BISTABLE AND OSCILLATORY DYNAMICS OF NICHOLSON'S BLOWFLIES EQUATION WITH ALLEE EFFECT

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Abstract. The bistable dynamics of a modified Nicholson's blowflies delay differential equation with Allee effect is analyzed. The stability and basins of attraction of multiple equilibria are studied by using Lyapunov-LaSalle invariance principle. The existence of multiple periodic solutions are shown using local and global Hopf bifurcations near positive equilibria, and these solutions generate long transient oscillatory patterns and asymptotic stable oscillatory patterns.

1. **Introduction.** The growth of a biological population is often described by a delay differential equation [8, 13, 29, 31]

$$u'(t) = -\mu u(t) + f(u(t - \tau)), \tag{1}$$

where $u(t)$ is the population density at time t, μ is the constant mortality rate, and $f(u)$ is a density-dependent population growth function but depends on the population density at a past-time $t - \tau$ for some $\tau > 0$. Prominent examples of such delay differential equation models include Nicholson's blowflies model [7, 25, 38], and Mackey-Glass model of physiological control systems [20, 35]. Similar models also appear in the context of economic growth models [3, 21, 22].

Typically the growth function $f(u)$ satisfies $f'(0) > 0$ which indicates the population could have an overall positive growth rate in low density. But in many other situations, the biological species may have smaller growth rate in low density because of low mating rate or weak resistance to predators, which is termed as an Allee effect in the population growth [1, 5]. It is typical that in such a system, there exists a threshold under which the species will go to extinction, and there are multiple stable equilibrium points. Study on the dynamic behaviors of the

mathematical model with Allee effect is helpful for preventing the extinction of endangered species, and it could play a significant role in the sustainable development of ecological environment.

In this paper we consider the dynamical behavior of the following case of (1):

$$u'(t) = -\mu u(t) + \beta u^k(t-\tau)e^{-pu(t-\tau)}. \tag{2}$$

Here μ, β, p are positive parameters, and $k > 0$. The growth function in (2) is of Ricker type. When $k = 1$, it becomes the classical Nicholson's blowflies equation which has been extensively studied in the literature [2, 6, 28, 30, 32, 38, 42] and references cited therein. For the multiple-patch Nicholson's blowflies model, corresponding results can be found in [10, 11, 17, 18, 27, 40, 41] and references cited therein. When $k \neq 1$, equation (2) appears as a model for the process of generation and degeneration of red blood cells [14, 37]. When $k > 1$, the population growth rate is negative or decreasing function at low population size or density, which was found by Allee [1] and is termed as the strong Allee effect [33]. For the model (2) with Allee effect $k > 1$, Terry [36] considered a special case of $k = 2$ and found conditions of population extinction and persistence. Huang et al. [12] (see also Liz and Ruiz-Herrera [16]) characterized the basins of attraction of locally stable equilibria and showed the existence of heteroclinic orbits. Their approach combines the idea of relating the dynamics of a map to the dynamics of a delay differential equation and invariance arguments for the solution semiflow under the assumption that the equilibria exist. Sullivan et al. [34] presented numerical simulations of spreading dynamics of the model (2) with diffusion when $k > 1$. For the case of $0 < k < 1$, Buedo-Fernández and Liz [3] established sharp global stability conditions for the positive equilibrium of equation (2). However, there are very few results for the existence of the equilibria and the bifurcation for general k, especially for the stability of the equilibria by using the characteristic method, which we consider in this paper.

In this paper, we analyze dynamics of model (2) with $k > 1$, including the existence and the stability of the equilibria, and the coexistence of the equilibrium and the stable periodic solution, which is a remarkable phenomenon in biological systems [15, 26]. By analyzing the distribution of the eigenvalues of associated characteristic equations, the stability of the equilibria and the condition under which Hopf bifurcations occur are obtained by taking the time delay τ as the bifurcation parameter. The global stability of the equilibria is obtained by using Lyapunov functional and Lyapunov-LaSalle invariance principle, which is different from the approach in [12]. The global existence of the periodic solutions for all possible time delay values τ is established by applying the global Hopf bifurcation theorem of Wu [39]. Our main conclusions include the following:

(i) In addition to the extinction equilibrium $u_0 = 0$, there exist two positive equilibria $u_2 > u_1 > 0$ when the growth rate parameter $\beta > \beta_*$ and there is no positive equilibria when $\beta < \beta_*$. The species goes to extinction if β is small ($\beta < \beta_*$), and it persists if β is large and the initial population is appropriate.

(ii) The extinction equilibrium u_0 is always locally stable, and it is globally asymptotically stable when β is small; the intermediate equilibrium u_1 is always unstable; and the large equilibrium u_2 is locally stable for $\beta_* < \beta < \beta^*$ and all $\tau > 0$, but it becomes unstable for $\beta > \beta^*$ and large τ. Moreover, u_2 attracts all large initial values regardless of τ for a more restricted range of β.

(iii) When β is large, Hopf bifurcations inducing oscillatory patterns occur near both positive equilibria u_1 and u_2 if the time delay τ increases, generating unstable and stable periodic solutions around respective equilibria. For large τ, unstable periodic solutions around u_1 cause long transient oscillatory patterns before solutions eventually converge to one of asymptotic stable states: the extinction state or the persistence state, which makes a bistable structure. The persistence state can be either the equilibrium u_2 or a stable limit cycle around u_2.

(iv) For small $\beta > 0$, either a small or large initial density of the population could lead to eventual extinction, while an intermediate initial density results in population persistence; and for large $\beta > 0$, a large initial density always keeps the population persist in an oscillatory fashion.

Our results confirm that the dynamics of system (2) is bistable due to the Allee effect structure. We also find parameter conditions for the occurrence of long transient oscillations and asymptotic stable oscillations, which has been of great interest in recent ecological studies [9, 23, 24]. Numerically we also find that for intermediate growth rate β, a large initial population leads to eventual population extinction, which appears to be a signature for delayed population model with Allee effect (see [4]).

The rest of our paper is organized as follows. Some preliminaries needed in the following are present in Section 2. In Section 3, we prove our main conclusions on the dynamic behaviors of the model, such as the global stability of the equilibria and the occurrence of Hopf bifurcation; and in Section 4, we show the global Hopf bifurcation of periodic solutions. Finally, we show some numerical simulations to illustrate our conclusions in Section 5, and conclude our results and discuss some future work in Section 6.

2. **Preliminaries.** In this section, we first give some preliminaries for the following Nicholson's blowflies equation with Allee effect:

$$
\begin{cases}
u'(t) = -u(t) + \beta u^k(t-\tau)e^{-u(t-\tau)}, & t > 0, \\
u(\theta) = \phi(\theta), & -\tau \le \theta \le 0.
\end{cases}
\tag{3}
$$

System (3) is obtained by changing the variables in system (2):

$$
\hat{u} = pu, \quad \hat{t} = \mu t, \quad \hat{\tau} = \mu\tau, \quad \hat{\beta} = \frac{\beta}{\mu p^{k-1}}
$$

and removing the hat. The initial function $\phi \in \Xi_1$ which is defined as

$$
\Xi_1 := \{\phi \in C([-\tau, 0], \mathbb{R}) : \ \phi(\theta) \ge (\not\equiv)0 \text{ and } \phi(0) > 0, \text{ for each } \theta \in [-\tau, 0]\}.
$$

First we have the following positivity and boundedness of solutions to system (3).

Lemma 2.1. *The solution of system (3) is positive for $t > 0$ and is ultimately uniformly bounded if $\phi \in \Xi_1$.*

Proof. Let

$$
f(u) := \beta u^k e^{-u}.
\tag{4}
$$

Then $f(0) = 0$, $f(+\infty) = \lim\limits_{u \to +\infty} f(u) = 0$. And from $f'(u) = \beta u^{k-1}e^{-u}(k-u)$, we have $f'(0) = 0 = f'(k)$, which shows that $0 < f(u) \le f_{max}$ for all $u > 0$ with the maximum of f is $f_{max} = f(k) = \beta k^k e^{-k}$ (see Figure 1).
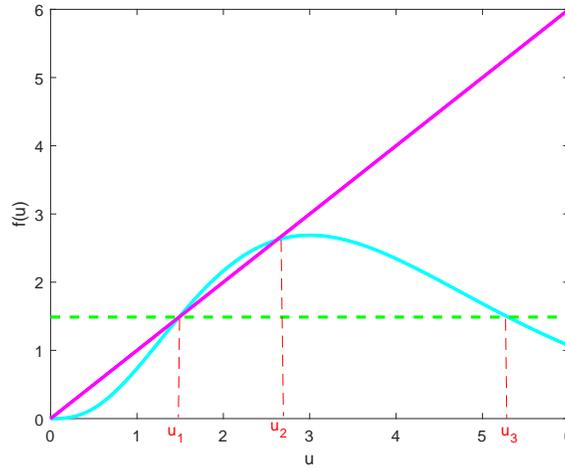
FIGURE 1. The graph of functions $f(u) = \beta u^k e^{-u}$ represented by the cyan curve, and $\tilde{f}(u) = u$ represented by the magenta curve. Here, $k = 3$ and $\beta = 2$.

Assume $u(t)$ is a solution of system (3). Then it satisfies

$$u'(t) = -u(t) + \beta u^k(t - \tau)e^{-u(t-\tau)} \geq -u(t), \tag{5}$$

which implies $u(t) \geq u(0)e^{-t} > 0$ for $t \in [0, \tau]$ as $\phi \in \Xi_1$. When $t \in [\tau, 2\tau]$, by inequality (5), we have $u(t) \geq u(\tau)e^{\tau-t} > 0$. Repeating the above step for $t \in [j\tau, (j+1)\tau]$ with $j \in \mathbb{N}$, we obtain that $u(t)$ is positive for all $t > 0$.

