# DYNAMICS OF A TWO-PATCH NICHOLSON'S BLOWFLIES MODEL WITH RANDOM DISPERSAL\*

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**Abstract** The global dynamics of the Nicholson's blowfly reaction-diffusion model with zero Dirichlet boundary condition is less understood. In this paper, we provide a discrete version of diffusive Nichlson's blowflies equation with zero Dirichlet boundary condition. Local and global stability of the equilibria are obtained by some comparison arguments, fluctuation method and the theory of exponential ordering. Hopf bifurcation at the positive equilibrium and the global existence of the periodic solutions are studied by local and global Hopf bifurcation theory.

**Keywords** Nicholson's blowflies model, Dirichlet boundary condition, stability, Hopf bifurcations.

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### 1. Introduction

Gurney et al. [9] proposed the following delayed model

$$\frac{du(t)}{dt} = -\delta u(t) + pu(t-\tau)e^{-au(t-\tau)}$$
(1.1)

to describe the population dynamics of the Australian sheep-blowfly, hoping to explain the oscillatory phenomena in Nicholson's laboratory experiments [15]. Here p is the maximum per capita daily egg production rate, 1/a is the size at which the blowfly population reproduces at its maximum rate,  $\delta$  is the per capita daily adult death rate, and  $\tau$  is the generation time. Since the numerical solutions of (1.1) in [9] agree with the real data of the Nicholson's laboratory experiments [15] very well, (1.1) has been widely quoted as the Nicholson blowflies equation and has been extensively studied in the literature, see e.g. [2, 12, 23] and references therein. Considering the mobility of the adults and immobility of eggs, Yang and So [27] extended (1.1) to the following diffusive form

$$\frac{du(t,x)}{dt} = d\Delta u(t,x) - \delta u(t,x) + pu(t-\tau)e^{-au(t-\tau)}, \ x \in \Omega,$$
(1.2)

which is known as the diffusive Nicholson's blowfly model. For (1.2) with Neumann boundary condition, Yang and So [27] obtained results on the global attractivity of

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positive steady state and the existence of Hopf bifurcations. When zero Dirichlet boundary condition

$$u(t,x) = 0, \text{ on } (0,\infty) \times \partial\Omega, \tag{1.3}$$

is imposed, numerics suggests there is rich dynamics that is less understood. So and Yang [20] and Yi et al. [28] studied the global attractivity of the steady states. In particular, they obtained that:

(R) Assume  $p/\delta \in (1, e^2]$ , if  $p > d\lambda_1 + \delta$  then there exists a unique positive steady state which attracts all solutions of (1.2)-(1.3) with the positive initial value, where  $\lambda_1$  is the principle eigenvalue of  $-\Delta$ .

This result implies that for any delay  $\tau$ , the newly bifurcated positive steady state is globally asymptotically stable when the diffusion coefficient d is small enough. Then a natural question is : when  $p \gg d\lambda_1 + \delta$ , would the stability of the positive steady state depends on time delay  $\tau$ ? In such a case, So et al. [19] proposed a numerical scheme to verify that time delay can destabilize the positive steady state due to the occurrence of periodic solutions.

In 1996, Busenberg and Huang [3] first studied the Hopf bifurcating periodic solutions arising from the positive steady state of the delayed reaction diffusion equation with the zero Dirichlet boundary condition. For the following Hutchison equation:

$$\begin{cases} \frac{\partial u(t,x)}{\partial t} = \frac{\partial^2 u(t,x)}{\partial^2 x^2} + ku(t,x)[1-u(t-r,x)], \ t > 0, \\ u(t,0) = u(t,\pi) = 0, \ t \ge 0. \end{cases}$$

Combining the Lyapunov-Schmidt reduction and the implicit function theorem, they proved that for each fixed k > 1,  $0 < k - 1 \ll 1$ , there is an r(k) > 0 such that the steady state  $u_k$  is locally stable if  $0 \le r < r(k)$  and unstable if r > r(k). Moreover, there exists a sequence  $\{r_{k_n}\}_{n=0}^{\infty}$ ,  $r(k) = r_{k_0} < r_{k_1} < \cdots$ , such that there is a Hopf bifurcation arising from  $u_k$  as the delay r monotonically passes through each  $r_{k_n}$ . Then, motivated by the methods of Busenberg and Huang [3], many researchers obtained similar results for different delayed population models with the zero Dirichlet boundary condition (see e.g. [14, 21, 22, 25, 26, 31]), for the models with nonlocal or distributed delay (see e.g. [1, 5-8, 29]) and for reaction-diffusionadvection models (see [4] and [11]). Note that in the aforementioned works, the Hopf bifurcation analysis are only available when the bifurcated steady state is close to zero. Therefore, these methods can not be applied to answer the question for the Nicholson's blowflies model, i.e. when  $p \gg d\lambda_1 + \delta$ , would the stability of the positive steady state of (1.2)-(1.3) depends on time delay  $\tau$ ?

Liao and Lou [13] proposed a discrete analogue of the Hutchinson equation and studied the bifurcation problems. The obtained results has deep implications for the original diffusive equation. This motivates us to consider a two-patch Nicholson's blowfly model, as a discretized approximation of (1.2)-(1.3), aiming to understand the numerical observations for (1.2)-(1.3). With the variable changes  $\tilde{u} = au$ ,  $\tilde{\tau} = \delta \tau$ ,  $\beta = p/\delta$ ,  $\tilde{t} = \delta t$  for dimensionless, (1.1) can be written as

$$\frac{du(t)}{dt} = -u(t) + \beta u(t-\tau)e^{-u(t-\tau)}.$$
(1.4)

Using the method in [13], we consider a two-patch Nicholson's blowflies model. Let  $u_i$  denote the population density of a single species in patch i (i = 1, 2), d denote

the dispersal rate from patch to patch. Corresponding to the Dirichlet boundary condition, the two-patch model will be

$$\begin{cases} \frac{du_1(t)}{dt} = d[u_2(t) - 2u_1(t)] - u_1(t) + \beta u_1(t-\tau)e^{-u_1(t-\tau)}, \\ \frac{du_2(t)}{dt} = d[u_1(t) - 2u_2(t)] - u_2(t) + \beta u_2(t-\tau)e^{-u_2(t-\tau)}. \end{cases}$$
(1.5)

Define the positive parameter

$$\mu := \frac{\beta}{d+1}.\tag{1.6}$$

Given  $\phi \in C([-\tau, 0], \mathbb{R}^2_+) \setminus \{0\}$ , we often write  $\phi = (\phi_1, \phi_2)$  when its components are used. Let  $u(t, \phi) = (u_1(t, \phi), u_2(t, \phi))$  be the solution of (1.5) staring from  $\phi$ . The first result of this paper is about the global convergence of solutions to equilibrium.

**Theorem 1.1.** (i) If  $\mu < 1$ , then  $u(t, \phi) \rightarrow (0, 0)$  exponentially as  $t \rightarrow \infty$ .

- (ii) If  $\mu = 1$ , then  $u(t, \phi) \to (0, 0)$  as  $t \to \infty$ .
- (iii) If  $\mu > 1$ , then (1.5) admits a unique positive equilibrium  $u^*$  with the following explicit form

$$u^* = (\ln \mu, \ln \mu).$$

Further,  $u(t,\phi) \rightarrow u^*$  exponentially as  $t \rightarrow \infty$  provided that either of the following holds:

- (a)  $\mu \in (1, e^2];$
- (b)  $\mu > e^2$  and  $\tau < \tau^*$ , where  $\tau^* = \max_{\eta > 2\beta\mu e^{-1}} \tau(\eta)$  with  $\tau(\eta)$  being the minimal solution to

$$\eta e^{-(d+1+\eta)\tau} (1+e^{-2d\tau}) + 2\beta \mu e^{-1} = 0.$$

Clearly,  $\lim_{\eta\to 2\beta\mu e^{-1}} \tau(\eta) = 0 = \lim_{\eta\to\infty} \tau(\eta)$ . Hence,  $\tau^* = \max_{\eta>2\beta\mu e^{-1}} \tau(\eta)$  is attained at some  $\eta^* > 2\beta\mu e^{-1}$ . Further,  $\tau^*$  is decreasing in  $\mu$  with

$$\lim_{\mu \to \infty} \tau^*(\mu) = 0$$

The second result is about the local and global Hopf bifurcations.

