Dynamics of a predator-prey model with discrete and distributed delay

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Abstract: This paper considers a predator-prey model with discrete time delay representing prey handling time and assumed equal to the predator maturation period, and a distributed time delay describing intra-species interactions. We show that due to the delayed logistic growth of the prey, it is impossible for the species to become extinct through predation. Conditions for existence and local stability of the co-existence equilibrium are derived in terms of system parameters. Using techniques of centre manifold reduction and the normal form theory, we establish the direction of Hopf bifurcation of the co-existence equilibrium, as well as the stability of the bifurcating period solution. Numerical bifurcation analysis and simulations are performed to illustrate regions of stability of the co-existence equilibrium, to investigate how the amplitude and the period of bifurcating periodic solutions depend on parameters, and to demonstrate different types of dynamics of the system.

Keywords: stability; discrete and distributed delay; predator-prey model; Hopf bifurcation; periodic solutions.

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1 Introduction

Predator-prey models are known to play a very important role in a number of areas of mathematical biology and ecology, it is therefore no surprise that the classical model of a single predator-prey species, first proposed by Lotka in 1910 and further investigated by both Lotka and Volterra, is one of the most universally recognised models in mathematics, Lotka (1926) and Volterra (1927). Sustaining a healthy and balanced biosphere is not only biologically important but absolutely crucial to Earth's biodiversity and arguably necessary for the survival of the human species. This is evident, as any changes in ecology and environment can often have devastating and unpredictable effects on the population growth of many different species (Xu and Liao, 2014). To mitigate this, the Lotka-Voltera family of models can often be used to study population dynamics, and due to their significance they can provide a valuable tool in controlling the delicate balance of the ecosystem.

There are many ways of making the classical Lotka-Volterra model more realistic and tractable both biologically and mathematically, with each addition or extension often leading to more interesting mathematical results (Xu et al., 2011). One option, is to include some time delay in the biological interactions (Xu and Liao, 2014). For example, in the classical model, the intrinsic time delay for the conversion of biomass from prey to predator population is ignored. From a biological perspective, the delay could represent the time necessary to mature or reproduce, i.e., from mating to new offspring, which is further complicated by the variety of body size growth rates and reproductive capabilities for each individual within the population (Turchin, 1990). In a similar way, time delays can also be used as a way to account for the density dependence of the growth rate of several insect and plant species (Turchin and Taylor, 1992). Some ecologists have also suggested that the inclusion of a delay could help to explain certain phenomena observed in long population cycles (Boonstra et al., 1998). Although this practice makes the analysis of these models more difficult, it broadens the spectrum of possible behavioural regimes and allows for more realistic results.

Many theoreticians and experimentalists have analysed the stability of predator-prey systems and, more specifically, have done so with time delays incorporated into the models (Xu and Li, 2015; Xu and Liao, 2013). Such delayed systems received great attention since it became fairly obvious that time delays can often have a very complicated impact on the dynamical behaviour of the system, such as a periodic and chaotic dynamics. In a variety of specific contexts, it is not only appropriate but also instructive to include time delays in such models to correctly account for certain individual biological properties of the dynamics. Time-delayed predator-prey models go back to the early works of Volterra (1927); Volterra and Brelot (1931), and they have been extensively discussed in a number of monographs, such as those by Cushing (2013), MacDonald (1978), Gopalsamy (2013) and Kuang (1993). Main advantage of including time delays lies in the fact that such models provide higher degree of biological realism, but at the same time they make mathematical analysis more challenging, as the phase space of time-delayed systems is infinite-dimensional, and compared to models without time delays they can exhibit a number of complex dynamical behaviours, such as Hopf bifurcations of multiple equilibria, Bogdanov-Takens bifurcation and chaos, see, e.g., Xiao and Ruan (2001), Nakaoka et al. (2006), Dadi (2017) for details. A review by Ruan (2009) surveys a number of predator-prey models with discrete time delays and different types of functional response, and discusses the distribution of zeros for transcendental polynomials representing characteristic equations for such models.

Time delays in predator-prey models can represent a number of different biological features, and their effects on the dynamics also depend on the type of functional response being considered by Ruan (2009). May (1973) has proposed and briefly discussed a model with a single discrete time delay in the prey population representing time associated with growth to maturity. More recently, Song and Wei (2005) have analysed the dynamics of that system using centre manifold reduction and normal form theory developed by Hassard et al. (1981). Nakaoka et al. (2006) and Karaoglu and Merdan (2014) have considered the case when both prey and predators can have different discrete time delays associated with intra-specific competition, while Faria (2001) has analysed the case when predate is characterised by two distinct time delays for prey and predator. Yan and Zhang (2008) have studied the situation where both intra-specific and predation terms are characterised by the same discrete time delay. Yan and Li (2006) and Yuan and Zhang (2010) have investigated stability and a global Hopf bifurcation in the case where predation is instantaneous, but intra-specific terms have equal discrete time delay.