From the boundedness of f, we have $u'(t) \leq -u(t) + f_{max}$, and

$$\limsup_{t \to +\infty} u(t) \leq f_{max} = \beta k^k e^{-k}, \tag{6}$$

which implies that $u(t)$ is ultimately bounded. $\square$

Assume $\tilde{u}$ is an equilibrium of system (3). Obviously $\tilde{u} = 0$ is always an equilibrium. If $\tilde{u} > 0$, then it satisfies

$$\tilde{u}^{k-1}e^{-\tilde{u}} = \frac{1}{\beta}.$$

Let $g(u) = u^{k-1}e^{-u}$. Then

$$g'(u) = u^{k-2}e^{-u}(k - 1 - u).$$

Obviously, $g(0) = 0$, $g(+\infty) = 0$, $g'(0) = 0$, $g'(k-1) = 0$, $g'(u) > 0$ if $u \in (0, k-1)$ and $g'(u) < 0$ if $u \in (k-1, +\infty)$. And the maximum value of $g(u)$ is

$$g_{max} := g(k-1) = (k-1)^{k-1}e^{1-k}. \tag{7}$$

So we have the following results on the existence and multiplicity of nonnegative equilibria of (3) (see Figure 2).

Proposition 1. *For system* (3), $u_0 = 0$ *is an equilibrium for all* $\beta > 0$. *Moreover,*

(i) *If* $\beta < \beta_* := e^{k-1}(k-1)^{1-k}$, *there is no positive equilibrium.*

(ii) *If* $\beta = \beta_*$, *there exists a unique positive equilibrium* $u_* = k - 1$.
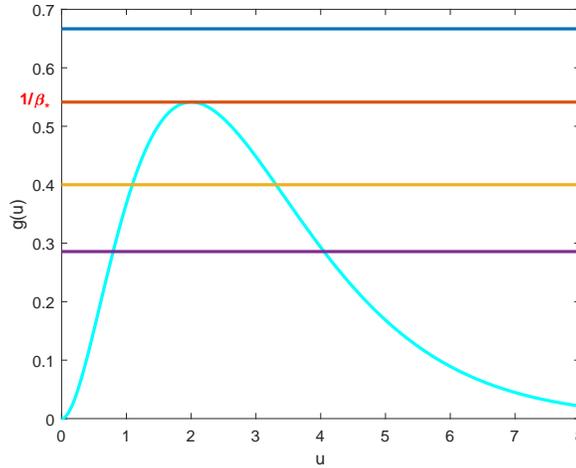
FIGURE 2. The existence of positive equilibria of (3) when $k = 3$ and $\beta > \beta_* = 1.847$.

(iii) *If $\beta > \beta_*$, there are exactly two distinctive positive equilibria u_1 and u_2 satisfying $0 < u_1 < k - 1 < u_2$.*

3. **Stability analysis of the constant equilibria.** In this section, we establish the stability of equilibria of (3) by analyzing the distribution of the eigenvalues and using Lyapunov-LaSalle invariance principle.

First we have

Lemma 3.1. *Assume that $\beta > \beta_*$, and let $0 < u_1 < u_2$ be the two positive equilibria of (3).*

(i) *Assume the initial function satisfies*

$$0 \leq \phi(\theta) \leq u_1 \text{ for any } \theta \in [-\tau, 0] \text{ and } 0 < \phi(0) < u_1. \tag{8}$$

Then the solution of system (3) satisfies $0 < u(t) < u_1$ for $t \geq 0$.

(ii) *Let u_3 be the unique value such that $u_3 > u_2$ and $f(u_3) = f(u_1) = u_1$. Assume the initial function satisfies*

$$u_1 \leq \phi(\theta) \leq u_3 \text{ for any } \theta \in [-\tau, 0] \text{ and } u_1 < \phi(0) < u_3. \tag{9}$$

Then the solution of system (3) satisfies $u_1 < u(t) < u_3$ for all $t \geq 0$.
Moreover, assume $\beta < \hat{\beta} := e^k k^{1-k}$ and the initial function ϕ satisfies

$$u_1 \leq \phi(\theta) \leq k \text{ for any } \theta \in [-\tau, 0] \text{ and } u_1 < \phi(0) < k. \tag{10}$$

Then the solution of system (3) satisfies $u_1 < u(t) < k$ for $t \geq 0$.

Proof. If $u(t)$ is a solution of system (3), then it satisfies

$$u(t) = u(t_0)e^{t_0 - t} + \int_{t_0}^{t} e^{s-t} f(u(s - \tau)) ds, \ t > t_0 \geq 0. \tag{11}$$

(i) Choose $t_0 = 0$ and $t \in (0, \tau]$ in (11), then by using the monotonicity of the function f when $0 < u < u_1$ and $f(u_1) = u_1$, we have

$$u(t) = \phi(0)e^{-t} + \int_0^t e^{s-t} f(u(s - \tau)) ds \leq \phi(0)e^{-t} + f(u_1)(1 - e^{-t}) = u_1 + (\phi(0) - u_1)e^{-t}.$$

Thus $\phi(0) < u_1$ implies $u(t) < u_1$. Repeating the above steps for any $t_0 = j\tau$ and $t \in (j\tau, (j+1)\tau]$ for $j \in \mathbb{N}$, we get $0 < u(t) < u_1$ for any $t > 0$.

(ii) Again we choose $t_0 = 0$ and $t \in (0, \tau]$ in (11), then

$$u(t) = \phi(0)e^{-t} + \int_0^t e^{s-t} f(u(s - \tau)) ds \geq u_1 + (\phi(0) - u_1)e^{-t} > u_1,$$

and

$$u(t) = \phi(0)e^{-t} + \int_0^t e^{s-t} f(u(s - \tau)) ds \leq f_{max} + (u_3 - f_{max})e^{-t} \leq u_3,$$

as $u_3 \geq f_{max}$ which is true by the monotone property of the function $f(u)$. Repeating the above steps for any $t_0 = j\tau$ and $t \in (j\tau, (j+1)\tau]$ for $j \in \mathbb{N}$, we obtain $u_1 < u(t) < u_3$ for any $t > 0$.

Finally we assume that $\beta < \hat{\beta}$. By doing similar calculation as above and the fact that

$$u(t) = \phi(0)e^{-t} + \int_0^t e^{s-t} f(u(s - \tau)) ds < f_{max} + (k - f_{max})e^{-t} \leq k,$$

as $f_{max} < k$ if and only if $\beta < \hat{\beta}$, we obtain the conclusion that $u_1 < y(t) < k$ for any $t > 0$. $\qquad \square$

Lemma 3.1 (i) shows that when the initial function is less than the smaller positive equilibrium, the solution will converge to 0, which implies that the population will become extinct when the initial density of the population is small. This phenomenon is an important manifestation of Allee effect.

Let $\tilde{u}$ be one of the equilibria obtained in Proposition 1. The linearized equation of system (3) at $\tilde{u}$ is

$$\varphi'(t) = -\varphi(t) + \beta e^{-\tilde{u}} \tilde{u}^{k-1}(k - \tilde{u})\varphi(t - \tau),$$

and the corresponding characteristic equation is

$$\lambda - \beta(k - \tilde{u})e^{-\tilde{u}} \tilde{u}^{k-1} e^{-\lambda\tau} + 1 = 0. \tag{12}$$

When $\tilde{u} = u_0$, the unique eigenvalue of equation (12) is $\lambda^{[0]} = -1$, which implies that u_0 is always locally asymptotically stable. Furthermore, we have

Theorem 3.2. $u_0 = 0$ *is locally asymptotically stable with respect to* (3) *for all* $\beta > 0$ *and* $\tau > 0$. *Moreover,* u_0 *is globally asymptotically stable when* $\beta < \beta_*$ *and* $\tau > 0$.

Proof. We only need to establish the global stability of u_0 by constructing a Lyapunov functional $V_1 : \Xi_1 \to \mathbb{R}$ as

$$V_1(u) = u(t) + \int_{-\tau}^0 \beta u^k(t + s)e^{-u(t+s)} ds.$$

By taking the time derivative of V along solutions of system (3), we have

$$V_1'(u)|_{(3)} = u(t)(\beta g(u(t)) - 1) \leq u(t)(\beta g_{max} - 1) \leq 0,$$

if $\beta \leq \beta_* = 1/g_{max}$ and g_{max} is defined in (7). And $V_1'(u)|_{(3)} = 0$ if and only if $u = 0$. Thus, by the Lyapunov-LaSalle invariance principle [8, 13], u_0 is globally asymptotically stable. $\qquad\square$

We remark that the global stability of $u_0 = 0$ was also proved in Theorem 3.2 of [12] and Theorem 3.1 of [16] by using a map related to the dynamics of (3). Our proof is based on Lyapunov method.

For the stability of positive equilibria of (3), we have the following results.

Theorem 3.3. *For system* (3)*, the following stability conclusions are true:*

(i) *u_1 is unstable for all $\beta > \beta_*$ and $\tau > 0$; When $\tau = \tau_j^{[1]}(j \in \mathbb{N}^0)$ defined in* (18)*, (unstable) periodic solutions of system* (3) *bifurcate near u_1.*

(ii) *u_2 is locally asymptotically stable if one of the following statements holds: (a) $\tau \geq 0$ and $\beta_* < \beta < \beta^* := (k+1)^{1-k}e^{k+1}$, or (b) $0 \leq \tau < \tau_0^{[2]}$ and $\beta > \beta^*$; and when $\tau > \tau_0^{[2]}$ and $\beta > \beta^*$, u_2 is unstable. Moreover, when $\beta > \beta^*$ and $\tau = \tau_j^{[2]}$ ($j \in \mathbb{N}^0$) defined in* (20)*, system* (3) *undergoes a Hopf bifurcation at u_2, and periodic solutions of system* (3) *bifurcate near u_2.*

Proof. When $\tilde{u} = u_l$ for $l = 1, 2$, equation (12) becomes

$$\lambda^{[l]} - (k - u_l)e^{-\tau\lambda^{[l]}} + 1 = 0, \tag{13}$$

with u_l satisfying $\beta e^{-u_l} u_l^{k-1} = 1$.

