{2} y^2(t - 1) - \frac{aN^* - 3}{6} y^3(t - 1) \right] + O(y^4(t - 1)) \\ &= \frac{\tau_0 \gamma (aN^* - 2)}{2} \left[e^{-2i\omega_0 \tau_0} z^2 + e^{2i\omega_0 \tau_0} \bar{z}^2 + 2z\bar{z} + 2e^{-2i\omega_0 \tau_0} W_{11}(-1) z^2 \bar{z} \right. \\ &\quad \left. + e^{2i\omega_0 \tau_0} W_{20}(-1) z^2 \bar{z} \right] - \frac{\tau_0 \gamma (aN^* - 3)}{6} 3e^{-i\omega_0 \tau_0} z^2 \bar{z} + \dots \end{aligned}$$

This relation and (22) imply

$$\begin{aligned} g(z, \bar{z}) = \bar{q}^*(0) f_0 = \bar{q}^*(0) &\left\{ \frac{\tau_0 \gamma (aN^* - 2)}{2} e^{-2i\omega_0 \tau_0} z^2 + \tau_0 \gamma (aN^* - 2) z \bar{z} \right. \\ &+ \frac{\tau_0 \gamma (aN^* - 2)}{2} e^{2i\omega_0 \tau_0} \bar{z}^2 + \left[\frac{\tau_0 \gamma (aN^* - 2)}{2} (2e^{-2i\omega_0 \tau_0} W_{11}(-1) \right. \\ &\left. \left. + e^{2i\omega_0 \tau_0} W_{20}(-1)) - \frac{\tau_0 \gamma (aN^* - 3)}{2} e^{-i\omega_0 \tau_0} \right] \right\} + \dots \end{aligned}$$

Comparing coefficients with (22) and using $\bar{q}^*(0) = \bar{D}$, we have

$$\begin{aligned}
 g_{20} &= \bar{D}\tau_0\gamma(aN^* - 2)e^{-2i\omega_0\tau_0}, \\
 g_{11} &= \bar{D}\tau_0\gamma(aN^* - 2), \\
 g_{02} &= \bar{D}\tau_0\gamma(aN^* - 2)e^{2i\omega_0\tau_0}, \\
 g_{21} &= \bar{D}[\tau_0\gamma(aN^* - 2)(e^{-i\omega_0\tau_0}W_{11}(-1) + e^{i\omega_0\tau_0}W_{20}(-1)) \\
 &\quad - \tau_0\gamma(aN^* - 3)e^{-i\omega_0\tau_0}].
 \end{aligned}
 \tag{25}$$

Since, for $\theta \in [-1, 0)$,

$$\begin{aligned}
 H(z, \bar{z}, \theta) &= -\bar{q}^*(0)f_0q(\theta) - q^*(0)\bar{f}_0\bar{q}(\theta) \\
 &= -g(z, \bar{z})q(\theta) - \bar{g}(z, \bar{z})\bar{q}(\theta),
 \end{aligned}$$

comparing coefficients with (23) we get,

$$\begin{aligned}
 H_{20}(\theta) &= -g_{20}q(\theta) - \bar{g}_{02}\bar{q}(\theta), \\
 H_{11}(\theta) &= -g_{11}q(\theta) - \bar{g}_{11}\bar{q}(\theta).
 \end{aligned}$$

Substituting these relations into (24) we can derive the following equation

$$W'_{20}(\theta) = 2i\omega_0\tau_0W_{20}(\theta) + g_{20}e^{i\omega_0\tau_0\theta} + \bar{g}_{02}e^{-i\omega_0\tau_0\theta}.$$

Solving for $W_{20}(\theta)$ we obtain

$$W_{20}(\theta) = -\frac{g_{20}}{i\omega_0\tau_0}e^{i\omega_0\tau_0\theta} - \frac{\bar{g}_{02}}{3i\omega_0\tau_0}e^{-i\omega_0\tau_0\theta} + E_1e^{2i\omega_0\tau_0\theta}.
 \tag{26}$$

Similarly,

$$W_{11}(\theta) = \frac{g_{11}}{i\omega_0\tau_0}e^{i\omega_0\tau_0\theta} - \frac{\bar{g}_{11}}{i\omega_0\tau_0}e^{-i\omega_0\tau_0\theta} + E_2,
 \tag{27}$$

where E_1 and E_2 are constants and will be determined in the following. From

$$H(z, \bar{z}, 0) = -2\operatorname{Re}\{\bar{q}^*(0)f_0q(0)\} + f_0,$$

we have

$$H_{20} = -g_{20} - \bar{g}_{02} + \tau_0\gamma(aN^* - 2)e^{-2i\omega_0\tau_0},$$