In this paper, we consider a predator-prey model with discrete and distributed time delays of the form

$$\begin{aligned}\dot{x}_1(t) &= x_1(t)\left[r_1 - a_{11}\int_{-\infty}^{t} F(t-s)x_1(s)\mathrm{d}s - a_{12}x_2(t-\tau)\right],\\ \dot{x}_2(t) &= x_2(t)\left[-r_2 + a_{21}x_1(t-\tau) - a_{22}\int_{-\infty}^{t} F(t-s)x_2(s)\mathrm{d}s\right].\end{aligned} \tag{1}$$

Here, $x_1(t)$ and $x_2(t)$ denote the population densities of prey and predator at time t, respectively, $r_1 > 0$ is the constant growth rate of the prey in the absence of predation, $a_{11} > 0$ is the self-regulation rate for the prey, $a_{12} > 0$ is the rate of predation, $r_2 > 0$ is the constant death rate of the predators when there is no prey, $a_{21} > 0$ is the conversion rate for predators, and $a_{22} \geq 0$ is the intra-specific competition among the predators. The discrete time delay τ represents prey handling time (or hunting delay), which is taken to be the same as the predator maturation time (c.f. the work by Faria (2001) where they were taken to be distinct, but that work assumed instantaneous intra-specific interactions). $F(\cdot)$ is a non-negative continuous delay kernel defined and integrable on the interval $[0,\infty)$,

$$F(s) \geq 0 \text{ for } s \geq 0, \qquad \int_0^{\infty} F(s)\mathrm{d}s = 1,$$

which describes intra-specific competition, i.e., weighting of available resource with respect to past prey and predator densities. For simplicity, this kernel is taken to be the same for both prey and predators. In the trivial case $\tau = 0$ and $F(s) = \delta(s)$, the system (1) reduces to a Lotka-Volterra system with logistic growth in prey. Several related models have already been studied in the literature. Song amd Yuan (2006) have analysed the situation when the intra-specific terms are instantaneous, while the predation term is represented by a discrete time delay in the prey equation and a distributed delay in the predator equation. Ma et al. (2009) have considered a model where both intra-specific and predation terms all have the same discrete time delay, and the prey population has an additional intra-specific competition term with a distributed delay. Xu and Shao (2012) have recently analysed a model where predation term in the prey equation and an intra-specific predator competition have the same discrete time delay, and the predation term in the predator, as well as an intra-specific prey competition have the same distributed delay.

As it has been mentioned above, several authors have considered the delay kernel in the form of Dirac δ-function, which results in an intra-specific competition which is either instantaneous or has a discrete time delay. Another biologically realistic choice for the delay kernel is given by a gamma distribution (Cushing, 2013)

$$F(s) = \frac{s^{p-1}\alpha^p e^{-\alpha s}}{(p-1)!}, \tag{2}$$

for some integer power p. Models with gamma distributed time delay have been originally proposed in the context of population biology (Blythe et al., 1985; Cooke and Grossman, 1982; Cushing, 2013) and have subsequently been used to study intracellular dynamics of HIV infection (Mittler et al., 1998), epidemics (Blyuss and Kyrychko, 2010), neural network (Rahman et al., 2015), traffic dynamics with delayed driver response (Sipahi et al., 2007) and time-delayed feedback control (Kyrychko et al., 2011, 2013; Xu and Li, 2018).

The mean time delay for a gamma distribution is given by

$$\tau_m = \int_0^\infty sF(s)\mathrm{d}s = p/\alpha,$$

so the distribution parameter α plays the role of the inverse time delay. For a particular choice of $p = 1$ known as the *weak kernel*, gamma distribution becomes an exponential distribution

$$F(s) = \alpha e^{-\alpha s}, \quad \alpha > 0, \tag{3}$$

with the largest contribution to intra-specific competition coming from the present values of prey and predator densities. When $p > 1$ (which in the case of $p = 2$ is usually referred to as the *strong kernel*), the largest contribution comes from prey and predator densities evaluated at $t - (p-1)/\alpha$.

The outline of this paper is as follows. Section 2 presents linear stability analysis of the steady states of the system (1) with a weak distribution kernel and established conditions for the existence of Hopf bifurcation of a co-existence steady state. In Section 3, explicit formulae are derived for determining the stability of the bifurcating periodic solutions and the direction of the Hopf bifurcation using the normal form theory and the center manifold reduction. Section 4 contains results of numerical simulations of the model, and the paper concludes in Section 5 with discussion of results.

2 Steady states and linear stability analysis

In the rest of this paper we will be concerned with the analysis of system (1) with the weak kernel (3). It is possible to convert a scalar delay differential equation with a distributed delay into a non-delayed system of equations by using the so-called *linear chain trick* described in MacDonald (1978). The linear chain trick allows one to replace the system with distributed delays by the system of ordinary differential equations. Suppose that $F(s)$ in (2) is a general gamma distribution, and let

$$\begin{aligned} x_3(t) &= \int_{-\infty}^t \alpha e^{-\alpha(t-s)} x_1(s)\mathrm{d}s, \\ x_4(t) &= \int_{-\infty}^t \alpha e^{-\alpha(t-s)} x_2(s)\mathrm{d}s. \end{aligned} \tag{4}$$