Assume $\tau = 0$. The unique eigenvalue of (13) at u_1 is

$$\lambda^{[1]} = k - 1 - u_1, \tag{14}$$

and the unique eigenvalue of (13) at u_2 is

$$\lambda^{[2]} = k - 1 - u_2. \tag{15}$$

From (iii) of Proposition 1, $\lambda^{[1]} > 0$ and $\lambda^{[2]} < 0$, which implies u_1 is unstable.

Assume $\tau \neq 0$ and $\lambda^{[l]} = \omega^{[l]}i$ ($\omega^{[l]} > 0, l = 1, 2$) is a root of equation (13). Then

$$\sin(\omega^{[l]}\tau) = \frac{\omega^{[l]}}{u_l - k}, \ \cos(\omega^{[l]}\tau) = -\frac{1}{u_l - k}. \tag{16}$$

That is, $(\omega^{[l]})^2 = (k - 1 - u_l)(k + 1 - u_l)$. When $l = 1$, $k - 1 - u_1 > 0$ implies $k + 1 - u_1 > 0$. Thus, $\omega^{[1]}$ exists and satisfies

$$\omega^{[1]} = \sqrt{(k - u_1)^2 - 1}, \tag{17}$$

and

$$\tau_j^{[1]} = \frac{1}{\omega^{[1]}}\left((2j+1)\pi + \arccos\left(\frac{1}{u_1 - k}\right)\right), \ j \in \mathbb{N}^0 := \mathbb{N} \cup \{0\}. \tag{18}$$

When $l = 2$, $k - 1 - u_2 < 0$. If $u_2 \leq k + 1$ (equivalently $\beta_* \leq \beta \leq \beta^*$), then $(\omega^{[2]})^2 \leq 0$ and there exists no purely imaginary root of (13). If $u_2 > k + 1$ (equivalently $\beta > \beta^*$), then the imaginary part of the purely imaginary root is

$$\omega^{[2]} = \sqrt{(u_2 - k)^2 - 1}, \tag{19}$$

and the delay τ must equal to

$$\tau_j^{[2]} = \frac{1}{\omega^{[2]}}\left((2j+1)\pi - \arccos\left(\frac{1}{u_2 - k}\right)\right), \ j \in \mathbb{N}^0. \tag{20}$$

Differentiating (13) with respect to τ for $l = 1, 2$, we obtain

$$\frac{\mathrm{d}\lambda^{[l]}}{\mathrm{d}\tau} - (k - u^{[l]})e^{-\tau\lambda^{[l]}} \left(-\lambda^{[l]} - \tau\frac{\mathrm{d}\lambda^{[l]}}{\mathrm{d}\tau}\right) = 0,$$

that is,

$$\left(\frac{\mathrm{d}\lambda^{[l]}}{\mathrm{d}\tau}\right)^{-1} = \frac{e^{\tau\lambda^{[l]}} + \tau(k - u^{[l]})}{\lambda^{[l]}(u^{[l]} - k)}.$$

By applying (16)-(20) and separating the real part and the imaginary part of the derivative at $\tau = \tau_j^{[l]}$, we have

$$\left(\frac{\mathrm{d}\mathrm{Re}\lambda^{[l]}}{\mathrm{d}\tau}\right)^{-1}\Bigg|_{\tau=\tau_j^{[l]}} = \frac{\sin(\omega^{[l]}\tau_j^{[l]})}{\omega^{[l]}(u^{[l]} - k)} = \frac{1}{(\omega^{[l]})^2 + 1} > 0, \qquad (21)$$

which implies the transversality condition for the Hopf bifurcation holds. $\qquad \square$

We remark that the local stability of u_2 was also shown in Proposition 2 of [16]. By Theorem 3.2 and Theorem 3.3, under the condition of (ii) in Theorem 3.3, the two equilibria u_0 and u_2 are both locally stable, so the system is bistable. This is another manifestation of the Allee effect.

By restricting the range of β, we can show that the convergence to the large equilibrium u_2 is "global" in a sense as it attracts all initial conditions in $[u_1, k]$ defined in Lemma 3.1.

Theorem 3.4. *Assume that $\beta_* < \beta < \hat{\beta}$, $\tau > 0$ and the initial function ϕ satisfies* (10). *Let $u(t)$ be the solution of* (3). *Then $\lim_{t\to\infty} u(t) = u_2$.*

Proof. Denote

$$\Xi_2 = \{\phi \in \Xi_1 : u_1 < \phi(\theta) < k, \text{ for each } \theta \in [-\tau, 0]\},$$

which implies that Ξ_2 is positively invariant by the conclusion in (ii) of Lemma 3.1.

In the following, we will prove this theorem in several steps.

Step 1. If $u_1 < u < k$, then $\widetilde{V_2}(u) < \widetilde{V_2}(u_1)$, where $\widetilde{V_2} : [u_1, k] \to \mathbb{R}$ and

$$\widetilde{V_2}(u) = u - u_2 \ln u + \int_{-\tau}^0 (f(u) - f(u_2)\ln f(u)) \, \mathrm{d}s$$

$$= u - u_2 \ln u + \tau (f(u) - f(u_2)\ln f(u)).$$

Taking the direct derivative of $\widetilde{V_2}$ with respect to u, we get

$$\widetilde{V_2}'(u) = \frac{u - u_2}{u} + \tau\frac{f'(u)}{f(u)}(f(u) - f(u_2)).$$

It is not difficult to see that $u_2 < k$ if and only if $\beta < \hat{\beta}$ and $(u-u_2)(f(u)-f(u_2)) > 0$ for each $u \in [u_1, k]$, which implies that $\widetilde{V_2}(u) \geq 0$ and $u = u_2$ is the global minimum of $\widetilde{V_2}(u)$ in $[u_1, k]$.

Next, we verify that $\widetilde{V_2}(u_1) > \widetilde{V_2}(k)$. In fact,

$$\widetilde{V_2}(u_1) - \widetilde{V_2}(k) = u_1 - u_2 \ln u_1 + \tau(f(u_1) - f(u_2)\ln f(u_1))$$
$$- (k - u_2 \ln k + \tau(f(k) - f(u_2)\ln f(k)))$$
$$= Z_1(u_1) + Z_2(u_1),$$

where

$$Z_1(u_1) = u_1 - k + u_2(\ln k - \ln u_1),$$
$$Z_2(u_1) = \tau(f(u_1) - f(k) + f(u_2)\ln f(k) - f(u_2)\ln f(u_1)).$$

Taking the derivative of Z_1 and Z_2 with respect to u_1, respectively, then we obtain

$$Z_1'(u_1) = 1 - \frac{u_2}{u_1} < 0, \quad Z_2'(u_1) = \frac{\tau f'(u_1)}{f(u_1)}(f(u_1) - f(u_2)) < 0,$$

as $f(u_1) = u_1$, $f(u_2) = u_2$ and $f'(u_1) > 0, f(u_1) < f(u_2)$ when $u_2 < k$. Then as $u \in [u_1, k]$, the minimum values of functions $Z_1(u)$ and $Z_2(u)$ are both obtained at the point $u = k$ and $Z_1(k) = 0$, $Z_2(k) = 0$, which implies that $\widetilde{V_2}(u_1) > \widetilde{V_2}(k)$.

Step 2. Define

$$\widetilde{G} = \left\{ \psi \in \Xi_2 : \ \widetilde{V_2}(\psi) < \widetilde{V_2}(k) \right\}.$$

Then by Step 1 and (ii) of Lemma 3.1, $\widetilde{G}$ is invariant, $u_1 \notin \overline{\widetilde{G}}$ and $|u| < k$ for each $\phi \in \widetilde{G}$, where $|\cdot|$ represents the norm of $C([-\tau, 0], \mathbb{R})$.

Define a Lyapunov functional $V_2 : \widetilde{G} \to \mathbb{R}$ as

$$V_2(u) = u(t) - u_2\ln u(t) + \int_{-\tau}^0 [f(u(t+s)) - f(u_2)\ln f(u(t+s))]\, \mathrm{d}s,$$

where f is defined in (4). Then V_2 is a Lyapunov functional for (2) on $\widetilde{G}$. In fact, taking the time derivative of V_2 along a positive solution of system (3), we have

$$V_2'(u)|_{(3)} = -u(t) + u_2 - \frac{u_2}{u(t)}f(u(t-\tau)) + f(u(t)) - f(u_2)\ln f(u(t)) + f(u_2)\ln f(u(t-\tau)).$$

Denote $h(x) = x - 1 - \ln x$ and notice $f(u_2) = u_2$, then we have

$$\begin{aligned} V_2'(u(t))|_{(3)} ={}& -u(t) - u_2 h\left(\frac{u_2 f(u(t-\tau))}{u(t)f(u_2)}\right) - u_2 \ln\left(\frac{u_2 f(u(t-\tau))}{u(t)f(u_2)}\right) \\ &+ f(u(t)) - u_2\ln f(u(t)) + u_2\ln f(u(t-\tau)) \\ ={}& -u(t) + f(u(t)) - u_2 h\left(\frac{u_2 f(u(t-\tau))}{u(t)f(u_2)}\right) + u_2\ln\left(\frac{u(t)f(u_2)}{u_2 f(u(t))}\right) \\ ={}& -u(t) + f(u(t)) - u_2 h\left(\frac{u_2 f(u(t-\tau))}{u(t)f(u_2)}\right) - u_2 h\left(\frac{u(t)f(u_2)}{u_2 f(u(t))}\right) \\ &+ u_2\frac{u(t)f(u_2)}{u_2 f(u(t))} - u_2 \\ :={}& -u_2 h\left(\frac{u_2 f(u(t-\tau))}{u(t)f(u_2)}\right) - u_2 h\left(\frac{u(t)f(u_2)}{u_2 f(u(t))}\right) + A, \end{aligned}$$

where

$$A = -u(t) + f(u(t)) + u_2\frac{u(t)f(u_2)}{u_2 f(u(t))} - u_2 = u(t)\left(\frac{f(u(t))}{f(u_2)} - 1\right)\left(\frac{u_2}{u(t)} - \frac{f(u_2)}{f(u(t))}\right).$$

If $u \in \Xi_2$, then $u(t) < k$ and f is monotonic increasing in $(0, k)$, which implies $A \leq 0$. It is well known that $h(x) \geq 0$ for $x > 0$ and $h(x) = 0$ if and only if $x = 1$. Thus, $V_2'|_{(3)}(u) \leq 0$ for all $u \in \widetilde{G}$, which implies V_2 is a Lyapunov functional on $\widetilde{G}$.