and

$$H_{11} = -g_{11} - \bar{g}_{11} + \tau_0\gamma(aN^* - 2).$$

From (24) and the definition of A we obtain

$$\begin{aligned}
 &\int_{-1}^0 d\eta(\theta) \left[\frac{ig_{20}}{\omega_0\tau_0}e^{i\omega_0\tau_0\theta} + \frac{i\bar{g}_{02}}{3\omega_0\tau_0}e^{i\omega_0\tau_0\theta} + E_1e^{2i\omega_0\tau_0\theta} \right] \\
 &= 2i\omega_0\tau_0 \left[\frac{ig_{20}}{\omega_0\tau_0} + \frac{i\bar{g}_{02}}{3\omega_0\tau_0} + E_1 \right] + g_{20} + \bar{g}_{02} - \tau_0\gamma(aN^* - 2)e^{-2i\omega_0\tau_0\theta}
 \end{aligned}$$

and

$$\int_{-1}^0 d\eta(\theta) \left[\frac{g_{11}}{\omega_0 \tau_0} e^{i\omega_0 \tau_0 \theta} + \frac{\bar{g}_{11}}{\omega_0 \tau_0} e^{-i\omega_0 \tau_0 \theta} + E_2 \right] = g_{11} + \bar{g}_{11} - \tau_0 \gamma (aN^* - 2).$$

Thus,

$$E_1 = \frac{\tau_0 \gamma (aN^* - 2) e^{-2i\omega_0 \tau_0 \theta}}{2i\omega_0 \tau_0 - \int_{-1}^0 e^{2i\omega_0 \tau_0 \theta} d\eta(\theta)}$$

and

$$E_2 = \frac{\tau_0 \gamma (aN^* - 2)}{\int_{-1}^0 d\eta(\theta)}.$$

From the definition of $\eta(\theta)$, we have

$$E_1 = \frac{\gamma (aN^* - 2) e^{-2i\omega_0 \tau_0 \theta}}{2i\omega_0 + \gamma [1 + (aN^* - 1) e^{-i\omega_0 \tau_0 \theta}]}$$

and

$$E_2 = \frac{aN^* - 2}{aN^*}.$$

Substituting E_1 and E_2 into (26) and (27), respectively, we obtain

$$W_{20}(-1) = \frac{ig_{20}}{\omega_0 \tau_0} e^{i\omega_0 \tau_0} + \frac{i\bar{g}_{02}}{3\omega_0 \tau_0} e^{i\omega_0 \tau_0} + \frac{\gamma (aN^* - 2)}{2i\omega_0 + \gamma [1 + (aN^* - 1) e^{-2i\omega_0 \tau_0}]}$$

and

$$W_{11}(-1) = \frac{ig_{11}}{\omega_0 \tau_0} e^{-i\omega_0 \tau_0} + \frac{i\bar{g}_{11}}{\omega_0 \tau_0} e^{i\omega_0 \tau_0} + \frac{aN^* - 2}{aN^*}.$$

Hence we get

$$\begin{aligned} g_{21} = \bar{D} \left\{ \tau_0 \gamma (aN^* - 2) \left[-\frac{2ig_{11}}{\omega_0 \tau_0} e^{-2i\omega_0 \tau_0} + \frac{2i\bar{g}_{11}}{\omega_0 \tau_0} + \frac{2(aN^* - 2)}{aN^*} e^{-i\omega_0 \tau_0} \right] \right. \\ \left. + \frac{ig_{20}}{\omega_0 \tau_0} + \frac{i\bar{g}_{02}}{3\omega_0 \tau_0} e^{2i\omega_0 \tau_0} + \frac{\gamma (aN^* - 2) e^{i\omega_0 \tau_0}}{2i\omega_0 + \gamma [1 + (aN^* - 1) e^{-2i\omega_0 \tau_0}]} \right] \\ \left. - \tau_0 \gamma (aN^* - 3) e^{-i\omega_0 \tau_0} \right\}. \end{aligned} \tag{28}$$

Substituting expressions for g_{20} , g_{11} , g_{02} and (28) into the following relation

$$C_1(0) = \frac{i}{2\omega_0 \tau_0} \left(g_{20} g_{11} - 2|g_{11}|^2 - \frac{1}{3} |g_{02}|^2 \right) + \frac{g_{21}}{2},$$

we have

$$\begin{aligned}
 C_1(0) = & -i \frac{D\bar{D}\tau_0\gamma(aN^* - 2)}{6\omega_0} + \frac{\gamma}{2(aN^* - 1)} \left\{ \frac{\tau_0(aN^* - 2)^2}{3\Delta^2\omega_0\gamma^3(aN^* - 1)^3} \right. \\
 & \times \{ [4\omega_0\gamma(\gamma^2 - \omega_0^2)((1 + \tau_0\gamma)^2) - \omega_0^2\tau_0^2] \\
 & + 2\omega_0\tau_0(1 + \tau_0\gamma)(\gamma^4 + \omega_0^4 - 6\omega_0^2\gamma^2) \\
 & + i[(1 + \tau_0\gamma)^2 - \omega_0^2\gamma^2](\gamma^4 + \omega_0^4 - 6\omega_0^2\gamma_0^2) \\
 & - 8\omega_0^2\gamma\tau_0(1 + \tau_0\gamma)(\gamma^2 - \omega_0^2) \} \\
 & - \frac{2\tau_0(aN^* - 2)^2}{\Delta aN^*\gamma} \{ [\gamma(1 + \tau_0\gamma) + \omega_0^2\tau_0] + i[\omega_0(1 + \tau_0\gamma) - \omega_0\tau_0\gamma] \} \\
 & + \frac{\tau_0(aN^* - 3)}{\Delta\gamma} \{ [\gamma(1 + \tau_0\gamma) + \omega_0^2\tau_0] + i[\omega_0(1 + \tau_0\gamma) - \omega_0\tau_0\gamma] \} \\
 & \left. + \frac{\tau_0(aN^* - 2)^2}{\Delta} \frac{[\omega_0^2\tau_0 - \gamma(1 + \tau_0\gamma)] + i[\omega_0(1 + \tau_0\gamma) + \omega_0\tau_0\gamma]}{\gamma + \frac{\gamma^2 - \omega_0^2}{\gamma(aN^* - 1)} + i2\omega_0 \frac{aN^*}{aN^* - 1}} \right\},
 \end{aligned}$$