Differentiate $x_3(t)$ and $x_4(t)$ in (4) with respect to t

$$\begin{aligned} \dot{x}_3(t) &= \alpha x_1(t) - \int_{-\infty}^t \alpha^2 e^{-\alpha(t-s)} x_1(s)\mathrm{d}s = \alpha[x_1(t) - x_3(t)], \\ \dot{x}_4(t) &= \alpha x_2(t) - \int_{-\infty}^t \alpha^2 e^{-\alpha(t-s)} x_2(s)\mathrm{d}s = \alpha[x_2(t) - x_4(t)]. \end{aligned} \tag{5}$$

The model (1) with gamma distributed kernel now becomes

$$\begin{aligned}
\dot{x}_1(t) &= x_1(t)[r_1 - a_{11}x_3(t) - a_{12}x_2(t-\tau)],\\
\dot{x}_2(t) &= x_2(t)[-r_2 + a_{21}x_1(t-\tau) - a_{22}x_4(t)],\\
\dot{x}_3(t) &= \alpha[x_1(t) - x_3(t)],\\
\dot{x}_4(t) &= \alpha[x_2(t) - x_4(t)].
\end{aligned} \tag{6}$$

The system (6) has at most three equilibria: a trivial steady state $E_1^0 = (0,0,0,0)$ corresponding to extinction of both prey and predators, a single-species steady state $E_2^0 = (r_1/a_{11}, 0, r_1/a_{11}, 0)$ characterised by the absence of predators, and a non-trivial steady state $E^* = (x_1^*, x_2^*, x_3^*, x_4^*)$ with

$$x_1^* = x_3^* = \frac{r_1 a_{22} + r_2 a_{12}}{a_{11}a_{22} + a_{12}a_{21}},$$

$$x_2^* = x_4^* = \frac{r_1 a_{21} - r_2 a_{11}}{a_{11}a_{22} + a_{12}a_{21}}.$$

The co-existence steady state E^* is only biological feasible if the following relation between system parameters holds

$$r_1 a_{21} > r_2 a_{11}. \tag{7}$$

As a first step, we analyse the stability of the trivial steady state $E_1^0 = (0,0,0,0)$. The characteristic equation of the linearisation near this steady state is given by

$$(\lambda - r_1)(\lambda + r_2)(\lambda + a)^2 = 0,$$

which immediately implies that this steady state is unstable for any values of system parameters. Biologically, this means that provided one starts with non-zero numbers of prey and predators, it is impossible for both the prey and predators to become extinct, independently of the strength of predation. The reason behind this is the fact that in the absence of predation, prey experience logistic growth with time-delayed intra-specific competition, and this is what keeps them away from extinction, and in turn provides resource for predators.

Similarly, the characteristic equation of the linearisation of the system (6) about the single-species steady state $E_2^0 = (r_1/a_{11}, 0, r_1/a_{11}, 0)$ has the form

$$\lambda^4 + b_0\lambda^3 + b_1\lambda^2 + b_2\lambda + b_3 = 0.$$

where $b_0 = 2\alpha - l_2$, $\;b_1 = \alpha^2 - (2l_2 + l_1)\alpha$, $\;b_2 = (l_2 - \alpha)\alpha l_1 - l_2\alpha^2$, $\;b_3 = l_1 l_2 \alpha^2$, $l_1 = -r_1$, $l_2 = \frac{a_{21}}{a_{11}} r_1 - r_2$. Using Routh-Hurwitz criterion (Murray, 2002), conditions for stability of the steady state E_2^0 can be found as follows

$$\begin{aligned}
&B_0 = 2\alpha - l_2 > 0,\\
&B_1 = 2(\alpha - l_2)^2 - l_1\alpha > 0,\\
&B_2 = (2\alpha - l_1)(\alpha - l_2)(l_2^2 - (l_1 + l_2)\alpha) > 0,\\
&B_3 = l_1 l_2 \alpha^2 > 0.
\end{aligned}$$

Since $r_1 > 0$, this implies that $l_1 < 0$, which implies $B_1 > 0$ for any parameter values. In the light of this, the only possibility to satisfy the condition $B_3 > 0$ is by requiring $l_2 < 0$, which then implies that $B_0 > 0$ and $B_2 > 0$. Hence, for stability of the steady state E_2^0 it is necessary and sufficient to require

$$l_2 < 0 \Longrightarrow r_1 a_{21} < r_2 a_{11}.$$

It is noteworthy that this condition for stability of the single-species steady state E_2^0 is independent of the time delay τ and the inverse mean time delay α. It is also the condition that ensures the co-existence steady state E^* is not biologically feasible, as determined by the condition (7).