**Theorem 1.2.** There exists  $\tau_0^-$  and  $\tau_1^-$  ( $\tau_1^- > \tau_0^- > \tau^*$ ) such that the following statements hold.

- (i) For  $\mu > e^2$ , (1.5) undergoes a Hopf bifurcation at  $u^*$  when  $\tau = \tau_0^-$ . Further, it is a supercritical (subcritical) Hopf bifurcation if  $ReC_1(0) < 0$  ( $ReC_1(0) > 0$ ), where  $ReC_1(0)$  will be given in (3.11) in the Appendix.
- (ii) For  $\mu \in (e^2, e^{\frac{4d+2}{d+1}}]$ , (1.5) has at least one periodic solution when  $\tau > \tau_1^-$ .

The rest of this paper is organized as follows. In Section 2 the local and global stability of the equilibria are investigated for the two-patch model. Section 3 deals with the Hopf bifurcations and their global continuation of the branch of periodic solutions from Hopf bifurcation. The derivation of the results on the direction of the Hopf bifurcations and the stability of bifurcating periodic solutions are provided in the Appendix.

## 2. Convergence to equilibrium

In this section, we first study the existence of equilibria and their linear stability. Then we establish the convergence to equilibrium by appealing to some useful tools, including the monotone dynamics system theory, super and sub solutions method, exponential ordering for delay differential equations as well as the fluctuation method.

Clearly, (0,0) is an equilibrium of (1.5). Linearizing it at (0,0) yields

$$\begin{cases} u_1'(t) = d[u_2(t) - 2u_1(t)] - u_1(t) + \beta u_1(t - \tau), \\ u_2'(t) = d[u_1(t) - 2u_2(t)] - u_2(t) + \beta u_2(t - \tau), \end{cases}$$
(2.1)

which admits the comparison principle since the quasi-monotone condition for delay differential equation is satisfied. Thus, the solution of (2.1) provides a super solution of (1.5) thanks to the inequality  $\beta s \geq \beta s e^{-s}, s \geq 0$ . Let  $\lambda^*$  be the unique real solution of

$$\lambda + d + 1 - \beta e^{-\lambda \tau} = 0.$$

Consequently,  $(u_1(t), u_2(t)) := (le^{\lambda^* t}, le^{\lambda^* t}), l > 0$  solves (2.1). Moreover,  $\lambda^* < 0$  if  $\mu < 1$ . As such, we have the following convergence to (0, 0).

**Lemma 2.1.** If  $\mu < 1$ , then  $u(t, \phi)$ , solution of (1.5), converges to (0,0) exponentially as  $t \to \infty$ .

**Proof.** Choose  $l > ||\phi||$ . Then by the comparison principle we obtain  $0 \le u(t, \phi) \le (le^{\lambda^* t}, le^{\lambda^* t})$ . Since  $\lambda^* < 0$ , the proof is complete.

When  $\mu > 1$ , we see that (0,0) is linearly unstable. This gives rise to the existence of positive equilibrium.

**Lemma 2.2.** If  $\mu > 1$ , then (1.5) admits a unique positive equilibrium, having the explicit form  $(u_1^*, u_2^*) = (\ln \mu, \ln \mu)$ .

**Proof.** An equilibrium  $(u_1^*, u_2^*)$  must satisfy

$$\begin{cases} d[u_2^* - 2u_1^*] - u_1^* + \beta u_1^* e^{-u_1^*} = 0, \\ d[u_1^* - 2u_2^*] - u_2^* + \beta u_2^* e^{-u_2^*} = 0. \end{cases}$$
(2.2)

Assuming  $u_1^* = u_2^*$  yields that  $(\ln \mu, \ln \mu)$  is the unique solution of (2.2). It then suffices to prove that any equilibrium has the same components. Let  $u_1^*/u_2^* := w$ . Next we prove w = 1. Using (2.2) we obtain that  $(u_2^*, w)$  satisfies the following system:

$$\begin{cases} d[1/w-2] - 1 + \beta e^{-u_2^* w} = 0, \\ d[w-2] - 1 + \beta e^{-u_2^*} = 0. \end{cases}$$
(2.3)

From the first equation of (2.3) we have  $u_2^* = \ln[\beta/(1-dw+2d)]$ , which is increasing in w. From the second equation of (2.3) we have  $u_2^* = \ln[\beta/(1-d/w+2d)]/w$ , which is decreasing in w. These two functions have only one intersection at w = 1.  $\Box$ 

Linearizing (1.5) at  $(u_1^*, u_2^*) = (\ln \mu, \ln \mu)$  we obtain

$$\begin{cases} u_1'(t) = d[u_2(t) - 2u_1(t)] - u_1(t) + (d+1)(1 - \ln\mu)u_1(t-\tau), \\ u_2'(t) = d[u_1(t) - 2u_2(t)] - u_2(t) + (d+1)(1 - \ln\mu)u_2(t-\tau), \end{cases}$$
(2.4)

of which, the characteristic equation is

$$\Delta(\lambda,\tau) := \det(\lambda I - A - He^{-\lambda\tau}) = 0,$$

where

$$A = \begin{pmatrix} -2d - 1 & d \\ d & -2d - 1 \end{pmatrix}, \quad H = \begin{pmatrix} (d+1)(1 - \ln\mu) & 0 \\ 0 & (d+1)(1 - \ln\mu) \end{pmatrix}. \quad (2.5)$$

By direct computations, we obtain

$$\Delta(\lambda,\tau) = \lambda^2 + \beta_1 \lambda + e^{-\lambda\tau} (\eta_1 \lambda + \eta_0) + \delta_0 e^{-2\lambda\tau} + \gamma$$
(2.6)

where

$$\begin{split} \beta_1 &:= 2(2d+1), \\ \eta_1 &:= 2(d+1) \big( \ln \mu - 1 \big), \\ \gamma &:= 3d^2 + 4d + 1, \\ \eta_0 &:= 2(2d+1)(d+1) \big( \ln \mu - 1 \big), \\ \delta_0 &:= (d+1)^2 \big( \ln \mu - 1 \big)^2. \end{split}$$

By analyzing the characteristic equation, we obtain the sufficient and necessary conditions for the linear stability of the positive equilibrium.

**Lemma 2.3.** All roots of the characteristic equation (2.6) have negative real parts if and only if  $\mu \in (1, e^2]$  or  $\mu > e^2$  with  $\tau < \tau_0^-$ , where

$$\tau_0^- := \frac{1}{\left(d+1\right)\sqrt{\left(1-\ln\mu\right)^2 - 1}} \arccos\frac{1}{1-\ln\mu}.$$
(2.7)

**Proof.** We employ a continuation method [16, corollary 2.4] with  $\tau$  being the parameter. As  $\tau = 0$ , we see that the characteristic equation reduces to

$$\lambda^2 + (\beta_1 + \eta_1)\lambda + \eta_0 + \delta_0 + \gamma = 0.$$

Solving it we obtain two solutions

$$\lambda_{+} = -2d - (d+1)\ln\mu, \quad \lambda_{-} = -(d+1)\ln\mu.$$

Clearly  $\lambda_{\pm} < 0$ . As  $\tau$  increases from 0 to  $\infty$ , a necessary condition to ensure that (2.6) admits a root with positive real part is the following: there exists  $\tau' > 0$  such that at  $\tau = \tau'$  equation (2.6) admits roots with zero real parts. Next we find the minimal value of  $\tau$  so that this condition holds.

Since  $\Delta(0,\tau) = 2d(d+1)\ln\mu + (d+1)^2(\ln\mu)^2 > 0$  for all  $\tau \ge 0$ , it then suffices to consider the possible purely imaginary roots  $i\omega$  with  $\omega > 0$ .