and its real part

$$\begin{aligned}
 \text{Re}C_1(0) = & \frac{\gamma}{2(aN^* - 1)} \left\{ \frac{\tau_0(aN^* - 2)^2}{3\Delta^2\omega_0\gamma^3(aN^* - 1)^3} [2\gamma(\gamma^2 - \omega_0^2)(1 + \tau_0\gamma)^2 - \omega_0^2\tau_0^2] \right. \\
 & + \tau_0(1 + \tau_0\gamma)(\gamma^4 + \omega_0^4 - 6\omega_0^2\gamma_0^2) - \frac{2\tau_0(aN^* - 2)^2}{\Delta aN^*\gamma} (\gamma + \tau_0\gamma^2 + \omega_0^2\tau_0) \\
 & + \frac{\tau_0(aN^* - 3)}{\Delta\gamma} (\gamma + \tau_0\gamma^2 + \omega_0^2\tau_0) + \frac{\tau_0(aN^* - 2)^2}{\Delta} \\
 & \left. \times \frac{(\omega^2\tau_0 - \gamma - \tau_0\gamma^2) \frac{\gamma^2 aN^* - \omega_0^2}{\gamma(aN^* - 1)} + (\omega_0 + 2\omega_0\tau_0\gamma)2\omega_0 \frac{aN^*}{aN^* - 1}}{\frac{(\gamma^2 aN^* - \omega_0^2)^2}{(\gamma(aN^* - 1))^2} + 4\omega^2 \frac{aN^{*2}}{(aN^* - 1)^2}} \right\}, \tag{29}
 \end{aligned}$$

where

$$\Delta = (1 + \tau_0\gamma)^2 + \omega_0^2\tau_0^2.$$

Set

$$\beta_2 = 2 \text{Re} C_1(0), \quad \mu_2 = \frac{-\text{Re} C_1(0)}{\tau_0\alpha'(\tau_0)}, \tag{30}$$

where

$$\alpha'(\tau_0) = \frac{1}{\Delta} (aN^* - 1)\omega_0 \sin \omega_0\tau_0.$$

Then a general result for the direction and stability of Hopf bifurcation, see e.g. Hassard et al. [10, Chapter 1, Section 4], implies that the direction of the Hopf bifurcation is determined by the sign of β_2 , and the stability of the bifurcating periodic solutions is determined by the sign of μ_2 . Since $\alpha'(\tau_0) > 0$, we thus have the following result.

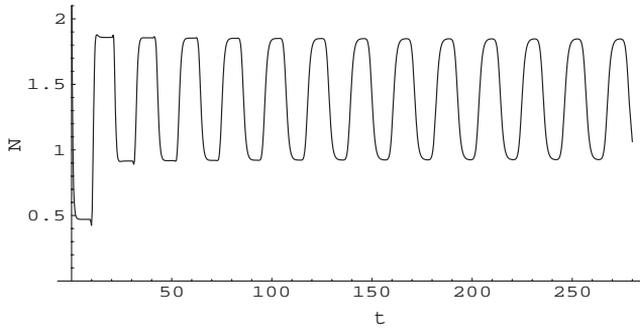


Fig. 1. A Mathematica simulation of a periodic solution to system (1) with $\tau = 10.2$ and $a = 1.5$, $\gamma = 2$, $p = 16$. The delay τ is between the two Hopf bifurcation values $\tau_1 = 8.20$ and $\tau_2 = 15.93$.