Next, we assume that the condition (7) is satisfied and consider the co-existence equilibrium E^*. Linearisation of the system 6 near this steady state E^* yields the following characteristic equation

$$\lambda^4 + p_0\lambda^3 + p_1\lambda^2 + p_2\lambda + p_3 + (q_0\lambda^2 + q_1\lambda + q_2)e^{-2\lambda\tau} = 0, \tag{8}$$

where

$$\begin{array}{l} p_0 = 2\alpha,\ p_1 = \alpha^2 - \alpha(m_3 + n_4),\ p_2 = -\alpha^2(m_3 + n_4),\ p_3 = \alpha^2 m_3 n_4, \\ q_0 = -m_2 n_1,\ q_1 = -2\alpha m_2 n_1,\ q_2 = -\alpha^2 m_2 n_1. \end{array} \tag{9}$$

and

$$m_2 = -a_{12}x_1^*, m_3 = -a_{11}x_1^*, n_1 = a_{21}x_2^*, n_4 = -a_{22}x_2^*,$$

In the case of instantaneous intra-specific competition ($\tau = 0$), the characteristic equation (8) reduces to

$$\lambda^4 + p_0\lambda^3 + (p_1 + q_0)\lambda^2 + (p_2 + q_1)\lambda + (p_3 + q_2) = 0. \tag{10}$$

By using the Routh-Hurwitz criteria, we have the following necessary and sufficient conditions for all roots of the equation (10) to have negative real part

$$\begin{array}{l} H_1 = p_0 > 0, \\ H_2 = p_0(p_1 + q_0) - (p_2 + q_1) > 0, \\ H_3 = p_0[(p_1 + q_0)(p_2 + q_1) - p_0(p_3 + q_2)] - (p_2 + q_1)^2 > 0, \\ H_4 = p_3 + q_2 > 0. \end{array}$$

Since $p_0 = \alpha$, this means that the condition $H_1 > 0$ is always satisfied. Using the definitions of p_i and q_i in equation (9), one can find

$$H_2 = \alpha^2[2\alpha - (m_3 + n_4)] > 0, \qquad H_4 = \alpha^2(m_3 n_4 - m_2 n_1) > 0,$$

and

$$H_3 = -\alpha^3 \left[2\alpha^2(m_3 + n_4) - \alpha(m_3 - n_4)^2 - 2m_2 n_1(m_3 + n_4)\right] > 0.$$

This means that whenever the co-existence steady state E^* exists, it is linearly asymptotically stable for $\tau = 0$.

Now that it has been established that the steady state E^* is linearly asymptotically stable for $\tau = 0$, the next question is whether this steady state can lose stability for $\tau > 0$. Substituting $\lambda = 0$ into the characteristic equation (8) gives the left-hand side as $p_3 + q_2$, which is always strictly positive. This means that a steady state bifurcation of E^* cannot happen, hence, the only possibility for the steady state E^* to lose stability is via Hopf bifurcation, in which case a pair of complex conjugate roots crosses the imaginary axis for some value of the time delay τ. To identify this critical value of the time delay, we look for roots of the characteristic equation (8) in form $\lambda = i\omega$ ($\omega > 0$). Substituting this into the characteristic equation (8) gives

$$\begin{aligned}\omega^4 - ip_0\omega^3 - p_1\omega^2 + ip_2\omega + p_3 \\ +(-q_0\omega^2 + iq_1\omega + q_2)\left[\cos(2\omega\tau) - i\sin(2\omega\tau)\right] = 0.\end{aligned} \tag{11}$$

Separating this equation into real and imaginary parts yields

$$\begin{aligned}&\omega^4 - p_1\omega^2 + p_3 = (q_0\omega^2 - q_2)\cos(2\omega\tau) - q_1\omega\sin(2\omega\tau), \\ &p_0\omega^3 - p_2\omega = (q_0\omega^2 - q_2)\sin(2\omega\tau) + q_1\omega\cos(2\omega\tau).\end{aligned} \tag{12}$$

Squaring and adding both sides of the above system, we have the following equation for the Hopf frequency ω

$$\omega^8 + s_0\omega^6 + s_1\omega^4 + s_2\omega^2 + s_3 = 0, \tag{13}$$

where $s_0 = p_0^2 - 2p_1$, $s_1 = p_1^2 + 2p_3 - 2p_0p_2 - q_0^2$, $s_2 = p_2^2 + 2q_0q_2 - 2p_1p_3 - q_1^2$, $s_3 = p_3^2 - q_2^2$. Introducing an auxiliary variable $z = \omega^2$, the equation (13) can be recast in the form

$$h(z) = z^4 + s_0z^3 + s_1z^2 + s_2z + s_3 = 0. \tag{14}$$

Differentiating function $h(z)$ gives

$$\frac{dh(z)}{dz} = 4z^3 + 3s_0z^2 + 2s_1z + s_2 = g(z).$$

Using Cardano's formulas, the roots of $g(z)$ can be found as follows,

$$\begin{aligned}z_1 &= K_1 + K_2 - \frac{s_0}{4}, \\ z_2 &= -\frac{K_1 + K_2}{2} - \frac{3s_0}{12} + \frac{i\sqrt{3}}{2}(K_1 - K_2), \\ z_3 &= -\frac{K_1 + K_2}{2} - \frac{3s_0}{12} - \frac{i\sqrt{3}}{2}(K_1 - K_2),\end{aligned} \tag{15}$$

where

$$K_1 = \sqrt[3]{R + \sqrt{D}}, \qquad K_2 = \sqrt[3]{R - \sqrt{D}},$$

and

$$D = Q^3 + R^2, \qquad Q = \frac{24s_1 - 9s_0^2}{144}, \qquad R = \frac{216s_0s_1 - 432s_2 - 54s_0^3}{3456}.$$

When $D > 0$, the equation $g(z) = 0$ has one real root, namely, $z_1^* = z_1$ and two complex conjugate roots; if $D = 0$, then all roots of $g(z) = 0$ are real, and at least two are equal, namely, $z_1^*, z_2^* = z_3^*$, where $z_2^* = \max\{z_1, z_2\}$; if $D < 0$, then all roots of $g(z) = 0$ are real and distinct, namely, z_1^*, z_2^*, z_3^*, where $z_3^* = \max\{z_1, z_2, z_3\}$.