Let $S = \left\{\phi \in \overline{\widetilde{G}} : \ \dot{V_2}(\phi) = 0\right\}$ and M be the largest invariant subset in S with respect to (3). Then a direct calculation shows that $M = \{u_2\}$. By the Lyapunov-LaSalle invariance principle (Theorem 5.3.2 in [8]), we have that the omega limit sets of solutions are contained in M, which ends the proof. $\qquad\square$

We remark that the global stability of u_2 was also proved in Theorem 3.4 of [12] and Theorem 3.1 of [16] by using a map related to the dynamics of (3). Our proof is based on a different Lyapunov method.
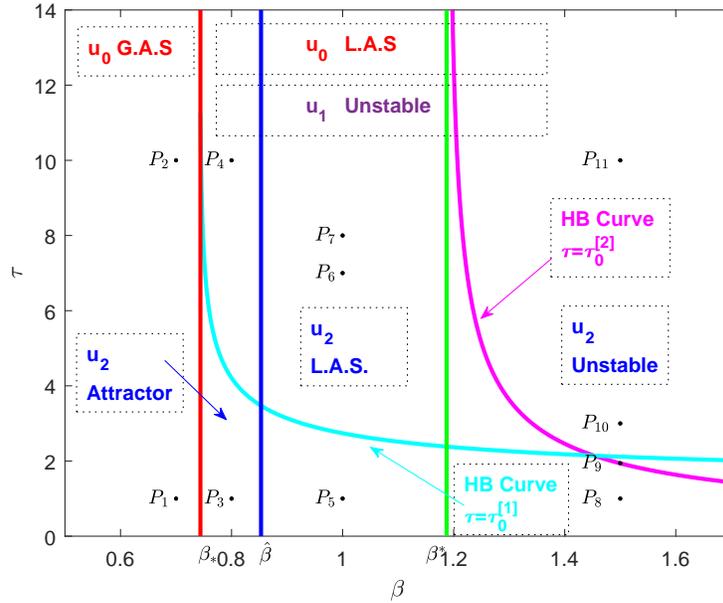
FIGURE 3. Dynamics of system (3) with $k = 4$ in the $\beta - \tau$ plane. The critical values are $\beta_* = 0.7439$, $\hat{\beta} = 0.8531$ and $\beta^* = 1.1873$. We choose eleven points in $\beta - \tau$ plane to perform the numerical simulations in Section 5: $P_1 = (0.7, 1)$, $P_2 = (0.7, 10)$, $P_3 = (0.8, 1)$, $P_4 = (0.8, 10)$, $P_5 = (1, 1)$, $P_6 = (1, 7)$, $P_7 = (1, 8)$, $P_8 = (1.5, 1)$, $P_9 = (1.5, 1.94)$, $P_{10} = (1.5, 3)$, $P_{11} = (1.5, 10)$. Here L.A.S. stands for locally asymptotically stable, and G.A.S. stands for globally asymptotically stable. HB curve $\tau = \tau_0^{[1]}$ and HB curve $\tau = \tau_0^{[2]}$ represent the Hopf bifurcation curves $\tau = \tau_0^{[1]}$ at u_1 and $\tau = \tau_0^{[2]}$ at u_2, respectively.

The local/global stability of equilibria and convergence results in Theorems 3.2, 3.3 and 3.4 can be visualized in Figure 3 to see the effect of β and τ on the dynamics of (3). In particular, there are three bifurcation values in β: β_* (saddle node bifurcation) $< \hat{\beta}$ (global to local dynamics transition) $< \beta^*$ (absolute to conditional stability), and one bifurcation value in τ: $\tau_0(\beta)$ (Hopf bifurcation) when $\beta > \beta^*$.

4. **Global Hopf bifurcations.** Theorem 3.3 shows that the periodic solutions bifurcate from the positive equilibrium when τ is near the bifurcation value under some conditions. Here we consider the global extension of the branches of periodic orbits to τ far away from bifurcation values.

Denote $\tilde{u}$ as one of the positive equilibria and τ_j with $j \in \mathbb{N}^0$ as one of the bifurcation value corresponding to the equilibrium $\tilde{u}$. Let $\mathbb{R}_+ = [0, \infty)$ and $\mathcal{C} = C([-\tau, 0], \mathbb{R}_+)$ be the Banach space of bounded and continuous functions equipped with the standard supermum norm.

Rewrite system (3) as the following general functional differential equation

$$u'(t) = F(u_t, \tau, T), \ (u_t, \tau, T) \in \mathcal{C} \times \mathbb{R}_+^2, \tag{22}$$

where $\mathbb{R}_+^2 = \mathbb{R}_+ \times \mathbb{R}_+$, $u_t(\theta) = u(t + \theta) \in \mathcal{C}$ and $F : \mathcal{C} \times \mathbb{R}_+^2 \to \mathbb{R}$ is defined as

$$F(\phi, \tau, T) = -\phi(0) + \beta\phi(-\tau)^k e^{-\phi(-\tau)}.$$

Identifying the subspace of $\mathcal{C}$ consisting of all constant mappings with $\mathbb{R}_+$, we have a restricted mapping $\hat{F} = F|_{\mathbb{R}_+^3} : \mathbb{R}_+^3 \to \mathbb{R}$ defined as $\hat{F}(x, \tau, T) = -x + \beta x^k e^{-x}$, where $\mathbb{R}_+^3 = \mathbb{R}_+ \times \mathbb{R}_+ \times \mathbb{R}_+$. It is easy to see that $\hat{F}$ is twice continuously differentiable, that is, the assumption (A1) in Chapter 3 of [39] is satisfied.

Set $S(F)$ be the set of the stationary solutions of equation (22):

$$S(F) = \{(u_0, \tau, T), (u_1, \tau, T), (u_2, \tau, T) : \tau > 0, T > 0\}.$$

For any stationary solution $(\tilde{u}, \tau, T) \in S(F)$, the characteristic equation is

$$\Delta_{(\tilde{u}, \tau, T)}(\lambda) = \lambda - \beta(k - \tilde{u})e^{-\tilde{u}}\tilde{u}^{k-1}e^{-\lambda\tau} + 1.$$

It is easy to see that $\lambda = 0$ is not a root of $\Delta_{(\tilde{u}, \tau, T)}(\lambda){=}0$ for all $(\tilde{u}, \tau, T) \in S(F)$, which implies the assumption (A2) in Chapter 3 of [39] holds.

By the definition of $F(u, \tau, T)$ and $\Delta_{(\tilde{u}, \tau, T)}(\lambda)$, the smoothness assumption (A3) of Chapter 3 in [39] is satisfied. Thus, for $(u_l, \tau, T) \in S(F)$, there exist $\varepsilon > 0$ and a continuously differentiable mapping $v : B_\varepsilon(\tau_j^{[l]}, T^{[l]}) \to \mathbb{R}_+$ satisfying $\hat{F}(v(\tau, T), \tau, T) = 0$ for $(\tau, T) \in B_\varepsilon(\tau_j^{[l]}, T^{[l]}) = (\tau_j^{[l]} - \varepsilon, \tau_j^{[l]} + \varepsilon) \times (T^{[l]} - \varepsilon, T^{[l]} + \varepsilon)$, where $T^{[l]} = 2\pi/\omega^{[l]}$ and $l = 1, 2$.