Note that (2.6) can be factored into

$$\Delta(\lambda,\tau) = \Delta_{+}(\lambda,\tau) \cdot \Delta_{-}(\lambda,\tau) = 0, \qquad (2.8)$$

where

$$\Delta_{+}(\lambda,\tau) = \lambda + 3d + 1 - (d+1)(1 - \ln\mu)e^{-\lambda\tau}$$
(2.9)

and

$$\Delta_{-}(\lambda,\tau) = \lambda + d + 1 - (d+1)(1 - \ln\mu)e^{-\lambda\tau}.$$
(2.10)

As such, it remains to study the purely imaginary solutions of  $\Delta_{\pm}(\lambda, \tau) = 0$ . Note that  $\lambda = i\omega$  solves  $\Delta_{\pm}(\lambda, \tau) = 0$  if and only if

$$i\omega + 3d + 1 - (d+1)(1 - \ln\mu)e^{-i\omega\tau} = 0,$$

in which, separating the real and imaginary parts yields

(

$$\begin{cases} 3d + 1 - (d+1)(1 - \ln \mu)\cos(\omega \tau) = 0, \\ \omega + (d+1)(1 - \ln \mu)\sin(\omega \tau) = 0, \end{cases}$$

leading to

$$(3d+1)^2 + \omega^2 = (d+1)^2 (1 - \ln \mu)^2,$$

and consequently,

$$\omega = \omega^{+} := \sqrt{(d+1)^{2} (1 - \ln \mu)^{2} - (3d+1)^{2}}$$
(2.11)

subject to the condition

$$\ln \mu > \frac{4d+2}{d+1}.$$

With such a condition, we compute to have a sequence of values of  $\tau$ , at which  $\Delta_+(\lambda, \tau) = 0$  admits purely imaginary solutions  $i\omega^+$ :

$$\tau_k^+ := \frac{1}{\omega^+} \left[ \arccos \frac{3d+1}{(d+1)(1-\ln\mu)} + 2k\pi \right], \text{ for } k = 0, 1, \cdots.$$
 (2.12)

Similarly, we compute to have a sequence of values of  $\tau$ , at which  $\Delta_{-}(\lambda, \tau) = 0$  admits purely imaginary solutions  $i\omega^{-}$ :

$$\tau_k^- := \frac{1}{\omega^-} \left[ \arccos \frac{1}{1 - \ln \mu} + 2k\pi \right], \text{ for } k = 0, 1, \cdots,$$
 (2.13)

where

$$\omega^{-} := (d+1)\sqrt{(\ln \mu - 2)\ln \mu}, \qquad (2.14)$$

subject to the condition

$$\ln \mu > 2.$$

Since for any  $d \ge 0$ ,

$$\frac{4d+2}{d+1} \ge 2, \quad \omega^- \ge \omega^+, \quad \frac{\pi}{2} > \arccos \frac{3d+1}{(d+1)(1-\ln\mu)} \ge \arccos \frac{1}{1-\ln\mu} > 0,$$

we can infer that  $\tau_0^+ \geq \tau_0^-$ . Hence, as  $\tau$  increases from zero to infinity, the first value of  $\tau$ , at which purely imaginary roots emerges, is  $\tau_0^-$ . Meanwhile,  $\ln \mu > 2$  is necessary.

Therefore, all roots of (2.6) have negative real parts provided that either  $\ln \mu < 2$  or  $\tau < \tau_0^-$  holds.

When  $\mu = 1$ , we see from the proof of Lemma 2.2 that no equilibria other than zero exist. In such a case, below we show that all solutions converges to zero as t tends to infinity.

**Lemma 2.4.** If  $\mu = 1$ , then  $u(t, \phi) \rightarrow (0, 0)$  as  $t \rightarrow \infty$ .

**Proof.** Define an auxiliary function

$$h(z) := \begin{cases} \beta z e^{-z}, & z < 1\\ \beta e^{-1}, & z \ge 1 \end{cases}$$

Clearly,  $h : \mathbb{R}^+ \to \mathbb{R}^+$  is nondecreasing (see Fig. 1).



Figure 1. Function h(z).

Consider

$$\begin{cases} v_1'(t) = d[v_2(t) - 2v_1(t)] - v_1(t) + h(u_1(t-\tau)), \\ v_2'(t) = d[v_1(t) - 2v_2(t)] - v_2(t) + h(u_2(t-\tau)). \end{cases}$$
(2.15)

By a similar proof to Lemma 2.2 we can show that (2.15) admits a unique equilibrium that is (0,0). Then by using the generic convergence theory on the solutions of delay differential equations [17], we can infer that any solution  $v(t,\phi)$  of (2.15) converges to (0,0). By the comparison principle,  $0 \le u(t,\phi) \le v(t,\phi)$ . The proof is complete.

**Remark 2.1.** For  $\mu > 1$ , the auxiliary equation (2.15) admits a unique positive equilibrium  $(v_1^*, v_2^*)$ , which equals  $(\ln \mu, \ln \mu)$  when  $\mu \leq e$  and  $(\mu e^{-1}, \mu e^{-1})$  when  $\mu > e$ . By the generic convergence theory again, we infer that any solution  $v(t, \phi)$  with  $\phi \neq 0$  converges to  $(v_1^*, v_2^*)$  as  $t \to \infty$ . Then by the comparison principle we have  $0 \leq u(t, \phi) \leq v(t, \phi)$ , and hence, we conclude that for any  $M > v_1^*$  and  $\phi \neq 0$ , there exists  $t_0 = t_0(M, \phi) > 0$  such that

$$0 \le u(t,\phi) \le [0,M]^2, \quad t \ge t_0.$$
(2.16)

When  $\mu \leq 1$ , there is no positive equilibrium and we have established the global converge to zero in Lemmas 2.1 and 2.4. When  $\mu > 1$ , a unique positive equilibrium emerges. Next we consider the possible global convergence to it. From Lemma 2.3, we have seen that it is locally stable if and only if either  $\mu \in (1, e^2]$  or  $\mu > e^2$  with  $\tau < \tau_0^-$ . Then it is mandatory to restrict our attention on the following two cases:

- (a)  $\mu \in (1, e^2];$
- (b)  $\mu > e^2$  and  $\tau < \tau_0^-$ .

We employ a fluctuation argument to deal with case (a).

**Lemma 2.5.** For  $\mu \in (1, e^2]$  and  $\phi \neq 0$ ,  $u(t, \phi) \rightarrow (\ln \mu, \ln \mu)$  exponentially as  $t \rightarrow \infty$ .

**Proof.** We first write (1.5) as the following integral form:

$$\begin{cases} u(t) = e^{At}u(0) + \int_0^t e^{As}F(u(t-s-\tau))ds, & t > 0, \\ u(t) = \phi(t), & t \in [-\tau, 0]. \end{cases}$$
(2.17)

where A is the 2 × 2 matrix defined as in (2.5) and  $F : \mathbb{R}^2 \to \mathbb{R}^2$  is defined by

$$F(v) = (f(v_1), f(v_2))^T$$
, with  $f(s) = \beta s e^{-s}$ . (2.18)

Define  $g: \mathbb{R}^2_+ \to \mathbb{R}_+$  by

$$g(x,y) = \begin{cases} \inf_{z \in [x,y]} f(z), & x \le y, \\ \sup_{z \in [y,x]} f(z), & y \le x. \end{cases}$$

Clearly, g(x, y) is non-decreasing in x and non-increasing in y. Moreover, g(x, x) = f(x). Define

$$u_i^\infty = \limsup_{t \to \infty} u_i(t), \quad u_{i\infty} = \liminf_{t \to \infty} u_i(t), \quad i = 1, 2.$$

Note that all eigenvalues of matrix A are negative. It then follows that  $\lim_{t\to\infty} e^{At}u(0) \to (0,0)^T$  as  $t\to\infty$ . Hence, from (2.17) we have

$$u_i^{\infty} = \limsup_{t \to \infty} \int_0^t \left( e^{As} F(u(t-s-\tau))_i \right) ds.$$

In view of the positivity of  $e^{As}$  and the property of g, we employ the Fatou lemma to obtain

$$\begin{pmatrix} u_1^{\infty} \\ u_2^{\infty} \end{pmatrix} \le \int_0^{\infty} e^{As} \begin{pmatrix} g(u_1^{\infty}, u_{1\infty}) \\ g(u_2^{\infty}, u_{2\infty}) \end{pmatrix} ds.$$
(2.19)