Using Lemma 2.2 in Li and Hu (2011), we now have the following

Lemma 1:
1) If $s_3 < 0$, then equation (14) has at least one positive root.

2) If $s_3 \geq 0$, then equation (14) has no positive roots if and only if one of these conditions holds:

$$(a)\ D > 0 \text{ and } z_1^* \leq 0;\ (b)\ D = 0 \text{ and } z_2^* \leq 0;\ (c)\ D < 0 \text{ and } z_3^* \leq 0.$$

3) If $s_3 \geq 0$, then equation (14) has at least one positive root if and only if one of these conditions holds:

$$(a)\ D > 0,\ z_1^* > 0, \text{ and } h(z_1^*) < 0;\ (b)\ D = 0,\ z_2^* > 0 \text{ and } h(z_2^*) < 0;$$
$$(c)\ D < 0,\ z_3^* > 0 \text{ and } h(z_3^*) < 0.$$

Without loss of generality, let us suppose that equation (14) has four distinct positive real roots, given by $z_1,\ z_2,\ z_3,\ z_4$. In this case, equation (13) also has positive real roots, namely, $\omega_1 = \sqrt{z_1},\ \omega_2 = \sqrt{z_2},\ \omega_3 = \sqrt{z_3},\ \omega_4 = \sqrt{z_4}$.

Returning to the system (12), one find the critical time delay τ_0 as follows

$$\tau_{n,j} = \frac{1}{2\omega_n}\left[\arctan\left\{\frac{q_1\omega_n(\omega_n^4 - p_1\omega_n^2 + p_3) + (q_0\omega_n^2 - q_2)(p_0\omega_n^2 - p_2\omega_n)}{q_1\omega_n(p_0\omega_n^3 - p_2\omega_n) + (q_0\omega_n^2 - q_2)(\omega_n^4 - p_1\omega_n^2 + p_3)}\right\} + j\pi\right],$$

where $n = 1, 2, 3, 4,\ j = 0, 1, 2, ...$ Then $\tau_{n,j}$ are solutions of (11), and $\lambda = \pm i\omega_n$ are a pair of purely imaginary roots of the characteristic equation (8) with $\tau = \tau_{n,j}$. If we define

$$\tau_0 = \tau_{n_0,0} = \min_{1 \leq n \leq 4}\{\tau_{n,0}\},\ \omega_0 = \omega_{n_0}, \qquad n_0 \in \{1, 2, 3, 4\},$$

then τ_0 is the first value of the time delay τ such that the characteristic equation (8) has purely imaginary roots.

Let $\lambda(\tau)=\gamma(\tau)\pm i\omega(\tau)$ be the root of the characteristic equation (8) in the neighbourhood of $\tau=\tau_{n,j}$, satisfying $\gamma(\tau_{n,j})=0,\ \omega(\tau_{n,j})=\omega_n, n=1,2,3,4,\ j=0,1,2....$ Then the following result holds.

Lemma 2: *Suppose $h^{'}(z_n)\neq 0$ $(n=1,2,3,4)$, where $h(z)$ is defined by equation (14), then the following transversality condition holds:*

$$sgn\left\{\frac{dRe\{\lambda(\tau)\}}{d\tau}\right\}\Bigg|_{\tau=\tau_{n,j}} = sgn[h^{'}(z_n)]\neq 0.$$

Proof: Substituting $\lambda=\lambda(\tau)$ into the characteristic equation (8) and taking derivative with respect to τ gives

$$\left\{\frac{d\lambda(\tau)}{d\tau}\right\}^{-1}=\frac{\left(4\,\lambda^3+3\,p_0\lambda^2+2\,p_1\lambda+p_2\right)\mathrm{e}^{2\,\lambda\,\tau}+2\,q_0\lambda+q_1}{2\left(q_0\lambda^2+\,q_1\lambda+\,q_2\right)\lambda}-\frac{\tau}{\lambda}.$$