From Theorem 3.3, for each $j \in \mathbb{N}^0$, $(u_1, \tau_j^{[1]}, T^{[1]})$ is an isolated center [39] when $\beta > \beta_*$ and $(u_2, \tau_j^{[2]}, T^{[2]})$ is an isolated center when $\beta > \beta^*$. Thus, by Theorem 3.3 and (21), there exist $\varepsilon > 0, \delta > 0$ and smooth curves $\lambda^{[l]} : (\tau_j^{[l]} - \delta, \tau_j^{[l]} + \delta) \to \mathbb{C}$ (which represents the set of all complex numbers) such that $\Delta_{(v(\tau, T), \tau, T)}(\lambda^{[l]}(\tau)) = 0$ as $|\lambda^{[l]}(\tau) - i\omega^{[l]}| < \varepsilon$ and $\tau \in [\tau_j^{[l]} - \delta, \tau_j^{[l]} + \delta]$, where

$$\lambda^{[l]}(\tau_j^{[l]}) = i\omega^{[l]}, \ \frac{d\mathrm{Re}\lambda^{[l]}(\tau_j^{[l]})}{d\tau} > 0, \ l = 1, 2.$$

Let

$$\Omega_\varepsilon^{[l]} = \{(\alpha, T) : \ 0 < \alpha < \varepsilon, \ |T - T^{[l]}| < \varepsilon\}.$$

Then, by Theorem 3.3 and (21), it is not difficult to see that $\Delta_{(u_l, \tau, T)}(\alpha + 2\pi i/T) = 0$ as $|\tau - \tau_j^{[l]}| \le \delta$ and $(\alpha, T) \in \partial\Omega_\varepsilon^{[l]}$ if and only if $\tau = \tau_j^{[l]}, \alpha = 0$ and $T = T^{[l]}$. Denote

$$H^\pm(u_l, \tau_j^{[l]}, T^{[l]})(\alpha, T) = \Delta_{(u_l, \tau_j^{[l]} \pm \delta, T)}(\alpha + 2\pi i/T).$$

Then we obtain the cross number of the isolated center $(u_l, \tau_j^{[l]}, T^{[l]})$ is

$$\gamma_1^{[l]}\left(u_l, \tau_j^{[l]}, T^{[l]}\right) = \deg_B\left(H^-(u_l, \tau_j^{[l]}, T^{[l]}), \Omega_\varepsilon^{[l]}\right) - \deg_B\left(H^+(u_l, \tau_j^{[l]}, T^{[l]}), \Omega_\varepsilon^{[l]}\right) = -1,$$

for each $j \in \mathbb{N}^0$ and $l = 1, 2$, where $\deg_B$ represents the Brouwer degree. This verifies the assumption (A4) for $m = 1$ of Chapter 3 in [39] holds.

Define a closed subset of $\mathcal{C} \times \mathbb{R}_+^2$ by

$$\Sigma(F) = Cl\left\{(x, \tau, T) \in \mathcal{C} \times \mathbb{R}_+^2 : \ x \text{ is a } T\text{-periodic solution of system (22)}\right\},$$

and denote by $C(u_l, \tau_j^{[l]}, T^{[l]})$ the connected component of $\Sigma(F)$ containing the point $(u_l, \tau_j^{[l]}, T^{[l]})$ with $l = 1, 2$, where $T^{[l]} = 2\pi/\omega^{[l]}$, $\tau_j^{[l]}$ and $\omega^{[l]}$ are defined in (17)-(20). From Theorem 3.3, $C(u_l, \tau_j^{[l]}, T^{[l]})$ are nonempty subsets of $\Sigma(F)$.

From Theorem 3.3 in [39], one of the following alternatives holds:

(I) $C(u_l, \tau_j^{[l]}, T^{[l]})$ is unbounded in $\mathcal{C} \times \mathbb{R}_+^2$; or

(II) $C(u_l, \tau_j^{[l]}, T^{[l]})$ is bounded, $C(u_l, \tau_j^{[l]}, T^{[l]}) \cap S(F)$ is finite and

$$\sum_{(w, \tau, T) \in C(u_l, \tau_j^{[l]}, T^{[l]}) \cap S(F)} \gamma_1^{[l]}(w, \tau, T) = 0.$$

From (4), the alternative (II) cannot happen. Thus, the alternative (I) must happen for each of $C(u_l, \tau_j^{[l]}, T^{[l]})$, that is,

Lemma 4.1. $C\left(u_l, \tau_j^{[l]}, T^{[l]}\right)$ is unbounded in $\mathcal{C} \times \mathbb{R}_+^2$ for each center $\left(u_l, \tau_j^{[l]}, T^{[l]}\right)$ and $l = 1, 2$.

For further properties of the connected component $C\left(u_l, \tau_j^{[l]}, T^{[l]}\right)$, we prove several preliminary results. Lemma 2.1 implies that the boundedness of all the periodic solutions:

Lemma 4.2. All positive periodic solutions of system (3) are uniformly bounded.

We have the following non-existence results for the periodic solutions of (3) with certain periods.

Lemma 4.3. System (3) has no periodic solutions of period τ and 2τ.

Proof. Any nonconstant periodic solution $u(t)$ of (3) with period τ is a periodic solution of the ordinary differential equation $u'(t) = -u(t) + \beta u^k(t)e^{-u(t)}$ since $u(t - \tau) = u(t)$. It is well known that a first order autonomous ordinary differential equation has no non-constant periodic solutions so (3) has no periodic solutions of period τ.

We next prove the nonexistence of periodic solutions with period 2τ. Assume that $u(t)$ is a periodic solution of (3) with period 2τ. Let $v(t) = u(t - \tau)$, then $(u(t), v(t))$ is a periodic solution of the following system

$$\begin{aligned} u'(t) &= -u(t) + \beta v^k(t)e^{-v(t)}, \\ v'(t) &= -v(t) + \beta u^k(t)e^{-u(t)}. \end{aligned} \tag{23}$$

Denote $P(u, v) = -u + \beta v^k e^{-v}$ and $Q(u, v) = -v + \beta u^k e^{-u}$. A direct calculation leads to

$$\frac{\partial P}{\partial u} + \frac{\partial Q}{\partial v} = -2 < 0,$$

which implies system (23) has no non-constant periodic solutions by Bendixson's criterion. $\square$

Now we are in the position to describe the global Hopf bifurcations and existence of multiple periodic solutions of (3).

Theorem 4.4. For system (3), the following statements are true:

(i) Assume that $\beta_* < \beta \leq \beta^*$. Then system (3) has at least $j + 1$ non-constant periodic solutions when $\tau > \tau_j^{[1]}$ with $j \in \mathbb{N}^0$.

(ii) *Assume $\beta > \beta^*$. Then system (3) has at least $j + 2$ non-constant periodic solutions when $\tau > \max\{\tau_0^{[1]}, \tau_0^{[2]}, \min\{\tau_j^{[1]}, \tau_j^{[2]}\}\}$ with $j \in \mathbb{N}$; and it has at least 1 non-constant periodic solution when $\tau > \min\{\tau_0^{[1]}, \tau_0^{[2]}\}$.*

Proof. We first assume that $\beta > \beta^*$. In that case, Hopf bifurcations occur at both u_1 and u_2 when τ increases. By the definition of $\tau_j^{[l]}$ in (18) and (20) for $l = 1, 2$, we have that for $j \in \mathbb{N}^0$,

$$\tau_j^{[1]} \omega^{[1]} = (2j + 1)\pi + \arccos\left(\frac{1}{u_1 - k}\right),$$

$$\tau_j^{[2]} \omega^{[2]} = (2j + 1)\pi - \arccos\left(\frac{1}{u_2 - k}\right),$$

which implies that for $j \in \mathbb{N}^0$ and $l = 1, 2$,

$$\left(2j + \frac{3}{2}\right)\pi < \tau_j^{[1]} \omega^{[1]} < (2j + 2)\pi, \quad \left(2j + \frac{1}{2}\right)\pi < \tau_j^{[2]} \omega^{[2]} < (2j + 1)\pi. \quad (24)$$

Here we use the fact that $u_1 - k < -1$, $u_2 - k > 1$ when $\beta > \beta^*$ and the range of the function arccos is $[0, \pi]$. Thus, by (24), a direct calculation leads to for $j \in \mathbb{N}^0$,

$$\frac{\tau_j^{[1]}}{j + 1} < \frac{2\pi}{\omega^{[1]}} < \frac{4\tau_j^{[1]}}{4j + 3} < \frac{\tau_j^{[1]}}{j}, \quad \frac{\tau_j^{[2]}}{j + 1} < \frac{2\tau_j^{[2]}}{2j + 1} < \frac{2\pi}{\omega^{[2]}} < \frac{4\tau_j^{[2]}}{4j + 1} < \frac{\tau_j^{[2]}}{j}. \quad (25)$$

The relations in (25) imply that near the Hopf bifurcation point $\tau = \tau_j^{[l]}$, the period T of bifurcating periodic solutions on $C(u_l, \tau_j^{[l]}, T^{[l]})$ with $T^{[l]} = 2\pi/\omega^{[l]}$ satisfies

$$\frac{\tau}{j + 1} < T < \frac{\tau}{j}, \quad \text{if} \quad (u, \tau, T) \in C(u_l, \tau_j^{[l]}, T^{[l]}), \quad j \in \mathbb{N}, \quad l = 1, 2, \quad (26)$$

and

$$\begin{aligned} \tau < T < 2\tau, \quad &\text{if} \quad (u, \tau, T) \in C(u_1, \tau_0^{[1]}, T^{[1]}), \\ 2\tau < T < 4\tau, \quad &\text{if} \quad (u, \tau, T) \in C(u_2, \tau_0^{[2]}, T^{[2]}). \end{aligned} \quad (27)$$

From Lemma 4.3, the bounds of T in (26) hold for all periodic solutions on $C(u_l, \tau_j^{[l]}, T^{[l]})$, as T cannot equal to τ/j for any $j \in \mathbb{N}$ otherwise (3) has a periodic solution with period τ. Hence the periods of periodic solutions of system (3) on $C(u_l, \tau_j^{[l]}, T^{[l]})$ are uniformly bounded. In particular this also implies that

$$\begin{aligned} C(u_l, \tau_j^{[l]}, T^{[l]}) \cap C(u_l, \tau_i^{[l]}, T^{[l]}) = \emptyset, \quad &i \neq j, \quad l = 1, 2, \\ C(u_1, \tau_j^{[1]}, T^{[1]}) \cap C(u_2, \tau_i^{[1]}, T^{[2]}) = \emptyset, \quad &i \neq j. \end{aligned} \quad (28)$$