Theorem 3.1. *Let $\text{Re } C_1(0)$ be given in (29). Then,*

- (a) *the Hopf bifurcation occurs as τ crosses τ_0 to the right if $\text{Re } C_1(0) < 0$, and to the left if $\text{Re } C_1(0) > 0$; and*
- (b) *the bifurcating periodic solution is stable if $\text{Re } C_1(0) < 0$ and unstable if $\text{Re } C_1(0) > 0$.*

Theorem 3.1 provides an explicit algorithm for detecting the direction and stability of the Hopf bifurcation at $\tau = \tau_0$. For instance, if the parameter values are chosen as $a = 1.5$, $\gamma = 2$, and $p = 16$, then the relation $p > \gamma e^2$ holds. Furthermore, by (29) we have $\text{Re} C_1(0) \doteq -0.494456 < 0$ (and thus $\beta_2 < 0$ and $\mu_2 > 0$ by (30)). Therefore, by Theorem 3.1, the bifurcation takes place when τ crosses τ_0 to the right ($\tau > \tau_0$), and the bifurcating periodic solution is asymptotically stable. We have carried out numerical simulations on system (1) using Mathematica with these parameter values, and for different choices of initial conditions and for different delays. The simulations support our theoretical result. Moreover, the simulations consistently show the global existence of asymptotically periodic solutions: existence of periodic solutions for values of τ far away from τ_0 , and solutions from various initial conditions converge to the periodic solution. In Fig. 1, we show one of the simulations using $a = 1.5$, $\gamma = 2$, and $p = 16$. In this case it can be calculated that, for $k = 0, 1, 2, \dots$, $\tau_k \doteq 0.48, 8.20, 15.93, 23.66, 31.39, 39.12, \dots$. The delay $\tau = 10.2$ is between the two Hopf bifurcation values $\tau_1 = 8.20$ and $\tau_2 = 15.93$. A periodic solution of amplitude 1 is shown in Fig. 1. These numerical simulations also motivated our theoretical investigation of the global existence of periodic solutions in the next section.

4. Global Hopf bifurcation

In this section we study the global continuation of the local Hopf branch bifurcating from the point $(0, \tau_k)$, $k = 0, 1, 2, \dots$, for Eq. (10). For convenience of the reader, we copy Eq. (10) in the following.

$$y'(t) = -\gamma\tau[y(t) + aN^*(1 - e^{-y(t-1)}) - y(t-1)e^{-y(t-1)}]. \tag{31}$$

We use the following notations:

$$\mathcal{C} = C([-1, 0], \mathbb{R}),$$

$$\Sigma = \text{Cl}\{(y, \tau, T) : y \text{ is a } T\text{-periodic solution of (31)}\} \subset X \times \mathbb{R}_+ \times \mathbb{R}_+,$$

$$N = \{(\hat{y}, \tau, T) : \hat{y} + aN^*(1 - \hat{y}) - \hat{y}e^{-\hat{y}} = 0\}.$$

Let $C(0, \tau_k, 2\pi/(\tau_k\omega_0))$ denote the connected component of $(0, \tau_k, 2\pi/(\tau_k\omega_0))$ in Σ , where τ_k and ω_0 are defined in (8) and (9), respectively.

Lemma 4.1. *All periodic solutions to (31) are uniformly bounded.*

Proof. Let $y(t)$ be a nonconstant periodic solution to (31), and $y(t_1) = M$, $y(t_2) = m$ be its maximum and minimum, respectively. Then, $y'(t_1) = y'(t_2) = 0$, and by (31),

$$M = y(t_1 - 1)e^{-y(t_1-1)} - aN^*[1 - e^{-y(t_1-1)}], \tag{32}$$

$$m = y(t_2 - 1)e^{-y(t_2-1)} - aN^*[1 - e^{-y(t_2-1)}]. \tag{33}$$

We claim that $y(t_1 - 1) < 0$ and $y(t_2 - 1) > 0$. In fact, if $y(t_1 - 1) = 0$, then (32) implies $M = 0$, and thus $m < 0$ and $y(t_2 - 1) \leq 0$. Using (33) we know $y(t_2 - 1) < 0$, and thus

$$m > y(t_2 - 1)e^{-y(t_2-1)},$$

which contradicts the fact that m is the minimum. If $y(t_1 - 1) > 0$, then, by (32), we arrive at

$$M \leq M - aN^*(1 - e^{-y(t_1-1)}) < M,$$

a contradiction. Therefore, $y(t_1 - 1) < 0$. A similar argument can show that $y(t_2 - 1) > 0$. Therefore, we have $m < 0$ and $M > 0$. Again, by (32) and (33), we have

$$m > aN^*[e^{-M} - 1] > -aN^*. \tag{34}$$

Also by (32) we have

$$\begin{aligned} M &= -aN^* + (y(t_1 - 1) + aN^*)e^{-y(t_1-1)} \\ &= -aN^* + e^{aN^*}(y(t_1 - 1) + aN^*)e^{-(y(t_1-1)+aN^*)} \\ &\leq -aN^* + e^{aN^*}e^{-1} = -aN^* + e^{aN^*-1}. \end{aligned} \tag{35}$$

Here we have used the fact that $y(t_1 - 1) + aN^* > m + aN^* > 0$ and that $xe^{-x} < e^{-1}$ for $x \geq 0$. Relations (34) and (35) imply uniform boundedness of the periodic solutions. \square

Lemma 4.2. *Assume that $\gamma e^2 < p < \sqrt{2}\gamma e^2$. Then (31) has no periodic solutions of period 4.*