Taking real part of this equation, one obtains

$$\begin{aligned}
&\left\{\frac{d\mathrm{Re}\{\lambda(\tau)\}}{d\tau}\right\}^{-1}_{\tau=\tau_{n,j}}=\mathrm{Re}\left\{\frac{\left(4\,\lambda^3+3\,p_0\lambda^2+2\,p_1\lambda+p_2\right)\mathrm{e}^{2\,\lambda\,\tau}+2\,q_0\lambda+q_1}{2(\,q_0\lambda^2+\,q_1\lambda+\,q_2)\lambda}\right\}_{\tau=\tau_{n,j}}\\
&=\frac{\left(4\,\omega_n{}^5q_0-4\,\omega_n{}^3q_2-2\,p_1\omega_n{}^3q_0+2\,p_1\omega_n\,q_2+3\,q_1\omega_n{}^3p_0-q_1\omega_n\,p_2\right)\cos(2\,\omega_n\,\tau_{n,j})}{2(q_1{}^2\omega_n{}^2+q_0{}^2\omega_n{}^4-2\,q_0\omega_n{}^2q_2+q_2{}^2)\omega_n}\\
&+\frac{\left(3\,q_0\omega_n{}^4p_0-3\,q_2p_0\omega_n{}^2-q_0\omega_n{}^2p_2+q_2p_2-4\,q_1\omega_n{}^4+2\,q_1\omega_n{}^2p_1\right)\sin(2\,\omega_n\,\tau_{n,j})}{2(q_1{}^2\omega_n{}^2+q_0{}^2\omega_n{}^4-2\,q_0\omega_n{}^2q_2+q_2{}^2)\omega_n}\\
&+\frac{-2\,q_0{}^2\omega_n{}^3+2\,q_0\omega_n\,q_2-q_1{}^2\omega_n}{2(q_1{}^2\omega_n{}^2+q_0{}^2\omega_n{}^4-2\,q_0\omega_n{}^2q_2+q_2{}^2)\omega_n}.
\end{aligned}\tag{16}$$

Solving equation (12) yields

$$\cos(2\omega_n\tau_{n,j})=\frac{q_1\omega_n(p_0\omega_n^3-p_2\omega_n)+(q_0\omega_n^2-q_2)(\omega_n^4-p_1\omega_n^2+p_3)}{q_1^2\omega_n^2+(q_0\omega_n^2-q_2)^2},$$

$$\sin(2\omega_n\tau_{n,j})=\frac{q_1\omega_n(\omega_n^4-p_1\omega_n^2+p_3)+(q_0\omega_n^2-q_2)(p_0\omega_n^2-p_2\omega_n)}{q_1^2\omega_n^2+(q_0\omega_n^2-q_2)^2}.$$

Substituting these values together with the definitions of p_i and q_i from (9) into equation (16), we find

$$\begin{aligned}
&\left\{\frac{d\mathrm{Re}\{\lambda(\tau)\}}{d\tau}\right\}^{-1}_{\tau=\tau_{n,j}}=\frac{1}{\kappa}\Big[4\,\omega_n{}^6+\left(6\,\alpha^2+6\,\alpha\,n_4+6\,\alpha\,m_3\right)\omega_n{}^4\\
&+(2\,\alpha^4+4\,\alpha^3n_4+4\,\alpha^3m_3+2\,\alpha^2n_4{}^2+4\alpha^2m_3n_4-2n_1{}^2m_2{}^2\alpha^2m_3n_4\\
&+2\,\alpha^2m_3{}^2)\omega_n{}^2-2n_1{}^2m_2{}^2\alpha^4m_3n_4+\alpha^4n_4{}^2+\alpha^4m_3{}^2+2\,\alpha^4n_4m_3\Big]\\
&=\frac{1}{\kappa}[4z_n^3+3s_0z_n^2+2s_1z_n+s_2]=\frac{1}{\kappa}h^{'}(z_n),
\end{aligned}$$

where $\kappa = 2\alpha^2 n_1^2 m_2^2 n_4 m_3 \left(\alpha^2 + \omega^2\right)^2$. Since $n_4 < 0$ and $m_3 < 0$, this implies that $\kappa > 0$, and, therefore,

$$\operatorname{sgn}\left\{\frac{d\mathrm{Re}\{\lambda(\tau)\}}{d\tau}\right\}_{\tau=\tau_{n,j}} = \operatorname{sgn}\left\{\frac{d\mathrm{Re}\{\lambda(\tau)\}}{d\tau}\right\}_{\tau=\tau_{n,j}}^{-1} = \operatorname{sgn}\left[\frac{1}{\kappa}h^{'}(z_n)\right]$$
$$= \operatorname{sgn}[h^{'}(z_n)] \neq 0,$$

which completes the proof. □

The above analysis can be summarised as follows.

Theorem 3: *Suppose condition (7) holds. Then the co-existence steady state E^* is biologically feasible, and we have the following.*

- *The co-existence steady state E^* is linearly asymptotically stable for any values of the time delay $\tau \geq 0$ if $s_3 \geq 0$ and one of these conditions holds:*

  $$(a)\ D > 0 \textit{ and } z_1^* \leq 0;\ (b)\ D = 0 \textit{ and } z_2^* \leq 0;\ (c)\ D < 0 \textit{ and } z_3^* \leq 0.$$

- *The co-existence steady state E^* is linearly asymptotically stable for $\tau \in [0, \tau_0)$ if $s_3 < 0$, or if $s_3 \geq 0$ and one of the conditions below holds:*

  $$(a)\ D > 0,\ z_1^* > 0,\ \textit{and } h(z_1^*) < 0;\ (b)\ D = 0,\ z_2^* > 0 \textit{ and } h(z_2^*) < 0;$$
  $$(c)\ D < 0\ z_3^* > 0 \textit{ and } h(z_3^*) < 0.$$

  If additionally the condition of Lemma 2.2 holds, the co-existence steady state E^* undergoes Hopf bifurcation at $\tau = \tau_0$.