Combining Lemma 4.1, Lemma 4.2 and the boundedness of periods, $C(u_l, \tau_j^{[l]}, T^{[l]})$ is bounded in the projections onto u and T components, thus the projection of $C(u_l, \tau_j^{[l]}, T^{[l]})$ onto the τ-space must be unbounded for $l = 1, 2$. Also there is no nontrivial periodic solutions when $\tau > 0$ is small, thus we conclude that the projection of $C(u_l, \tau_j^{[l]}, T^{[l]})$ ($l = 1, 2$) onto τ-space includes $(\tau_j^{[l]}, +\infty)$. The bound of T in (26) does not exclude the possibility of $C(u_1, \tau_j^{[l]}, T^{[1]}) = C(u_2, \tau_j^{[l]}, T^{[2]})$ for $j \in \mathbb{N}$, so we conclude that there exists at least one periodic solution (u, τ, T) of (3) on $C(u_1, \tau_j^{[l]}, T^{[1]}) \cup C(u_2, \tau_j^{[l]}, T^{[2]})$ when $\tau > \min\{\tau_j^{[1]}, \tau_j^{[2]}\}$ with T satisfying (26). However for $j = 0$, (27) implies that $\tau < T < 2\tau$ for all periodic solutions of (3)

on $C(u_1, \tau_0^{[1]}, T^{[1]})$, and $T > 2\tau$ for all periodic solutions of (3) on $C(u_2, \tau_0^{[2]}, T^{[2]})$, hence

$$\mathcal{C}(u_1, \tau_0^{[1]}, T^{[1]}) \cap C(u_2, \tau_0^{[2]}, T^{[2]}) = \emptyset. \tag{29}$$

Thus there exists at least one periodic solution (u, τ, T) of (3) on $C(u_1, \tau_0^{[1]}, T^{[1]})$ when $\tau > \tau_0^{[1]}$, and there exists at least one periodic solution (u, τ, T) of (3) on $C(u_2, \tau_j^{[2]}, T^{[2]})$ when $\tau > \tau_0^{[2]}$ with T satisfying (27).

In summary system (3) has at least $j + 2$ non-constant periodic solutions when $\tau > \max\{\tau_0^{[1]}, \tau_0^{[2]}, \min\{\tau_j^{[1]}, \tau_j^{[2]}\}\}$ with $j \in \mathbb{N}$; and it has at least 1 non-constant periodic solution when $\tau > \min\{\tau_0^{[1]}, \tau_0^{[2]}\}$.

For the case of $\beta_* < \beta \le \beta^*$, the proof is same as above except that Hopf bifurcations only occur at u_1 not u_2, so only $C(u_1, \tau_j^{[1]}, T^{[1]})$ exist for $j \in \mathbb{N}^0$.   □

We remark that the estimates (25) can lead to a finer estimate of period T of periodic solutions on the bifurcation branches $C(u_1, \tau_j^{[l]}, T^{[1]})$ and $C(u_2, \tau_j^{[l]}, T^{[2]})$. But it is not known that whether (3) possesses periodic orbits with period 4τ when $\beta > \beta^*$. If that is the case, we can exclude the possibility of $C(u_1, \tau_j^{[l]}, T^{[1]}) = C(u_2, \tau_j^{[l]}, T^{[2]})$ for $j \in \mathbb{N}$, and there will be $2j + 2$ non-constant periodic solution when $\tau > \min\{\tau_j^{[1]}, \tau_j^{[2]}\}$ for $j \in \mathbb{N}^0$.

5. **Numerical simulations.** In this section, we show some numerical simulations to demonstrate our theoretical results in the previous sections and also explore more possible dynamics of (3). In the simulations, we use $k = 4$ and the bifurcation values calculated previously are $\beta_* = 0.7439$, $\hat{\beta} = 0.8531$ and $\beta^* = 1.1873$.
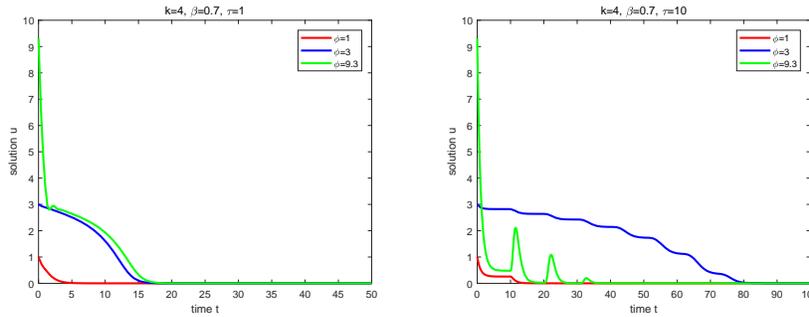
FIGURE 4. The global stability of u_0 of system (3) with $k = 4$, $\beta = 0.7 < \beta_*$. Left panel: $\tau = 1$ and $(\beta, \tau) = P_1$; right panel: $\tau = 10$ and $(\beta, \tau) = P_2$ as in Figure 3. Initial condition: $\phi(t) = 1 < u_1$ (red), $\phi(t) = 3 \in (u_1, u_3)$ (blue), and $\phi(t) = 9.3 > u_3$ (green).

When $\beta = 0.7 < \beta_*$, there is no positive equilibria and all solutions converge to $u_0 = 0$ as shown in Theorem 3.2; see Figure 4.

When $\beta > \beta_*$, the system has two distinctive positive equilibria $u_2 > u_1$. We also assume $\beta < \beta^*$. When the time delay τ is small, solutions of (3) converge to u_0 provided $\phi < u_1$ and converge to u_2 provided $\phi > u_1$ (Theorems 3.2 and 3.4). When τ is large, solutions of (3) converge to u_0 provided $\phi < u_1$ or ϕ is large enough, and they converge to u_2 provided $\phi > u_1$ but not large enough; see Figure 5 ($\beta = 0.8$) and Figure 6 ($\beta = 1$). In these two cases, transient oscillatory dynamics of
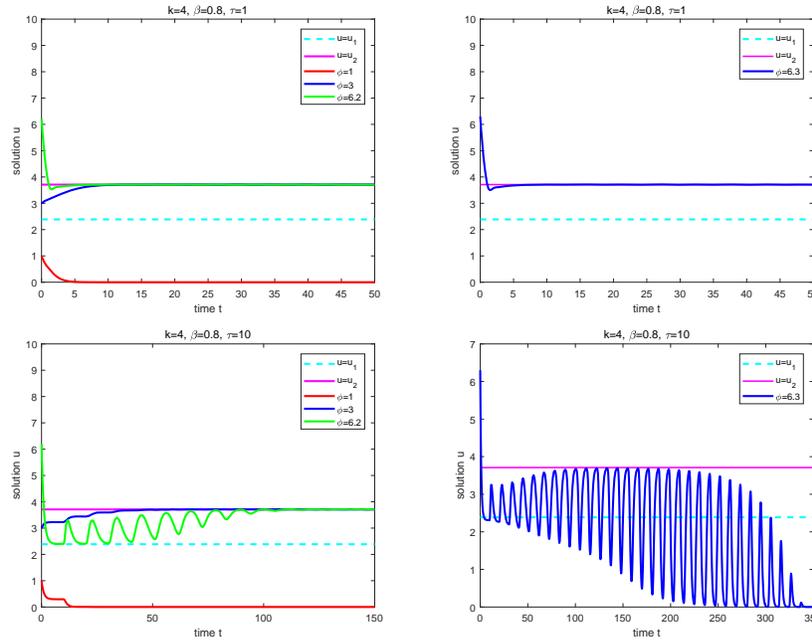
FIGURE 5. The dynamics of system (3) with $k = 4$ and $\beta = 0.8$. Upper row: $\tau = 1$ and $(\beta, \tau) = P_3$; lower row: $\tau = 10$ and $(\beta, \tau) = P_4$ as in Figure 3. Initial condition: (left column) $\phi(t) = 1 < u_1$ (red), $\phi(t) = 3 \in (u_1, u_3)$ (blue), and $\phi(t) = 6.2 > u_3$ (green); (right column) $\phi(t) = 6.3$ (blue). Here positive equilibria are $u_1 = 2.3817$ and $u_2 = 3.7093$.

system (3) occurs when the time delay τ is large, but the solution converges to the equilibrium u_0 or u_2 asymptotically. The transient oscillatory behavior corresponds to the unstable periodic solutions bifurcating from the unstable equilibrium u_1 through Hopf bifurcations (see Theorems 3.3 and 4.4). When $\tau = 8$ in Figure 6, a threshold phenomenon is shown: the solution converges to u_2 when ϕ is smaller than the threshold and it converges to u_0 when ϕ is larger than it.

For $\beta \in (\beta_*, \beta^*)$, all oscillatory behavior of solutions appear to be transient as indicated by unstable periodic solutions bifurcated from unstable equilibrium u_1. As the time delay τ gets larger, the transient oscillations also last longer. Figure 7 shows the long transient oscillations when $\beta = 1$ and $\tau = 50$. Similar oscillatory long transients have also been observed in [23], see also [9, 24].