Define  $w^* := \max\{u_1^{\infty}, u_2^{\infty}\}$  and  $w_* := \min\{u_{1\infty}, u_{2\infty}\}$ . By using the symmetry of A, we combine the two components of inequality (2.19) to obtain

$$w^* \le g(w^*, w_*) \int_0^\infty \left[ \left( e^{As} \right)_{11} + \left( e^{As} \right)_{12} \right] ds,$$

where  $(e^{As})_{ij}$  is the entry of matrix  $e^{As}$  in the *i*-th row and *j*-th column. By virtue of the Cayley-Hamilton theorem, we compute to have  $e^{As} = a_0(s)I + a_1(s)A$ , where

$$a_0(s) = \frac{\lambda_1 e^{\lambda_2 s} - \lambda_2 e^{\lambda_1 s}}{\lambda_1 - \lambda_2}, \quad a_1(s) = \frac{e^{\lambda_1 s} - e^{\lambda_2 s}}{\lambda_1 - \lambda_2}$$

with  $\lambda_1$  and  $\lambda_2$  being the two distinct eigenvalues of matrix A. As such,

$$(e^{As})_{11} + (e^{As})_{12} = a_0(s) - (d+1)a_1(s).$$

Consequently,

$$\begin{split} \int_{0}^{\infty} \left[ \left( e^{As} \right)_{11} + \left( e^{As} \right)_{12} \right] ds &= \int_{0}^{\infty} a_{0}(s) - (d+1)a_{1}(s)ds \\ &= \frac{-\frac{\lambda_{1}}{\lambda_{2}} + \frac{\lambda_{2}}{\lambda_{1}}}{\lambda_{1} - \lambda_{2}} - (d+1)\frac{-\frac{1}{\lambda_{1}} + \frac{1}{\lambda_{2}}}{\lambda_{1} - \lambda_{2}} \\ &= -\frac{\lambda_{1} + \lambda_{2} + d + 1}{\lambda_{1}\lambda_{2}} \\ &= \frac{1}{d+1}. \end{split}$$

Therefore, we have

$$w^* \le \frac{1}{d+1}g(w^*, w_*), \tag{2.20}$$

and similarly,

$$w_* \ge \frac{1}{d+1}g(w_*, w^*). \tag{2.21}$$

By the definition of g, inequalities (2.20) and (2.21) become, respectively,

$$w^* \le \frac{1}{d+1} \sup_{s \in [w_*, w^*]} f(s), \quad w_* \ge \frac{1}{d+1} \inf_{s \in [w_*, w^*]} f(s).$$

Thus, there exist  $x, y \in [w_*, w^*]$  such that  $f(x) = \sup_{s \in [w_*, w^*]} f(s)$  and  $f(y) = \inf_{s \in [w_*, w^*]} f(s)$ , and hence,  $w^* \leq \frac{1}{d+1} f(x)$  and  $w^* \geq \frac{1}{d+1} f(y)$ . This implies that

$$\frac{1}{d+1}\frac{f(x)}{x} \ge \frac{w^*}{x} \ge 1 = \frac{1}{d+1}\frac{f(\ln\mu)}{\ln\mu} = 1 \ge \frac{1}{d+1}\frac{f(y)}{y} \ge \frac{w_*}{y}.$$

Note that  $\frac{f(s)}{s}$  is decreasing. It then follows that  $w^* \ge y \ge \ln \mu \ge x \ge w_*$ . Finally, by the same arguments as in page 279 of [30], we obtain that  $w^* = w_* = \ln \mu$  provided that  $\mu \in (1, e^2]$ . Therefore,  $u(t, \phi) \to (\ln \mu, \ln \mu)$  as  $t \to \infty$ , which, together with the local stability established in Lemma 2.3, completes the proof.

**Remark 2.2.** It is unclear whether such a fluctuation method is extendable to the diffusive Nicholson blowfly equation with zero Dirichlet boundary condition since the solutions vanish in the boundary.

Case (b) in general is hard to be completely solved. It is related to the longstanding open conjecture by Wright. Here we try to construct an exponential ordering to cast (1.5) into the monotone dynamical system framework, in order to verify the folklore in delay differential equations that small delay does not influence the generic convergence to equilibria.

By Remark 2.1, we see that all solutions will eventually stay in the box  $[0, M]^2$  with  $M > \mu e^{-1}$ . And by the comparison principle,  $[0, M]^2$  is positively invariant for the solution semiflow of (1.5). For the sake of convenience, we pick up  $M = \mu e^{-1} + 1$ . Define

$$S := \{ \phi \in C([-\tau, 0], [0, M]^2) : \lim_{t \to \infty} u(t, \phi) \text{ is an equilibrium of } (1.5) \}.$$
(2.22)

By appealing to [18, Theorem 4.1], we obtain the following result.

**Lemma 2.6.** Assume that  $\mu > e^2$ . Then there exists  $\tau^* > 0$  such that the interior of S is dense in  $C([-\tau, 0], [0, M]^2)$ .

**Proof.** Recall that the nonlinearity G of (1.5) is

$$G[\phi] = A\phi(0) + F(\phi(-\tau)),$$

where A is defined in (2.5) and F is defined in (2.18). Clearly, the functional G is of  $C^1$ . By Remark 2.1, we see that all solutions eventually will stay in the box  $[0, M]^2$  with  $M > \mu e^{-1}$ . This implies that condition (T) of [18, Theorem 4.1] holds for (1.5). It then remains to construct a  $2 \times 2$  cooperative matrix B such that conditions  $(I'_B)$  and  $(SM'_B)$  of [18, Theorem 4.1] hold.

Indeed, for  $\eta > 0$ , define  $2 \times 2$  irreducible and cooperative matrix B by

$$B := \begin{bmatrix} -(2d+1+\eta), & d \\ d & -(2d+1+\eta) \end{bmatrix}.$$
 (2.23)

Since B is irreducible, we see that  $(SM'_B)$  implies  $(I'_B)$ . It then remains to find  $\eta > 0$  such that  $(SM'_B)$  holds. As in [18], we define

$$K_B := \{ \phi \in C([-\tau, 0], \mathbb{R}^2_+) : \phi(t) \ge e^{B(t-s)}\phi(s), \tau \le s \le t \le 0 \}.$$

We write  $\phi \ge_B \psi$  iff  $\phi - \psi \in K_B$  and  $\psi \gg 0$  iff  $\psi_i(\theta) > 0$  for  $i = 1, 2, \theta \in [-\tau, 0]$ .

Differentiating the functional G we obtain the differential operator DG below:

$$DG[\phi]\psi = A\psi(0) + \beta \begin{bmatrix} e^{-\phi_1(-\tau)}[1-\phi_1(-\tau)] & 0\\ 0 & e^{-\phi_2(-\tau)}[1-\phi_2(-\tau)] \end{bmatrix} \psi(-\tau).$$

Clearly, for every  $\phi \in C([-\tau, 0], \mathbb{R}^2_+)$  and  $\psi \in K_B$  with  $\psi \gg 0$ , we have

$$DG[\phi]\psi = (A - B)\psi(0) + \beta \begin{bmatrix} e^{-\phi_1(-\tau)}[1 - \phi_1(-\tau)] & 0\\ 0 & e^{-\phi_2(-\tau)}[1 - \phi_2(-\tau)] \end{bmatrix} \psi(-\tau)$$
  
$$\geq (A - B)e^{B\tau}\psi(-\tau) + \beta \begin{bmatrix} -|1 - \phi_1(-\tau)| & 0\\ 0 & -|1 - \phi_2(-\tau)| \end{bmatrix} \psi(-\tau)$$
  
$$= \eta e^{B\tau}\psi(-\tau) + \beta \begin{bmatrix} -|1 - \phi_1(-\tau)| & 0\\ 0 & -|1 - \phi_2(-\tau)| \end{bmatrix} \psi(-\tau).$$

Thus, for  $\phi \in [0, M]^2$  we obtain

$$DG[\phi]\psi \ge [\eta e^{B\tau} + \beta \mu e^{-1}I]\psi(-\tau).$$

Since  $e^{B\tau}$  is positive, it follows that  $DG[\phi]\psi \gg 0$  provided that the two diagonal entries of  $\eta e^{B\tau} - \beta \mu e^{-1}I$  are positive. Note that

$$B = \begin{bmatrix} -(d+1+\eta) & 0\\ 0 & -(d+1+\eta) \end{bmatrix} + \begin{bmatrix} -d & d\\ d & -d \end{bmatrix} := -(d+1+\eta)I + P$$

and IP = PI. Thus, by virtue of the Cayley-Hamilton theorem we compute to have

$$e^{B\tau} = e^{(-(d+1+\eta)I+P)\tau} = e^{-(d+1+\eta)\tau}e^{P\tau} = e^{-(d+1+\eta)\tau}\left(I + \frac{1-e^{-2d\tau}}{2d}P\right).$$

It then remains to check

$$\eta e^{-(d+1+\eta)\tau} (1+e^{-2d\tau}) + 2\beta \mu e^{-1} > 0.$$

which is true for every  $\eta > 2\beta\mu e^{-1}$  and  $\tau \le \tau(\eta)$ , where  $\tau(\eta)$  is the minimal value of  $\tau$  such that  $\eta e^{-(d+1+\eta)\tau}(1+e^{-2d\tau})+2\beta\mu e^{-1}=0$ . Clearly,  $\lim_{\eta\to\infty}\tau(\eta)=0$  and  $\lim_{\eta\to 2\beta\mu e^{-1}}\tau(\eta)=0$ . Therefore,  $\tau^*:=\max_{\eta>2\beta\mu e^{-1}}\tau(\eta)$  is positive and achieved at some  $\eta^*>2\beta\mu e^{-1}$ . The proof is complete.