Figures 1 and 2 illustrate regions of stability of the co-existence steady state E^* in the (τ, α) parameter plane, they are show that the maximum real part of the characteristic eigenvalues computed using pseudospectral approximation and implemented in the traceDDE suite (Breda et al., 2006). These figures suggest that increasing the rate of prey self-regulation a_{11} or decreasing the rate of predation a_{12} leads to an increase in the size of the parameter region where the steady state E^* is stable. Although the analysis presented earlier suggests that it may be possible for the steady state E^* to regain stability for higher values of the time delay through further Hopf bifurcations, numerical computation of the eigenvalues shown in Figures 1 and 2 suggests that this does not happen, and once stability is lost, this steady state remains unstable for arbitrarily large values of τ.

To better understand the behaviour of the system after Hopf bifurcation, we have used a numerical bifurcation software DDE-BIFTOOL to perform continuation of periodic orbits emerging at the Hopf bifurcation of E^*. These results are shown in Figures 1(c), 1(f) and 2(c), 2(f), and they suggest that once E^* undergoes Hopf bifurcation, both amplitude and period of the bifurcating periodic solution are growing with increasing discrete time delay τ.

Figure 1 (a), (b), (d) and (e) Stability region for the steady state E^* in the (τ, α)-plane, colour code denotes $[-\max[\mathrm{Re}(\lambda)]]$ for $\max[\mathrm{Re}(\lambda)] \leq 0$. Parameter values are $r_1 = 1$, $r_2 = 1$, $a_{12} = 0.6$, $a_{21} = 2$, $a_{22} = 0.5$. (a) $a_{11} = 1$, (b) $a_{11} = 1.2$, (d) $a_{11} = 1.4$, (e) $a_{11} = 1.6$, (c) and (f) illustrate the amplitude and period of periodic solutions, respectively, for $\alpha = 5$ (see online version for colours)

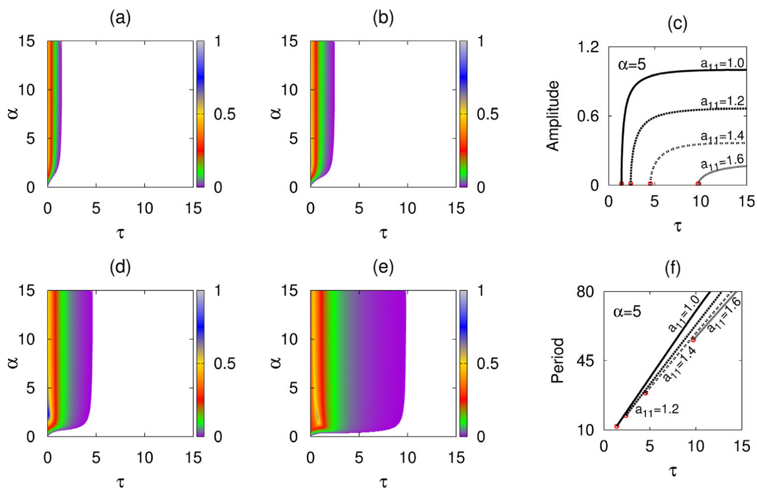
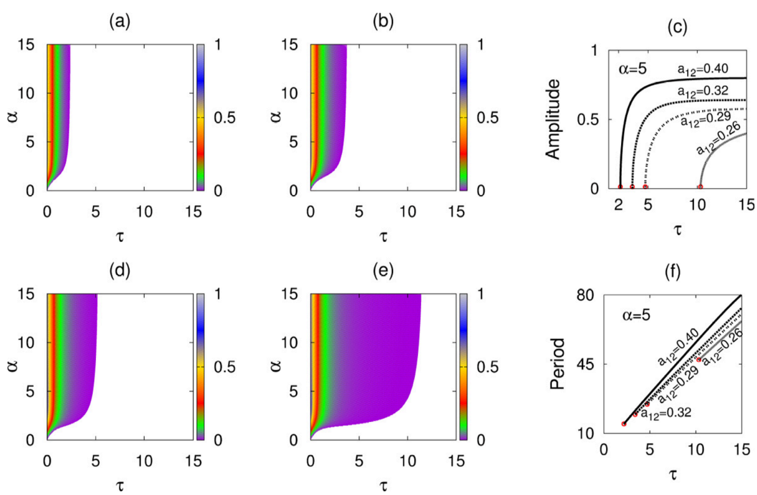


Figure 2 (a), (b), (d) and (e) Stability region for the steady state E^* in the (τ, α)-plane, colour code denotes $[-\max[\mathrm{Re}(\lambda)]]$ for $\max[\mathrm{Re}(\lambda)] \leq 0$. Parameter values are $r_1 = 1$, $r_2 = 1$, $a_{11} = 1$, $a_{21} = 2$, $a_{22} = 0.5$. (a) $a_{12} = 0.4$, (b) $a_{12} = 0.32$, (d) $a_{12} = 0.29$, (e) $a_{12} = 0.26$, (c) and (f) illustrate the amplitude and period of periodic solutions, respectively, for $\alpha = 5$ (see online version for colours)



3 Direction and stability of Hopf bifurcation

In this section, we investigate properties of the Hopf bifurcation of the coexistence steady state E^*, namely, its direction, the period of oscillations, as well as stability of the bifurcating periodic solution for the system (6) at the critical value τ_0. To make analytical progress, we employ the methodology of centre manifold reduction and normal form analysis, as discussed in Hassard et al. (1981).