When $\beta > \beta^*$, the larger equilibrium u_2 can lose its stability through Hopf bifurcation when τ increases, and sustained oscillations occur around u_2. See Figure 8 for the case of $\beta = 1.5$ and τ small. Here $\omega_0^{[2]} = 1.1753$, $\tau_0^{[2]} = 1.9364$ and $\tau_1^{[2]} = 7.2823$. So a solution with large initial value converges to u_2 when $\tau < \tau_0^{[2]}$, and it converges to a limit cycle when $\tau > \tau_0^{[2]}$. Using normal form theory of Hopf bifurcations, we can calculate that $\mu_2 = 2.113 > 0$, $\beta_2 = -0.423 < 0$, $T_2 = 0.464 > 0$ (using standard notation of normal forms), which implies that the Hopf bifurcation at $\tau = \tau_0^{[2]}$ is supercritical and the bifurcating periodic solution is locally asymptotically stable.
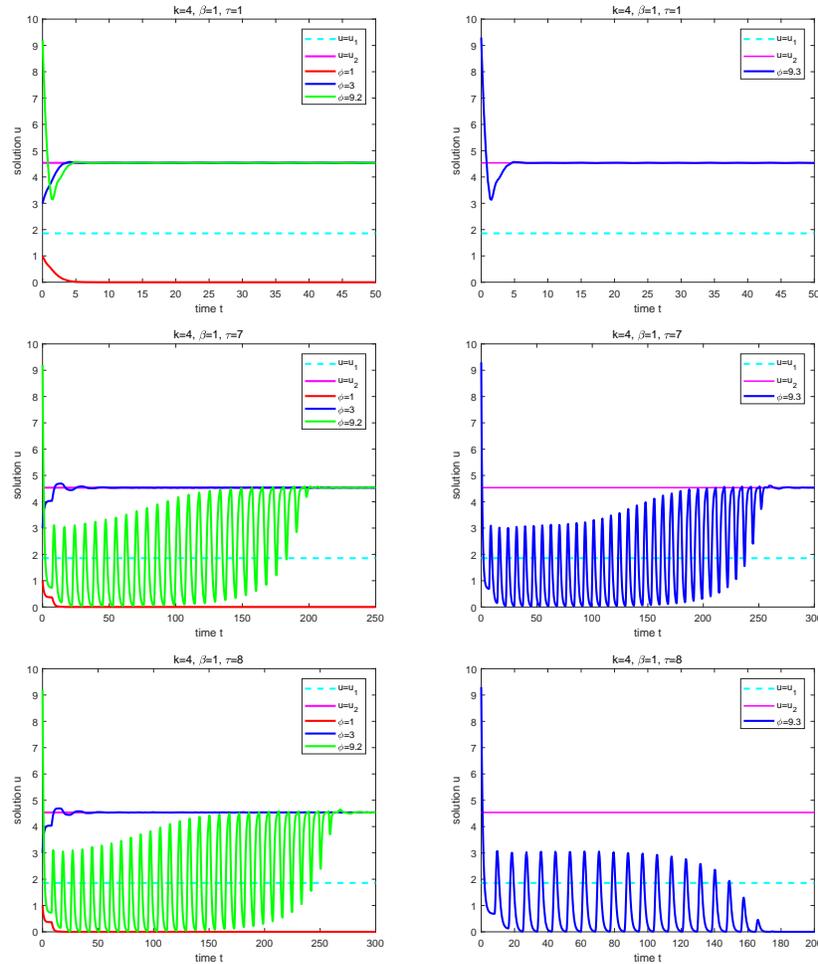
FIGURE 6. The dynamics of system (3) with $k = 4$ and $\beta = 1$. First row: $\tau = 1$ and $(\beta, \tau) = P_5$; Second row: $\tau = 7$ and $(\beta, \tau) = P_6$; Third row: $\tau = 8$ and $(\beta, \tau) = P_7$ as in Figure 3. Initial condition: (left column) $\phi(t) = 1 < u_1$ (red), $\phi(t) = 3 \in (u_1, u_3)$ (blue), and $\phi(t) = 9.2 > u_3$ (green); (right column) $\phi(t) = 9.3$ (blue). Here positive equilibria are $u_1 = 1.8572$ and $u_2 = 4.5364$.

For $\beta > \beta^*$, when the time delay τ increases, the simple sinusoidal oscillatory pattern around u_2 transits to a two-frequency oscillations with asymmetric peaks (see Figure 9 left column), and long transient of oscillations around u_1 also occurs but asymptotically transits into the oscillation pattern around u_2 (see Figure 9 right column). In the transition period from the transient oscillatory pattern around u_1 to the stable oscillatory pattern around u_2, both types of oscillations occur alternatively (see Figure 9 third row).

The solution orbits of (3) with different initial conditions are shown in Figure 10 and Figure 11 on the $u(t) - u(t - \tau)$ phase plane for different β and τ. Bistability in (3) is clearly demonstrated in all cases: for smaller β, u_0 and u_2 are both attractors;
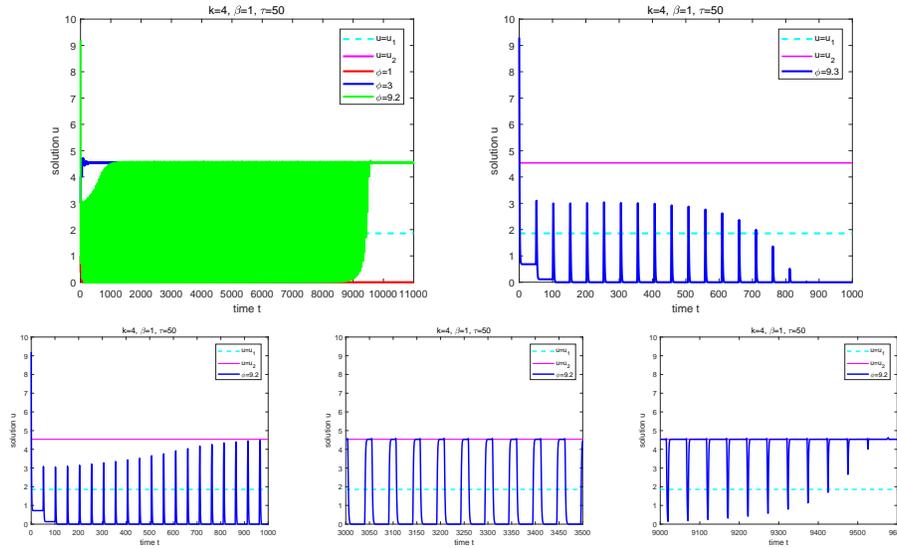
FIGURE 7. Transient oscillation dynamics of system (3) with $k = 4$, $\beta = 1$ and $\tau = 50$. Upper left: initial condition $\phi(t) = 1 < u_1$ (red), $\phi(t) = 3 \in (u_1, u_3)$ (blue), and $\phi(t) = 9.2 > u_3$ (green). Upper right: initial condition $\phi(t) = 9.3$ (blue). Lower row: snapshots of the solution with $\phi(t) = 9.2$ over different time intervals. Here positive equilibria are $u_1 = 1.8572$ and $u_2 = 4.5364$.
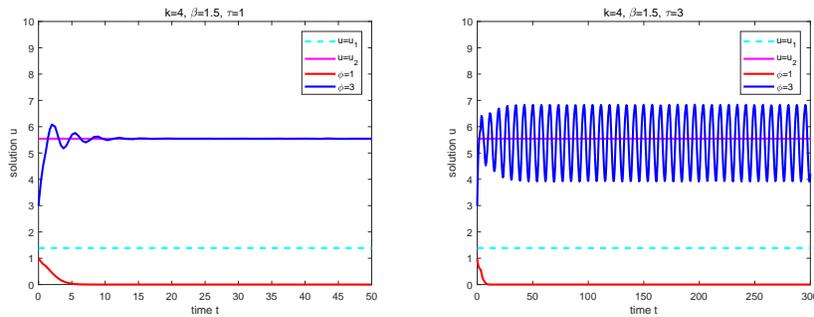
FIGURE 8. Oscillatory dynamics of (3) with $k = 4$ and $\beta = 1.5$. Left panel: $\tau = 1$ and $(\beta, \tau) = P_8$; right panel: $\tau = 3$ and $(\beta, \tau) = P_{10}$ as in Figure 3. Initial condition: $\phi(t) = 1 < u_1$ (red), and $\phi(t) = 3 \in (u_1, u_3)$ (blue). Here positive equilibria are $u_1 = 1.3871$ and $u_2 = 5.5432$.

and for larger β, u_0 and a limit cycle around u_2 are attractors. Long transient oscillations around u_1 can be observed for large $\tau(\approx 50)$ no matter what the value of β is, and stable oscillations around u_2 is the asymptotic limit of solutions of (3) when $\beta = 1.5$ and large τ. Figure 11 shows the complex dynamics of long transient oscillations around u_1 and eventual switching to stable oscillations around u_2 (corresponding to the same solution shown in Figure 9 right column and third row). The dynamics of $\beta = 0.8$ (or $\beta = 1$) and $\tau = 50$ also suggests the existence of a periodic pulse type solution oscillating between u_0 and u_2 (see also Figure 7
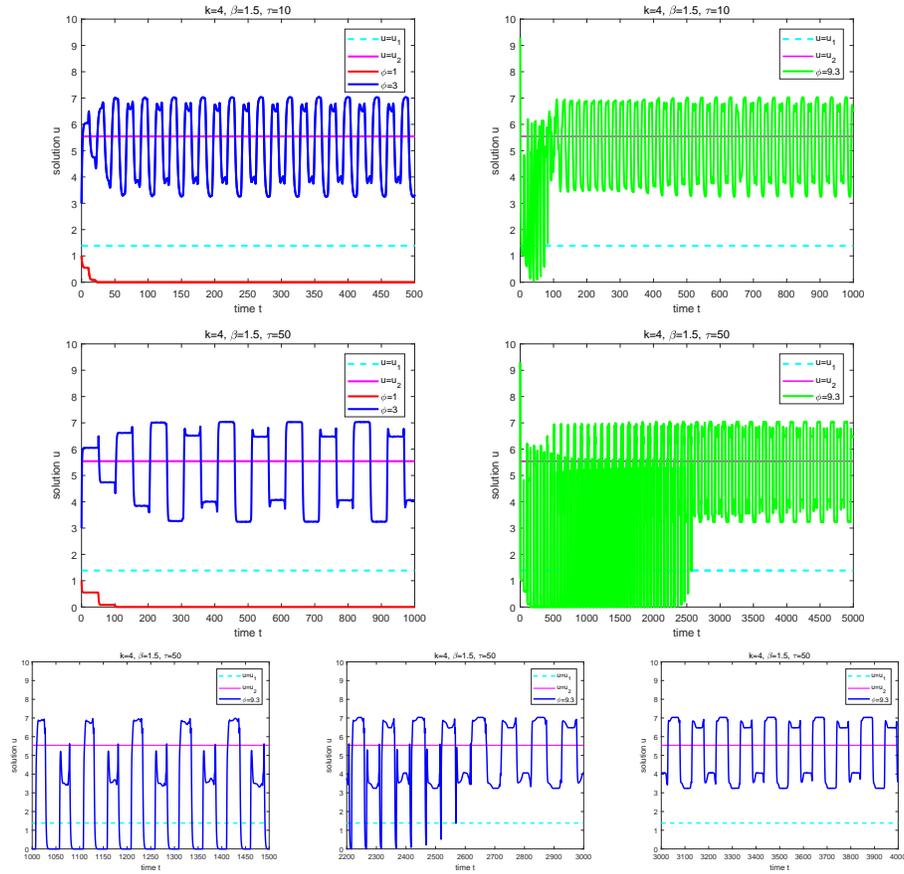
FIGURE 9. Two-frequency oscillations with asymmetric peaks and the transient oscillation dynamics of (3) with $k = 4$ and $\beta = 1.5$. First row: $\tau = 10$ and $(\beta, \tau) = P_{11}$ in Figure 3; Second row: $\tau = 50$; Third row: snapshots of the solution with the initial condition $\phi(t) = 9.3$ and $\tau = 50$ over different time intervals. Initial condition: $\phi(t) = 1 < u_1$ (red), $\phi(t) = 3 \in (u_1, u_3)$ (blue), and $\phi(t) = 9.3$ (green). Here positive equilibria are $u_1 = 1.3871$ and $u_2 = 5.5432$.