Proof. Let $y(t)$ be a periodic solution to (31) of period 4. Set $u_j(t) = y(t - j + 1)$, $j = 1, 2, 3, 4$. Then $u(t) = (u_1(t), u_2(t), u_3(t), u_4(t))$ is a periodic solution to the following system of ordinary differential equations:

$$u'_1(t) = -\gamma\tau[u_1(t) + aN^*(1 - e^{-u_2(t)}) - u_2(t)e^{-u_2(t)}]$$

$$\begin{aligned}
 u_2'(t) &= -\gamma\tau[u_2(t) + aN^*(1 - e^{-u_3(t)}) - u_3(t)e^{-u_3(t)}] \\
 u_3'(t) &= -\gamma\tau[u_3(t) + aN^*(1 - e^{-u_4(t)}) - u_4(t)e^{-u_4(t)}] \\
 u_4'(t) &= -\gamma\tau[u_4(t) + aN^*(1 - e^{-u_1(t)}) - u_1(t)e^{-u_1(t)}],
 \end{aligned}
 \tag{36}$$

whose orbit belongs to the region

$$G = \{u \in \mathbf{R}^4 \mid \bar{m} < |u_k| < \bar{M}, \quad k = 1, 2, 3, 4\}
 \tag{37}$$

where \bar{m} and \bar{M} are a pair of uniform bounds for periodic solutions of (31) obtained in Lemma 4.1. To rule out four-periodic solutions of (31), it suffices to prove the nonexistence of nonconstant periodic solutions of (36) in the region G . To do the latter, we use a general Bendixson’s criterion in higher dimensions developed in Li and Muldowney [18]. More specifically, we will apply Corollary 3.5 in [18]. The Jacobian matrix $J = J(u)$ of (36), for $u \in \mathbf{R}^4$, is

$$J(u) = -\gamma\tau \begin{pmatrix} 1 & f(u_2) & 0 & 0 \\ 0 & 1 & f(u_3) & 0 \\ 0 & 0 & 1 & f(u_4) \\ f(u_1) & 0 & 0 & 1 \end{pmatrix},$$

where

$$f(v) = (aN^* + v - 1)e^{-v}.
 \tag{38}$$

The second additive compound matrix $J^{[2]}(u)$ of $J(u)$ is, see ([3] and [20]),

$$J^{[2]}(u) = -\gamma\tau \begin{pmatrix} 2 & f(u_3) & 0 & 0 & 0 & 0 \\ 0 & 2 & f(u_4) & f(u_2) & 0 & 0 \\ 0 & 0 & 2 & 0 & f(u_2) & 0 \\ 0 & 0 & 0 & 2 & f(u_4) & 0 \\ -f(u_1) & 0 & 0 & 0 & 2 & f(u_3) \\ 0 & -f(u_1) & 0 & 0 & 0 & 2 \end{pmatrix}.$$

Choose a vector norm in \mathbf{R}^6 as

$$|(x_1, x_2, x_3, x_4, x_5, x_6)| = \max\{\sqrt{2}|x_1|, |x_2|, \sqrt{2}|x_3|, \sqrt{2}|x_4|, |x_5|, \sqrt{2}|x_6|\}.$$

Then, with respect to this norm, the Lozinskiĭ measure $\mu(J^{[2]}(u))$ of the matrix $J^{[2]}(u)$ is, see [1],

$$\begin{aligned}
 \mu(J^{[2]}(u)) &= \max\{\sqrt{2}\gamma\tau(-\sqrt{2} + |f(u_3)|), \sqrt{2}\gamma\tau(-\sqrt{2} + |f(u_4)|/2 + |f(u_2)|/2), \\
 &\quad \sqrt{2}\gamma\tau(-\sqrt{2} + |f(u_2)|), \sqrt{2}\gamma\tau(-\sqrt{2} + |f(u_4)|), \\
 &\quad \sqrt{2}\gamma\tau(-\sqrt{2} + |f(u_1)|/2 + |f(u_3)|/2), \sqrt{2}\gamma\tau(-\sqrt{2} + |f(u_1)|)\}.
 \end{aligned}
 \tag{39}$$

By Corollary 3.5 in [18], system (36) has no periodic orbits in G if $\mu(J^{[2]}(u)) < 0$ for all $u \in G$. From (39), we see that $\mu(J^{[2]}(u)) < 0$ if and only if

$$|f(u_j)| < \sqrt{2}, \quad j = 1, 2, 3, 4,
 \tag{40}$$

for $u \in G$. To establish (40), we first use the assumption $e^{aN^*} = p/\gamma < \sqrt{2}e^2$ to improve the lower bound m given in Lemma 4.1. In (33), we now have

$$y(t_2 - 1) + aN^* < M + aN^* < e^{aN^*-1} < \sqrt{2}e.$$

Using the fact that the function xe^{-x} is monotonically decreasing for $x > 1$ and that $y(t_2 - 1) + aN^* > 1$, we have

$$\begin{aligned} m &= -aN^* + e^{aN^*} (y(t_2 - 1) + aN^*)e^{-(y(t_2-1)+aN^*)} \\ &> -aN^* + e^{aN^*} \sqrt{2}e e^{-\sqrt{2}e} > -aN^* + 2e^2 \sqrt{2}e e^{-\sqrt{2}e} \\ &= -aN^* + 2\sqrt{2}e^{3-\sqrt{2}e}. \end{aligned}$$