**Proof of Theorem 1.1.** (i) It follows from Lemma 2.1 and 2.4. (ii) The existence and uniqueness of positive equilibrium follow from Lemma 2.2. The global convergence to  $(\ln \mu, \ln \mu)$  when  $\mu \in (1, e^2]$  follows from (2.5). Finally we show that for  $\mu > e^2$  and  $\tau < \tau^*$ , any solution  $u(t, \phi)$  with  $\phi \ge 0, \neq 0$  tends to  $(\ln \mu, \ln \mu)$  as  $t \to \infty$ . Indeed, we have established in Lemma 2.6 the generic convergence to  $(\ln \mu, \ln \mu)$  in  $[0, M]^2$ . Since in  $[0, M]^2$  there are only two equilibria that are ordered with respect to  $K_B$ . By [17, Remark 1.4.2] we then can conclude that every solution converges to one of the two equilibria. Meanwhile, by the eventually strong monotonicity we infer that  $u(t, \phi) \gg 0$  for all large t. Hence,  $u(t, \phi)$  converges to  $(\ln \mu, \ln \mu)$ , which, together with Remark 2.1, complete the proof.

# 3. Bifurcated periodic solutions and their global continuation

In the previous section, we have obtained the global convergence to equilibrium if  $\mu \in (0, e^2]$ . For  $\mu > e^2$ , using delay  $\tau$  as the parameter, we have seen that the positive equilibrium  $u^*$  is linearly stable when  $\tau < \tau_0^-$  and linearly unstable when  $\tau > \tau_0^-$ . In such a case, we have also shown that  $u^*$  is globally asymptotically stable when  $\tau \in [0, \tau^*]$  for some  $\tau^* < \tau_0^-$ . In this section, we seek for time periodic solutions when  $u^*$  lose its linear stability by analyzing the local Hopf bifurcations and their global continuation as  $\tau$  is far away from  $\tau_0^-$ .

From the proof of Lemma 2.3, we see that the characteristic equation admits pure imaginary roots if and only if  $\tau = \tau_k^{\pm}$ , which are defined by (2.12) and (2.13), and the corresponding imaginary roots are  $\pm i\omega^{\pm}$  that are given in (2.11) and (2.14). Let  $\lambda_k^{\pm}(\tau) = \alpha_k^{\pm}(\tau) \pm i\sigma_k^{\pm}(\tau)$  be the root of (2.6) when  $\tau$  is near  $\tau_k^{\pm}$ , respectively, such that  $\alpha_k^{\pm}(\tau_k^{\pm}) = 0$  and  $\sigma_k^{\pm}(\tau_k^{\pm}) = \omega^{\pm}$ .

By appealing to the standard Hopf bifurcation theory, we can infer that the following transversality property guarantees the bifurcated time periodic solutions when  $\tau$  is close to  $\tau_k^{\pm}$  from left-hand side or right-hand side.

Lemma 3.1.  $\frac{d\alpha_k^+}{d\tau}|_{\tau=\tau_k^+} > 0 \text{ and } \frac{d\alpha_k^-}{d\tau}|_{\tau=\tau_k^-} > 0.$ 

**Proof.** Differentiating both sides of (2.6) with respect to  $\tau$ , we have

$$\frac{d\lambda}{d\tau} = \frac{\lambda e^{-\lambda\tau}(\eta_1\lambda + \eta_0) + 2\delta_0\lambda e^{-2\lambda\tau}}{2\lambda + \beta_1 - \tau e^{-\lambda\tau}(\eta_1 + \eta_0) + \eta_1 e^{-\lambda\tau} - 2\tau\delta_0 e^{-2\lambda\tau}}.$$

By direct computations, we have

$$\frac{d\alpha_k^+}{d\tau}|_{\tau=\tau_k^+} = \frac{4(\omega^+)^2 d^2}{[2d+2\tau_k^+ d(3d+1)]^2 + 4(\tau_k^+)^2(\omega^+)^2 d^2}$$

and

Clearly, both

$$\begin{aligned} \frac{d\alpha_k^-}{d\tau}|_{\tau=\tau_k^-} &= \frac{4(\omega^-)^2 d^2}{[2d+2\tau_k^- d(3d+1)]^2 + 4(\tau_k^-)^2(\omega^-)^2 d^2}.\\ \frac{d\alpha_k^+}{d\tau}|_{\tau=\tau_k^+} \text{ and } \frac{d\alpha_k^-}{d\tau}|_{\tau=\tau_k^-} \text{ are positive.} \end{aligned}$$

**Remark 3.1.** (i) If  $\mu \in (e^2, e^{\frac{4d+2}{d+1}}]$ , then there exists only one sequence  $\{\tau_k^-\}_{k=0}^{+\infty}$  such that the characteristic equation (2.6) has a pair of purely imaginary roots  $\pm i\omega^-$ .

(ii) If  $\mu > e^{\frac{4d+2}{d+1}}$ , then there exist two sequences  $\{\tau_k^-\}_{k=0}^{+\infty}$  and  $\{\tau_k^+\}_{k=0}^{+\infty}$ , such that the characteristic equation (2.6) has a pair of purely imaginary roots  $\pm i\omega^-$  and  $\pm i\omega^+$ , respectively. Moreover,  $\{\tau_k^-\}_{k=0}^{+\infty}$  and  $\{\tau_k^+\}_{k=0}^{+\infty}$  are in following order:

 $\tau_0^- < \tau_1^-, \tau_0^+ < \tau_2^-, \tau_1^+ < \dots < \tau_k^-, \tau_{k+1}^+ < \dots$ 

With the transversal property in Lemma 3.1, we are led to the following results about local Hopf bifurcations, as an application of Hopf bifurcation theory in [10].

- **Lemma 3.2.** (i) If  $e^2 < \mu \leq e^{\frac{4d+2}{d+1}}$ , then (1.5) undergoes a Hopf bifurcation at  $(u_1^*, u_2^*)$  when  $\tau = \tau_k^-$ ,  $k = 0, 1, \cdots$ ; When  $\mu > e^{\frac{4d+2}{d+1}}$ , if  $\tau_k^- \neq \tau_{k+1}^+$  for any fixed k, then (1.5) undergoes a Hopf bifurcation at  $(u_1^*, u_2^*)$  when  $\tau = \tau_k^-$  and  $\tau = \tau_{k+1}^+$ .
  - (ii) (1.5) undergoes a Hopf bifurcation at  $(u_1^*, u_2^*)$  when  $\tau = \tau_0^-$ . Further, it is a supercritical (subcritical) Hopf bifurcation if  $ReC_1(0) < 0$  ( $ReC_1(0) > 0$ ), where  $ReC_1(0)$  will be given in (3.11) in the Appendix.