lower middle panel), and it appears to be asymptotically unstable but can stay for a long time.

For $\beta > \beta_*$, the dynamics of (3) is always bistable with one stable state being the extinction state $u_0 = 0$, and the other persistence state being either a stable positive equilibrium $u_2 > 0$ or a stable limit cycle around u_2. In general increasing the growth rate β shrinks the size of the basin of attraction of extinction state u_0 and enlarge the size of the basin of attraction of the persistence state. Figure 12 shows the partition of the set of constant initial conditions $\phi(t) \equiv \phi > 0$ for $t \in [-\tau, 0]$ according to the asymptotic limit of solutions starting from such initial conditions. We observe that for the case of $\beta = 0.8$ or $\beta = 1$, the basin of attraction of u_0 is split into region I and III, two disconnected regions. The phenomenon of population extinction for large initial conditions was also found in another delay
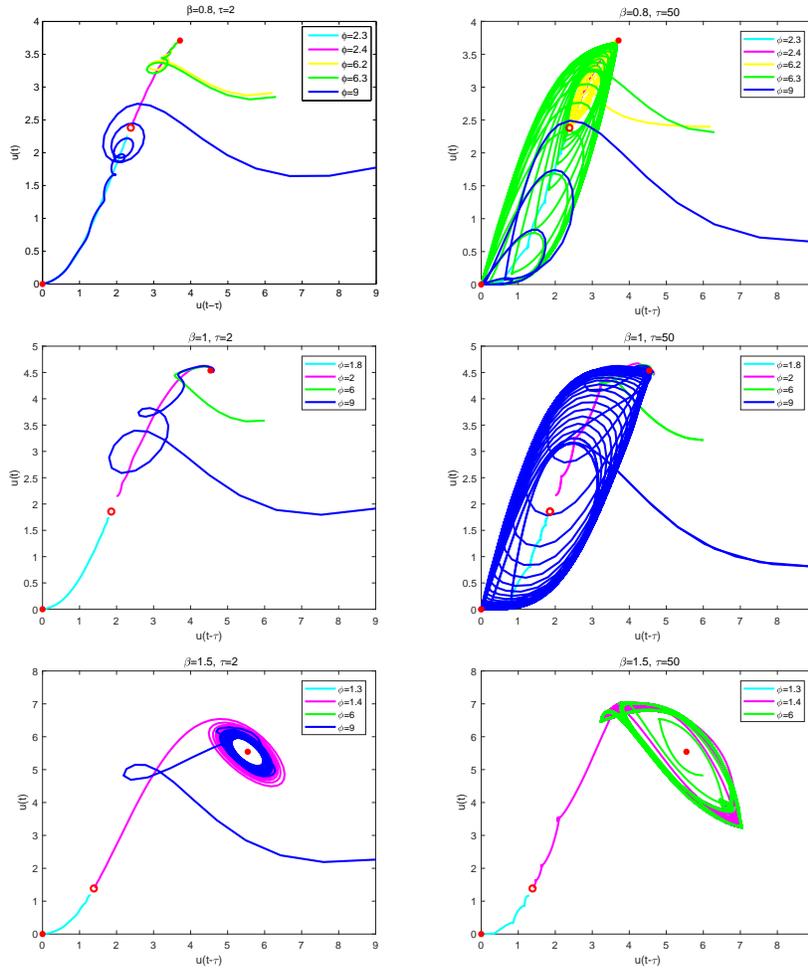
FIGURE 10. The $u(t) - u(t-\tau)$ phase planes of system (3) with $k = 4$. Upper left: $\beta = 0.8$, $\tau = 2$; Upper right: $\beta = 0.8$, $\tau = 50$; Middle left: $\beta = 1$, $\tau = 2$; Middle right: $\beta = 1$, $\tau = 50$; Bottom left: $\beta = 1.5$, $\tau = 2$. Bottom right: $\beta = 1.5$, $\tau = 50$. Solution orbits are shown for $0 \leq t \leq 1000$.

differential equation with different type of Allee effect [4]. Note that the region III satisfies that $\phi > u_3$ (see Lemma 3.1) and $\tau > \tilde{\tau}$. On the other hand, when $\beta > \beta^*$, it appears that all large initial conditions lead to a persistence state.

6. **Concluding remarks.** In this paper, we analyze the dynamical behavior and the effect of the delay of a scalar Nicholson's blowflies equation with Allee effect. The existence, stability and basins of attraction of multiple equilibria have been studied by using the characteristic method and Lyapunov-LaSalle invariance principle. Taking the time delay value as the bifurcating value, the existence of multiple periodic solutions are obtained using local and global Hopf bifurcations near the positive equilibria. Numerical simulations of the system have shown rich dynamics such as
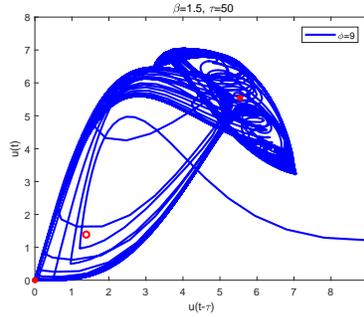
FIGURE 11. The $u(t) - u(t - \tau)$ phase plane of system (3) with $k = 4$, $\beta = 1.5$, $\tau = 50$ and $\phi = 9$. Solution orbits are shown for $0 \leq t \leq 1000$.
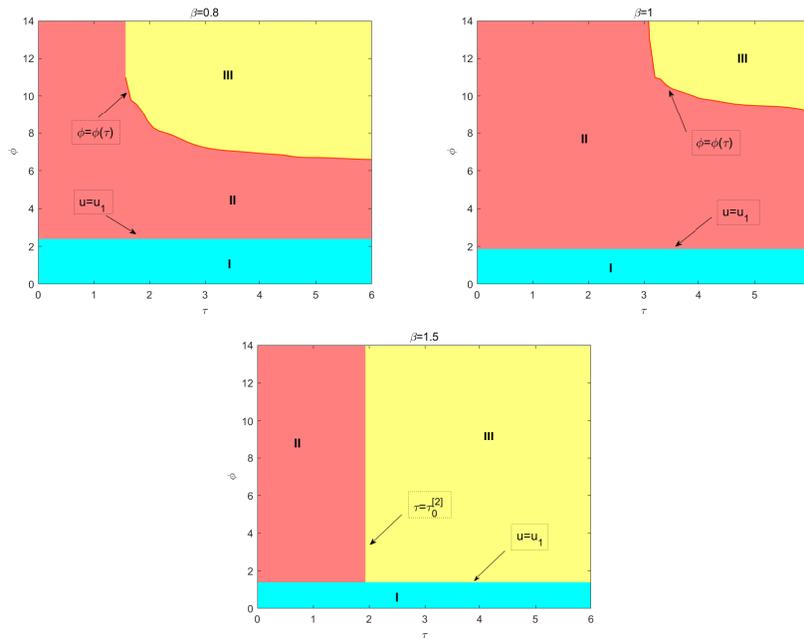
FIGURE 12. The domains of attraction of stable states on $\phi - \tau$ plane with $k = 4$, where ϕ is a constant initial condition. Upper left: $\beta = 0.8 \in (\beta_*, \hat{\beta})$; Upper right: $\beta = 1 \in (\hat{\beta}, \beta^*)$; and lower: $\beta = 1.5 > \beta^*$. Region I: converging to $u_0 = 0$; Region II: converging to $u_2 > 0$; and Region III: converging to $u_0 = 0$ for upper row, and oscillating for lower row.

long transient oscillations, and multiple-frequency oscillations which are generated from the interplay of bistability and time delay.

It should be noted that model (2) is also called the Lasota-Wazewska equation in biology, which describes the number of red blood cells when blood transfusion is conducted among the animal group [14]. It has an age structured equation with unimodal and delay feedback. Our conclusions obtained above can be applied to the Lasota-Wazewska equation, which coincides with the information in [19].

The model here is the kinetic equation of the reaction-diffusion model proposed in [34]. It is interesting to see the further effect of diffusion on the already complex dynamics caused by bistability and time delay, especially the phenomena of spatial-temporal pattern formation and spatial propagation.

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