Therefore, $u \in G$ satisfies

$$|u_i| > -aN^* + 2\sqrt{2}e^{3-\sqrt{2}e}.$$

For $\delta = 2\sqrt{2}e^{3-\sqrt{2}e} > 1$, we can verify

$$|f(-aN^* + \delta)| = e^{aN^*-\delta} |\delta - 1| = e^{aN^*-2} e^{2-\delta} (\delta - 1) < e^{aN^*-2}.$$

Using the graph of $f(v)$ we know that $f(v)$ has a global maximum $e^{aN^*-2} = e^{-2}p/\gamma$. Therefore, for $u \in G$,

$$|f(u_k)| \leq \max \{e^{aN^*-2}, |f(-aN^* + \delta)|\} \leq e^{aN^*-2} = \frac{P}{\gamma} e^{-2} < \sqrt{2}.$$

and (40) is satisfied, completing the proof. \square

Lemma 4.3. *Assume that $\gamma e^2 < p$. Then (31) has no periodic solutions of period 1 or 2.*

Proof. First note that any nonconstant 1-periodic solution $u(t)$ of (31) is also a nonconstant periodic solution of the ordinary differential equation

$$u'(t) = -\gamma\tau(1 - e^{-u(t)})(u(t) + aN^*). \tag{41}$$

A simple phase-line analysis shows that Eq. (41) has no nonconstant periodic solutions.

As in the proof of Lemma 4.2, if $u(t)$ is a periodic solution of (31) of period 2, then $u_1(t) = u(t)$ and $u_2(t) = u(t - 1)$ are periodic solution of the system of ordinary differential equations

$$\begin{aligned} u_1'(t) &= -\gamma\tau[u_1(t) + aN^*(1 - e^{-u_2(t)}) - u_2(t)e^{-u_2(t)}] \\ u_2'(t) &= -\gamma\tau[u_2(t) + aN^*(1 - e^{-u_1(t)}) - u_1(t)e^{-u_1(t)}]. \end{aligned} \tag{42}$$

Let $(P(u_1, u_2), Q(u_1, u_2))$ denote the vector field of (42), then

$$\frac{\partial P}{\partial u_1} + \frac{\partial Q}{\partial u_2} = -2\gamma\tau < 0$$

for all (u_1, u_2) . Thus the classical Bendixson's negative criterion implies that (42) has no nonconstant periodic solutions. \square

Theorem 4.4. *Suppose that $\gamma e^2 < p < \sqrt{2}\gamma e^2$ holds. Then, for each $\tau > \tau_k$, $k=0, 1, 2, \dots$, Eq. (31) has at least $k + 1$ periodic solutions, where τ_k is defined in (8).*

Proof. First note that

$$F(y^t, \tau, 1) := -\gamma\tau[y(t) + aN^*(1 - e^{y(t-1)}) - y(t-1)e^{-y(t-1)}]$$

satisfies the hypotheses (A_1) , (A_2) and (A_3) in Wu [30, p. 4813], with

$$(\hat{y}_0, \alpha_0, p_0) = \left(0, \tau_k, \frac{2\pi}{\tau_k\omega_0}\right),$$

$$\nabla_{(0, \tau_k, 2\pi/\tau_k\omega_0)}(z) = z + \tau\gamma + \tau\gamma[aN^* - 1]e^{-z}.$$

It can also be verified that $(0, \tau_k, 2\pi/\tau_k\omega_0)$ are isolated centers (see Wu [30, p. 4813]).

By Lemma 2.1 and Proposition 2.2, there exist $\varepsilon > 0$, $\delta > 0$, and smooth curve $z : (\tau_k - \delta, \tau_k + \delta) \rightarrow \mathbb{C}$ such that $\Delta(z(\tau)) = 0$, $|z(\tau) - i\tau_k\omega_0| < \varepsilon$ for all $\tau \in [\tau_k - \delta, \tau_k + \delta]$, and

$$z(\tau_k) = i\tau_k\omega_0, \quad \left. \frac{d \operatorname{Re} z(\tau)}{d\tau} \right|_{\tau=\tau_k} > 0.$$

Denote $T_k = 2\pi/(\tau_k\omega_0)$, and let

$$\Omega_\varepsilon = \{(0, T) : 0 < u < \varepsilon, |T - T_k| < \varepsilon\}.$$