Next, we shall study global continuation of periodic solutions bifurcating at  $\tau = \tau_k^-$ , k = 0, 1, 2, ..., for (1.5) using global Hopf bifurcation theorem given by [24]. We closely follow the notions used in [24] and assume  $\mu \in (e^2, e^{\frac{4d+2}{d+1}}]$ . Let  $x(t) = (u_1(\tau t), u_2(\tau t))$ , the (1.5) can be rewritten as a general functional differential equation in the following form

$$\dot{x}(t) = F(x^t, \tau, p) \tag{3.1}$$

with

$$F(x^{t},\tau,p) = \begin{pmatrix} d\tau[x_{2}(t) - 2x_{1}(t)] - \tau x_{1}(t) + \beta \tau x_{1}(t-1)e^{-x_{1}(t-1)} \\ d\tau[x_{1}(t) - 2x_{2}(t)] - \tau x_{2}(t) + \beta \tau x_{2}(t-1)e^{-x_{2}(t-1)} \end{pmatrix},$$

where  $x^t(s) = (x_1^t(s), x_2^t(s)) = (x_1(t+s), x_2(t+s)) \in X$ ,  $X = C([-1,0], \mathbb{R}^2_+)$ ,  $F: X \times \mathbb{R}_+ \times \mathbb{R}_+ \to \mathbb{R}^2$ . Identifying the subspace of X consisting of all constant mappings with  $\mathbb{R}^2_+$ , we obtain a mapping  $\hat{F} = F|_{\mathbb{R}^2_+ \times \mathbb{R}_+ \times \mathbb{R}_+} : \mathbb{R}^2_+ \times \mathbb{R}_+ \times \mathbb{R}_+ \to \mathbb{R}^2$ . Obviously,  $\hat{F}$  is twice continuously differentiable, i.e. the assumption (A1) in [24] holds. Denote  $\hat{x} = (u_1^*, u_2^*) = (\ln \mu, \ln \mu)$ , then  $(\hat{x}, \tau, p)$  is the stationary solution of (3.1). Define

$$\Delta_{(\hat{x},\hat{\tau},\hat{p})}(\gamma) = \gamma \mathrm{Id} - DF(\hat{x},\hat{\tau},\hat{p})(e^{\gamma} \mathrm{Id}), \qquad (3.2)$$

then det $\Delta_{(\hat{x},\hat{\tau},\hat{p})}(\gamma) = 0$  if and only is  $\gamma = \hat{\tau}\lambda$  which  $\lambda$  and  $\hat{\tau}$  satisfying the characteristic equation (2.6). Therefore, the assumption (A2) and (A3) hold duo to the properties of the eigenvalues of the characteristic equation (2.6). Moreover  $(\hat{x},\tau_k^-,\omega^-\tau_k^-), k = 0, 1, \cdots$ , are the isolated centers defined as in [24]. By the definitions of  $\tau_k^-$  and  $\omega_k^-$  and Lemma 3.1, (A4) in [24] hold for m = 1, and the corresponding

$$\gamma_1(\hat{x}, \tau_k^-, \omega^- \tau_k^-) = -1.$$

As in [24], let

 $\Sigma(F) = \operatorname{Cl}\{(x,\tau,p); x \text{ is a p-periodic solution of } (3.1)\} \subset X \times \mathbb{R}_+ \times \mathbb{R}_+,$  $N(F) = \{(\hat{x},\tau,p); F(\hat{x},\tau,p) = 0\}.$ 

We are now in the position to state the following global Hopf bifurcation theorem.

**Theorem 3.1.** For each fixed k,  $k = 0, 1, \cdots$ , denote by  $C(\hat{x}, \tau_k^-, \omega^- \tau_k^-)$  the connected component of  $(\hat{x}, \tau_k^-, \omega^- \tau_k^-)$  in  $\Sigma(F)$ , then  $C(\hat{x}, \tau_k^-, \omega^- \tau_k^-)$  is unbounded.

**Proof.** From Theorem 3.3 in [24], one of the following holds:

(i)  $C(\hat{x}, \tau_k^-, \omega^- \tau_k^-)$  is unbounded, or

(

(ii)  $C(\hat{x}, \tau_k^-, \omega^- \tau_k^-)$  is bounded,  $C(\hat{x}, \tau_k^-, \omega^- \tau_k^-) \cap N(F)$  is finite and

$$\sum_{(\hat{x},\tau,p)\in C(\hat{x},\tau_{k}^{-},\omega^{-}\tau_{k}^{-})\cap N(F)}\gamma_{m}(\hat{x},\tau,p) = 0$$
(3.3)

for all  $m = 1, 2, \cdots$ , where  $\mu_m(\hat{x}, \tau, p)$  is the *m*-th crossing number of  $(\hat{x}, \tau, p)$  if  $m \in J(\hat{x}, \tau, p), J(\hat{x}, \tau, p)$  denote the set of all positie integers *m* such that  $im\frac{2\pi}{p}$  is a characteristic value of  $(\hat{x}, \tau, p)$ , or it is zero if otherwise.

Note that  $\gamma_1(\hat{x}, \tau_k^-, \omega^- \tau_k^-) = -1$ , we have that for each fixed  $k, k = 0, 1, \cdots$ ,

$$\sum_{\hat{x},\tau,p)\in C(\hat{x},\tau_{k}^{-},\omega^{-}\tau_{k}^{-})\cap N(F)}\gamma_{1}(\hat{x},\tau,p)<0.$$

This is a contradiction to (3.3) with m = 1. Therefore the second alternative could not happen, and  $C(\hat{x}, \tau_k^-, \omega^- \tau_k^-)$  is unbounded for any k.

For the further structure of each  $C(\hat{x}, \tau_k^-, \omega^- \tau_k^-)$ , we prove the following properties of solutions of (1.5).

#### **Theorem 3.2.** (1.5) has no nontrivial positive periodic solution of period $\tau$ .

**Proof.** Note that any nontrivial positive  $\tau$ -periodic solution of (1.5) is also a nontrivial positive solution of the following ordinary differential system

$$\begin{cases} \frac{du_1(t)}{dt} = d[u_2(t) - 2u_1(t)] - u_1(t) + \beta u_1(t)e^{-u_1(t)}, \\ \frac{du_2(t)}{dt} = d[u_1(t) - 2u_2(t)] - u_2(t) + \beta u_2(t)e^{-u_2(t)}. \end{cases}$$
(3.4)

In the following, we prove that (3.4) has no periodic solution in  $\mathbb{R}^2_+$  using Bendixson-Dulac theorem. Let  $(f(u_1, u_2), g(u_1, u_2))$  denote the vector field of (3.4) and define the following Dulac function

$$B(u_1, u_2) = u_1^{-1} u_2^{-1} e^{u_1 + u_2}.$$

Then by direct computations we have

$$\frac{\partial(Bf)}{\partial u_1} + \frac{\partial(Bg)}{\partial u_2} = e^{u_1 + u_2} \left[ -du_1^{-2} - du_2^{-2} - (d+1)u_1^{-1} - (d+1)u_2^{-1} \right]$$
(3.5)

which is less than 0 duo to d > 0,  $(u_1, u_2) \in \mathbb{R}^2_+$ . Therefore, the classical Bendixson-Dulac theorem implies that (3.4) has no periodic solutions in  $\mathbb{R}^2_+$ . It follows that (1.5) has no nontrivial positive periodic solution of period  $\tau$ .

- **Remark 3.2.** (i) The proof of Theorem 3.2 implies that when  $\tau = 0$ , (1.5) (or equivalent (3.1)) has no any periodic solution.
- (ii) Theorem 3.2 derives that (3.1) has no nontrivial positive periodic solution of period 1. Since any nontrivial 1/m-periodic solution ( $m \in \mathbb{N}$ ) is also a non-trivial 1-periodic solution, then (3.1) has no nontrivial positive 1/m-periodic solution as well.

We now have the following global existence result for the periodic solution of (1.5).

**Lemma 3.3.** When  $\tau > \tau_1^-$ , (1.5) with  $\mu \in (e^2, e^{\frac{4d+2}{d+1}}]$  has at least one periodic solution.