Clearly, if $|\tau - \tau_k| \leq \delta$ and $(u, p) \in \partial\Omega_\varepsilon$ such that $\Delta_{(0, \tau, T)}(u + 2\pi i/T) = 0$, then $\tau = \tau_k$, $u = 0$, and $T = T_k$. This verifies assumption (A_4) in Wu [30] for $m = 1$. Moreover, if we put

$$H^\pm \left(0, \tau_k, \frac{2\pi}{\tau_k\omega_0}\right) (u, T) = \Delta_{(0, \tau_k \pm \delta, T)} \left(u + i \frac{2\pi}{T}\right),$$

then we have the cross number (see Wu [30])

$$\begin{aligned} \gamma_1 \left(0, \tau_k, \frac{2\pi}{\tau_k\omega_0}\right) &= \operatorname{deg}_B \left(H^- \left(0, \tau_k, \frac{2\pi}{\tau_k\omega_0}\right), \Omega_\varepsilon\right) \\ &\quad - \operatorname{deg}_B \left(H^+ \left(0, \tau_k, \frac{2\pi}{\tau_k\omega_0}\right), \Omega_\varepsilon\right) = -1. \end{aligned}$$

By Theorem 3.3 of Wu [30], we conclude that the connected component $C(0, \tau_k, 2\pi/(\tau_k\omega_0))$ through $(0, \tau_k, 2\pi/(\tau_k\omega_0))$ in Σ is nonempty. Meanwhile, we have

$$\sum_{(\hat{y}, \tau, T) \in C(0, \tau_k, \frac{2\pi}{\tau_k\omega_0})} p_1(\hat{y}, \tau, T) < 0,$$

and hence $C(0, \tau_k, 2\pi/(\tau_k\omega_0))$ is unbounded.

Lemma 4.1 implies that the projection of $C(0, \tau_k, 2\pi/(\tau_k\omega_0))$ onto the y -space is bounded. It can be verified using a phase-line analysis that, when $\tau = 0$, Eq. (31) has no nonconstant

periodic solutions. Therefore, the projection of $C(0, \tau_k, 2\pi/(\tau_k\omega_0))$ onto the τ -space is bounded below. From the definition of τ_k in (8) and that of ω_0 in (9), we obtain

$$\tau_k\omega_0 = \sin^{-1} \left(\frac{\sqrt{aN^*(aN^* - 2)}}{aN^* - 1} \right) + 2k\pi \quad (43)$$

for $k \geq 0$. Also, from (6) we know that $\sin \omega_0\tau_k > 0$ and $\cos \omega_0\tau_k < 0$, for $k \geq 0$. Hence

$$\frac{\pi}{2} < \omega_0\tau_0 < \pi, \quad \text{and} \quad 2\pi < \omega_0\tau_k < (2k + 1)\pi, \quad k \geq 1.$$

Therefore

$$2 < \frac{2\pi}{\tau_0\omega_0} < 4, \quad \text{and} \quad \frac{1}{k + 1} < \frac{2\pi}{\omega_0\tau_k} < 1, \quad k \geq 1. \quad (44)$$

Applying Lemmas 4.2 and 4.3 we know that $2 < T < 4$ if $(y, \tau, T) \in C(0, \tau_0, 2\pi/(\tau_0\omega_0))$, and that $1/(k + 1) < T < 1$ if $(y, \tau, T) \in C(0, \tau_k, 2\pi/(\tau_k\omega_0))$ for $k \geq 1$. This shows that in order for $C(0, \tau_k, 2\pi/(\tau_k\omega_0))$ to be unbounded, its projection onto the τ -space must be unbounded. Consequently, the projection of $C(0, \tau_k, 2\pi/(\tau_k\omega_0))$ onto the τ -space includes $[\tau_k, \infty)$. This shows that, for each $\tau > \tau_k$, Eq. (31) has $k + 1$ nonconstant periodic solutions, completing the proof of the theorem. \square

Remarks. 1. From the proof of Theorem 4.4, we know that the first global Hopf branch contains periodic solutions of period between 2 and 4. These are the slowly-oscillating periodic solutions. The τ_k branches, for $k \geq 1$, since the periods are less than 1, contain fast-oscillating periodic solutions.

2. For $k \geq 1$,

$$\frac{1}{k + 1} < \frac{2\pi}{\tau_k\omega_0} < 1$$

automatically holds. The bounds on the period T for $(y, \tau, T) \in C(0, \tau_k, 2\pi/(\tau_k\omega_0))$ hold without resulting to Lemma 4.2. Thus, the global extension of the τ_k -branch for $k \geq 1$ can be proved without the restriction $p < \sqrt{2}\gamma e^2$.

Acknowledgements

This research is supported in part by grants from the National Natural Science Foundation of China (J. Wei), the Natural Sciences and Engineering Research Council of Canada (M. Li), and the National Science Foundation (M. Li).

References

- [1] W.A. Coppel, *Stability and Asymptotic Behavior of Differential Equations*, Health, Boston, 1965.
- [2] Q.X. Feng, J.R. Yan, Global attractivity and oscillation in a kind of Nicholson's blowflies, *J. Biomath.* 17 (2002) 21–26.
- [3] M. Fiedler, Additive compound matrices and inequality for eigenvalues of stochastic matrices, *Czech. Math. J.* 99 (1974) 392–402.

- [4] S.A. Gourley, Travelling fronts in the diffusive Nicholson's blowflies equation with distributed delays, *Math. Comput. Modelling* 32 (2000) 843–853.
- [5] S.A. Gourley, S. Ruan, Dynamics of the diffusive Nicholson's blowflies equation with distributed delay, *Proc. Roy. Soc. Edinburgh Sect. A* 130 (2000) 1275–1291.
- [6] M.S. Gurney, S.P. Blythe, R.M. Nisbee, Nicholson's blowflies revisited, *Nature* 287 (1980) 17–21.
- [7] I. Györi, G. Ladas, *Oscillation Theory of Delay Differential Equations with Applications*, Oxford University Press, Oxford, 1991.
- [8] I. Györi, S.I. Trofimchuk, On the existence of rapidly oscillatory solutions in the Nicholson blowflies equation, *Nonlinear Anal. Ser. A: Theory Methods* 48 (2002) 1033–1042.
- [9] J.K. Hale, *Theory of Functional Differential Equations*, Springer, New York, 1977.
- [10] B.D. Hassard, N.D. Kazarinoff, Y.H. Wan, *Theory and Applications of Hopf Bifurcation*, Cambridge University Press, Cambridge, 1981.
- [11] V.Lj. Kocić, G. Ladas, Oscillation and global attractivity in a discrete model of Nicholson's blowflies, *Appl. Anal.* 38 (1990) 21–31.
- [12] G. Karakostas, Ch.G. Philos, Y.G. Sficas, The dynamics of some discrete population models, *Nonlinear Anal. Theory Methods Appl.* 17 (1991) 1069–1084.
- [13] M.R.S. Kulenovic, G. Ladas, Linearized oscillations in population dynamics, *Bul. Math. Bio.* 49 (1987) 615–627.
- [14] M.R.S. Kulenovic, G. Ladas, Y.G. Sficas, Global attractivity in population dynamics, *Comput. Math. Appl.* 18 (1989) 925–928.
- [15] M.R.S. Kulenovic, G. Ladas, Y.G. Sficas, Global attractivity in Nicholson's blowflies, *Appl. Anal.* 43 (1992) 109–124.
- [16] J. Li, Global attractivity in Nicholson's blowflies, *Appl. Math. Ser. B* 11 (1996) 425–434.
- [17] J. Li, Global attractivity in a discrete model of Nicholson's blowflies, *Ann. Differential Equations* 12 (1996) 173–182.
- [18] M.Y. Li, J.S. Muldowney, On Bendixson's criterion, *J. Differential Equations* 106 (1994) 27–39.
- [19] M. Li, J. Yan, Oscillation and global attractivity of generalized Nicholson's blowfly model, in: *Differential Equations and Computational Simulations* (Chengdu, 1999), World Sci. Publishing, River Edge, NJ, 2000, pp. 196–201.
- [20] J.S. Muldowney, Compound matrices and ordinary differential equations, *Rocky Mountain J. Math.* 20 (1990) 857–871.
- [21] S. Ruan, J. Wei, On the zeros of transcendental functions with applications to stability of delay differential equations, *Dynam. Cont. Discr. Impul. Sys. Series A: Math. Anal.*
- [22] S.H. Saker, S. Agarwal, Oscillation and global attractivity in a periodic Nicholson's blowflies model, *Math. Comput. Modelling* 35 (2002) 719–731.
- [23] J.W.-H. So, J.S. Yu, Global attractivity and uniform persistence in Nicholson's blowflies, *Diff. Equ. Dyn. Sys.* 2 (1994) 11–18.
- [24] J.W.-H. So, J.S. Yu, On the stability and uniform persistence of a discrete model of Nicholson's blowflies, *J. Math. Anal. Appl.* 193 (1995) 233–244.
- [25] J.W.-H. So, Y. Yang, Dirichlet problem for the diffusive Nicholson's blowflies equation, *J. Differential Equations* 150 (1998) 317–348.
- [26] J.W.-H. So, J. Wu, Y. Yang, Numerical steady state and Hopf bifurcation analysis on the diffusive Nicholson's blowflies equation, *Appl. Math. Comput.* 111 (2000) 33–51.
- [27] J.W.-H. So, X. Zou, Traveling waves for the diffusive Nicholson's blowflies equation, *Appl. Math. Comput.* 122 (2001) 385–392.
- [28] P. Weng, M. Liang, Existence and global attractivity of periodic solution of a model in population dynamics, *Acta Math. Appl. Sinica (English Ser.)* 12 (1996) 427–434.
- [29] J. Wu, *Theory and Applications of Partial Functional-Differential Equations*, Applied Mathematical Sciences, vol. 119, Springer, New York, 1996.
- [30] J. Wu, Symmetric functional differential equations and neural networks with memory, *Trans. Amer. Math. Soc.* 350 (1998) 4799–4838.
- [31] B.G. Zhang, H.X. Xu, A note on the global attractivity of a discrete model of Nicholson's blowflies, *Discrete Dyn. Nat. Soc.* 3 (1999) 51–55.