**Proof.** We have demonstrated that the connected component  $C(\hat{x}, \tau_k^-, \omega^- \tau_k^-)$  is unbounded for any  $k=0, 1, \cdots$ . Remark 2.1 implies that the projection of  $C(\hat{x}, \tau_k^-, \omega^- \tau_k^-)$  onto the *x*-space is bounded. Near the bifurcation point  $(\hat{x}, \tau_k^-, \omega^- \tau_k^-)$ , the period *p* of periodic solution is close to  $2\pi/(\omega^- \tau_k^-)$ . According to the definition of  $\omega^-$  and  $\tau_k^-$ , we have

$$\frac{2}{2k+1} = \frac{2\pi}{\pi + 2k\pi} < \frac{2\pi}{\omega^- \tau_k^-} < \frac{2\pi}{\pi/2 + 2k\pi} = \frac{4}{4k+1},$$

which derives that

$$\frac{1}{k+1} < \frac{2\pi}{\omega^- \tau_k^-} < \frac{1}{k},$$

for  $k \geq 1$ . From Remark 3.2-(ii) and the continuity of p on the connected component  $C(\hat{x}, \tau_k^-, \omega^-\tau_k^-), 1/(k+1) for any <math>(x, \tau, p) \in C(\hat{x}, \tau_k^-, \omega^-\tau_k^-)$  with  $k \geq 1$  which implies that the projection of  $C(\hat{x}, \tau_k^-, \omega^-\tau_k^-)$  onto the p-space is bounded for  $k \geq 1$ . Therefore, for the projection of  $C(\hat{x}, \tau_k^-, \omega^-\tau_k^-)$  with  $k \geq 1$  onto the  $\tau$ -space must be unbounded. From Remark 3.2-(i) and the continuity, the projection of  $C(\hat{x}, \tau_k^-, \omega^-\tau_k^-)$  with  $k \geq 1$  onto the  $\tau$ -space includes  $[\tau_k^-, +\infty)$ . Duo to the order of  $\tau_k^-$  for  $k \geq 1$ , the proof is completed.

**Proof of Theorem 1.2.** (i) It follows from Lemma 3.2; (ii) It follows from Lemma 3.3.

# Appendix: Derivation details of the explicit expression of $\mathcal{C}_1(0)$

Normalizing the time delay and transforming the equilibrium  $(u_1^*, u_2^*)$  to the origin, (1.5) is transformed to

$$\begin{cases} u_1'(t) = d\tau [u_2(t) - 2u_1(t)] - \tau u_1(t) + (d+1)\tau (u_1(t-1) + \ln[\beta/(d+1)])e^{-u_1(t-1)} \\ - (d+1)\tau \ln[\beta/(d+1)], \\ u_2'(t) = d\tau [u_1(t) - 2u_2(t)] - \tau u_2(t) + (d+1)\tau (u_2(t-1) + \ln[\beta/(d+1)])e^{-u_2(t-1)} \\ - (d+1)\tau \ln[\beta/(d+1)]. \end{cases}$$
(3.6)

Let  $\tau = \tau_0^- + \mu$ ,  $\mu \in \mathbb{R}$ , then  $\mu = 0$  is a Hopf bifurcation point for (1.5). For  $\phi = (\phi_1, \phi_2) \in C([-1, 0], \mathbb{R}^2)$ , let

$$L(\mu)\phi := (\tau_0^- + \mu)B\phi(0) + (\tau_0^- + \mu)C\phi(-1),$$

where B, C is defined in Section 2. By the Riesz Representation Theorem, there exists a function  $\eta(\theta, \mu)$  of bounded variation for  $\theta \in [-1, 0]$ , such that

$$L(\mu)\phi = \int_{-1}^{0} d\eta(\theta,\mu)\phi(\theta), \text{ for } \phi \in C([-1,0],\mathbb{R}^2).$$

In fact, we can choose

$$\eta(\theta,\mu) = \begin{cases} (\tau_0^- + \mu)B, & \theta = 0, \\ 0, & \theta \in (-1,0), \\ -(\tau_0^- + \mu)C, & \theta = -1. \end{cases}$$

For  $\phi = (\phi_1, \phi_2) \in C([-1, 0], \mathbb{R}^2)$ , define

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

and

$$R(\mu) = \begin{cases} 0, & \theta \in [-1,0), \\ (\tau_0^- + \mu) f(\mu, \phi), & \theta = 0, \end{cases}$$

where

$$\begin{split} f(\mu,\phi) &:= \\ \begin{pmatrix} (d+1)[(\ln[\beta/(d+1)]/2 - 1)\phi_1^2(-1) + (1/2 - \ln[\beta/(d+1)]/6)\phi_1^3(-1)] + O(\phi_1^4(-1)) \\ (d+1)[(\ln[\beta/(d+1)]/2 - 1)\phi_2^2(-1) + (1/2 - \ln[\beta/(d+1)]/6)\phi_2^3(-1)] + O(\phi_2^4(-1)) \end{pmatrix} \end{split}$$

Then we can rewrite (3.6) as

$$\dot{y}(t) = A(\mu)y^t + R(\mu)y^t,$$
(3.7)

where  $y^t(\theta) = y(t+\theta)$  for  $\theta \in [-1,0)$ . For  $\psi \in C^1([0,1], \mathbb{R}^2)$ , define

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

For  $\phi \in C([-1,0],\mathbb{R}^2), \psi \in C([0,1],\mathbb{R}^2)$ , define a bilinear form

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

where  $\eta(\theta) = \eta(\theta, 0)$ . In the following, we use similar notations in [10]. Note that  $\pm i\omega^-\tau_0^-$  are also eigenvalues of  $A^*$  and it can be verified that  $q(\theta) := (q_1(\theta), q_2(\theta))^{\mathrm{T}} e^{i\omega^-\tau_0^-\theta} = (1, 1)^{\mathrm{T}} e^{i\omega^-\tau_0^-\theta}$  is an eigenvector of eigenvector of A(0) with respect to the eigenvalue  $i\omega^-\tau_0^-$ , and  $q^*(s) := \frac{1}{D}(q_1^*(s), q_2^*(s))^{\mathrm{T}} e^{i\omega^-\tau_0^-s} = \frac{1}{D}(1, 1)^{\mathrm{T}} e^{i\omega^-\tau_0^-s}$  is an eigenvector of  $A^*$  with respect to the eigenvalue  $-i\omega^-\tau_0^-$ . Then by direct computations we have

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

and

$$D = 2[1 + (d+1)\tau_0^- + i\omega^-\tau_0^-].$$

We now compute the center manifold  $C_0$  at  $\mu = 0$ . Let  $y^t$  be the solution of (3.7) when  $\mu = 0$ . Define

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

then we have

$$\dot{z}(t) = i\omega^{-}\tau_{0}^{-}z + q^{*}(\theta)f(W + 2\operatorname{Re}\{z(t)q(\theta)\}).$$
(3.8)

For simplicity of notation, denote  $f_0(z, \bar{z}) := f(W + 2\text{Re}\{z(t)q(\theta)\})$ . Let

$$g(z,\bar{z}) := q^*(\theta) f_0(z,\bar{z}) := g_{20} \frac{z^2}{2} + g_{11} z \bar{z} + g_{02} \frac{\bar{z}^2}{2} + g_{21} \frac{z^2 \bar{z}}{2} + \cdots$$

Then, the Poincaré normal form for (3.7) has the following form:

$$\dot{z}(t) = \lambda(\mu) + C_1(\mu)z^2\bar{z} + \text{h.o.t.},$$

and

$$C_1(0) = \frac{i}{2\omega^- \tau_0^-} \left( g_{20}g_{11} - 2|g_{11}|^2 - \frac{|g_{02}|^2}{3} \right) + \frac{g_{21}}{2}.$$
 (3.9)

The remaining thing is the calculations of  $C_1(0)$ .

Using the centre manifold theorem given in [10], we know that on the centre manifold W(t, z) has the following form

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

and we denote  $W_{ij}(\theta) = (W_{ij}^{(1)}(\theta), W_{ij}^{(2)}(\theta))$  here. By expanding the series and comparing the corresponding coefficients, we obtain

$$\begin{split} g_{20} &= 2\tau_0^-(d+1)\big(\ln[\beta/(d+1)] - 2\big)e^{-2i\omega^-\tau_0^-}/D, \\ g_{11} &= 2\tau_0^-(d+1)\big(\ln[\beta/(d+1)] - 2\big)/D, \\ g_{02} &= 2\tau_0^-(d+1)\big(\ln[\beta/(d+1)] - 2\big)e^{2i\omega^-\tau_0^-}/D, \\ g_{21} &= \tau_0^-(d+1)[\beta/(d+1) - 2]v\big[q_1(0)\bar{q}_1^*(0)W_{11}^{(1)}(-1)e^{-i\omega^-\tau_0^-} + \bar{q}_1(0)\bar{q}_1^*(0)W_{20}^{(1)}(-1)e^{i\omega^-\tau_0^-} \\ &\quad + q_1(0)\bar{q}_1^*(0)W_{11}^{(2)}(-1)e^{-i\omega^-\tau_0^-} + \bar{q}_1(0)\bar{q}_1^*(0)W_{20}^{(2)}(-1)e^{-i\omega^-\tau_0^-}\big]/D \\ &\quad + 2(d+1)\big(3 - \ln[\beta/(d+1)]\big)q_1^2\bar{q}_1\bar{q}_1^*e^{-i\omega^-\tau_0^-}. \end{split}$$

By (3.7) and (3.8), we have

$$\begin{split} \dot{W} &= \dot{y}^t - \dot{z}q - \dot{\bar{z}}\bar{q} \\ &= \begin{cases} AW - 2\text{Re}\{\bar{q}^*(0)f_0q(\theta)\}, & \theta \in [-1,0), \\ AW - 2\text{Re}\{\bar{q}^*(0)f_0q(0) + f_0\}, & \theta = 0. \\ &:= AW + H(z, \bar{z}, \theta) \end{split}$$

where

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

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

$$(A - 2i\omega_*\tau_*)W_{20}(\theta) = H_{20}(\theta), AW_{11}(\theta) = -H_{11}(\theta), (A - 2i\omega_*\tau_*)W_{02}(\theta) = H_{02}(\theta), \dots$$
(3.10)

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

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

comparing the coefficients, we have

$$H_{20}(\theta) = -g_{20}q(\theta) - \bar{g}_{02}\bar{q}(\theta)$$
 and  $H_{11}(\theta) = -g_{11}q(\theta) - \bar{g}_{11}\bar{q}(\theta)$ .

Substituting these relations into (3.10) we can derive the following equation

$$\dot{W}_{20}(\theta) = 2i\omega^{-}\tau_{0}^{-}W_{20}(\theta) + g_{20}q(\theta) + \bar{g}_{02}\bar{q}(\theta).$$

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

$$W_{20}(\theta) = \frac{ig_{20}}{\omega^{-}\tau_{0}^{-}}q(0)e^{i\omega^{-}\tau_{0}^{-}\theta} + \frac{i\bar{g}_{02}}{3\omega_{0}\tau_{0}}\bar{q}(0)e^{-i\omega^{-}\tau_{0}^{-}\theta} + E_{1}e^{2i\omega^{-}\tau_{0}^{-}\theta},$$

and similarly,

$$W_{11}(\theta) = \frac{ig_{11}}{\omega^- \tau_0^-} q(0) e^{i\omega^- \tau_0^- \theta} + \frac{i\bar{g}_{11}}{\omega^- \tau_0^-} \bar{q}(0) e^{-i\omega^- \tau_0^- \theta} + E_2,$$

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

$$H_{20} = -g_{20}q(0) - \bar{g}_{02}\bar{q}(0) + \tau_0(d+1) \left( \ln[\beta/(d+1) - 2)e^{-2i\omega^-\tau_0^-\theta} \right),$$

and

$$H_{11} = -g_{11}q(0) - \bar{g}_{11}\bar{q}(0) + \tau_0(d+1) \left( \ln[\beta/(d+1) - 2] \right).$$

Using (3.10) and the definition of A, we obtain

$$\int_{-1}^{0} d\eta(\theta) \left[ \frac{ig_{20}}{\omega^{-}\tau_{0}^{-}} q(0)e^{i\omega^{-}\tau_{0}^{-}\theta} + \frac{i\bar{g}_{02}\bar{q}(0)}{3\omega^{-}\tau_{0}^{-}}e^{-i\omega^{-}\tau_{0}^{-}\theta} + E_{1}e^{2i\omega^{-}\tau_{0}^{-}} \right]$$
$$= 2i\omega^{-}\tau_{0}^{-} \left[ \frac{ig_{20}}{\omega^{-}\tau_{0}^{-}} q(0) + \frac{i\bar{g}_{02}}{3\omega^{-}\tau_{0}^{-}} + E_{1} \right] + g_{20}q(0) + \bar{g}_{02}\bar{q}(0)$$
$$-\tau_{0}^{-}(d+1)\left(\ln[\beta/(d+1)] - 2\right)e^{-2i\omega^{-}\tau_{0}^{-}\theta}$$

and

$$\int_{-1}^{0} d\eta(\theta) \left[ \frac{ig_{11}}{\omega^{-}\tau_{0}^{-}} q(0) e^{i\omega^{-}\tau_{0}^{-}\theta} + \frac{i\bar{g}_{11}}{\omega^{-}\tau_{0}^{-}} e^{-i\omega^{-}\tau_{0}^{-}\theta} + E_{2} \right]$$
  
=  $g_{11}q(0) + \bar{g}_{11}\bar{q}(0) - \tau_{0}^{-}(d+1) \left( \ln[\beta/(d+1)] - 2 \right).$ 

Thus,

$$E_{1} = \frac{(d+1)\left(\ln[\beta/(d+1)] - 2\right)e^{-2i\omega^{-}\tau_{0}^{-}\theta}}{2i\omega^{-} + (d+1)\left[1 + \left(\ln[\beta/(d+1)] - 1\right)e^{-i\omega^{-}\tau_{0}^{-}\theta}\right]} \begin{pmatrix} 1\\1 \end{pmatrix}$$

and

$$E_2 = \frac{\ln[\beta/(d+1)] - 2}{\ln[\beta/(d+1)]} \begin{pmatrix} 1\\ 1 \end{pmatrix}.$$

We now are in the position to substitute expressions for  $g_{20}$ ,  $g_{11}$ ,  $g_{02}$  and  $g_{21}$  into (3.9) and obtain

$$\begin{aligned} \operatorname{Re}C_{1}(0) \\ &= \frac{\tau_{0}^{-} \left(\ln[\beta/(d+1)]^{2} - 5\ln[\beta/(d+1)] + 8\right)[(d+1)(1 + (d+1)\tau_{0}^{-}) + (\omega^{-})^{2}\tau_{0}^{-}]}{\ln[\beta/(d+1)]\left(1 - \ln[\beta/(d+1)]\right)^{2}\tau_{0}^{-}\right]} \\ &- \frac{2\omega^{-} \left[d+1 + (d+1)^{2} \left(1 - \ln[\beta/(d+1)]\right)^{2}\tau_{0}^{-}\right]}{|D|^{2}(d+1)^{2} \left(1 - \ln[\beta/(d+1)]\right)^{2}} + \left[8(\omega^{-})^{2}(d+1)^{2} + 2(d+1)^{4}\right. \\ &+ 2\omega^{-}(d+1)^{3} \left(1 - \ln[\beta/(d+1)]\right)^{2}\tau_{0}^{-} - 2(\omega^{-})^{2}(d+1)\left(1 - \ln[\beta/(d+1)]\right)^{2}\right. \\ &+ 2(d+1)^{5} \left(1 - \ln[\beta/(d+1)]\right)^{2}\tau_{0}^{-} - (d+1)^{5} \left(1 - \ln[\beta/(d+1)]\right)^{4}\tau_{0}^{-} \\ &- (d+1)^{5} \left(1 - \ln[\beta/(d+1)]\right)^{5}\tau_{0}^{-} - 2(\omega^{-})^{2}(d+1)^{2} - (d+1)^{4} \left(1 - \ln[\beta/(d+1)]\right)^{2}\right. \\ &- (d+1)^{4} \left(1 - \ln[\beta/(d+1)]\right)^{3} \left[\frac{2\tau_{0}^{-}(d+1)^{3} \left(\ln[\beta/(d+1)] - 2\right)^{2} \left(1 - \ln[\beta/(d+1)]\right)}{\left[(1 + (d+1)\tau_{0}^{-})^{2} + (\omega^{-}\tau_{0}^{-})^{2}\right]M} \right] \end{aligned}$$

where

$$M = \left[4(\omega^{-})^{2}(d+1) + (d+1)^{3} - (d+1)(\omega^{-})^{2} - (d+1)^{3}\left(1 - \ln[\beta/(d+1)]\right)^{3}\right]^{2} + \left[2\omega^{-}(d+1)^{2} - 2(\omega^{-})^{3} - 2(d+1)^{2}\omega^{-}\right]^{2}.$$

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