We begin by rescaling time as $\overline{x}_i(t) = x_i(\tau t)$ and consider $\tau = \tau_0 + \sigma$, where τ_0 is the critical value of the time delay at which the steady state E^* undergoes Hopf bifurcation, and $\sigma \in \mathbb{R}$. Then the system (6) transforms into a functional differential equation in $C \in C([-1, 0], \mathbb{R}^4)$ as follows

Now, we rescale time by $\overline{x}_i(t) = x_i(\tau t)$ and consider $\tau = \tau_0 + \sigma$, where τ_0 is the value of the time delay at which the steady state E^* undergoes Hopf bifurcation, and $\sigma \in \mathbb{R}$. Then the system (6) transforms into a functional differential equation in $C \in C([-1, 0], \mathbb{R}^4)$ as follows

$$\dot{\overline{x}}(t) = L_\sigma(\overline{x}_t) + F(\sigma, \overline{x}_t), \tag{17}$$

where $\overline{x}(t) = (\overline{x}_1(t), \overline{x}_2(t), \overline{x}_3(t), \overline{x}_4(t))^T \in \mathbb{R}^4$ and $L_\sigma : \mathbb{C} \to \mathbb{R},\ F : \mathbb{R} \times \mathbb{C} \to \mathbb{R}$ are given below:

$$L_\sigma\phi = L_1\phi(0) + L_2\phi(-1),$$

where L_1 and L_2 are

$$L_1 = (\tau_0 + \sigma)\begin{pmatrix} 0 & 0 & m_3 & 0 \\ 0 & 0 & 0 & n_4 \\ \alpha & 0 & -\alpha & 0 \\ 0 & \alpha & 0 & -\alpha \end{pmatrix}, \qquad L_2 = (\tau_0 + \sigma)\begin{pmatrix} 0 & m_2 & 0 & 0 \\ n_1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \end{pmatrix},$$

and

$$F(\sigma, \phi) = (\tau_0 + \sigma)\begin{pmatrix} -a_{11}\phi_1(t)\phi_3(t) - a_{12}\phi_1(t)\phi_2(t-1) \\ a_{21}\phi_2(t)\phi_1(t-1) - a_{22}\phi_2(t)\phi_4(t) \\ 0 \\ 0 \end{pmatrix},$$

where $\phi(\theta) = (\phi_1(\theta), \phi_2(\theta), \phi_3(\theta), \phi_4(\theta))^T \in \mathbb{C}$. By the Riesz representation theorem, there exists a function $\eta(\theta, \sigma)$ of bounded variation for $\theta \in [-1, 0]$, such that

$$L_\sigma\phi = \int_{-1}^{0} \mathrm{d}\eta(\theta, \sigma)\phi(\theta), \qquad \text{for } \phi \in \mathbb{C}.$$

We can choose

$$\eta(\theta, \sigma) = L_1\delta(\theta) - L_2\delta(\theta + 1),$$

where $\delta(\theta)$ is the Dirac delta function defined as $\delta(\theta) = \begin{cases} 0, & \theta \neq 0, \\ 1, & \theta = 0 \end{cases}$. For $\phi \in C^1([-1, 0], \mathbb{R}^4)$, we define

$$A(\sigma)\phi = \begin{cases} \frac{d\phi(\theta)}{d\theta}, & \theta \in [-1, 0), \\ \int_{-1}^{0} \mathrm{d}\eta(s, \sigma)\phi(s), & \theta = 0, \end{cases} \qquad R(\sigma)\phi = \begin{cases} 0, & \theta \in [-1, 0), \\ F(\sigma, \phi), & \theta = 0, \end{cases}$$

which allows us to rewrite the system (17) as follows,

$$\dot{\overline{x}}_t = A(\sigma)\overline{x}_t + R(\sigma)\overline{x}_t,$$

where $\overline{x}_t(\theta) = \overline{x}(t+\theta)$, for $\theta \in [-1, 0)$.
For any function $\psi \in C^1([0,\tau], (\mathbb{R}^4)^*)$, we define

$$A^*\psi(s) = \begin{cases} -\dfrac{d\psi(s)}{ds}, & s \in (0,1], \\ \displaystyle\int_{-1}^{0} \mathrm{d}\eta(t,0)^T\psi(-t), & s = 0, \end{cases}$$

and a bilinear inner product

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

where we have used an abbreviation $\eta(\theta) = \eta(\theta, 0)$. It follows that $A = A(0)$ and A^* are adjoint operators. We know that $\pm i\omega_0\tau_0$ are eigenvalues of A, hence, they are also eigenvalues of A^*. As a next step, one has to compute the eigenvectors of A and A^* corresponding to $i\omega\tau$ and $-i\omega\tau$, respectively. Direct computations yield the following result.

Lemma 4: $q(\theta) = (1, \rho_1, \rho_2, \rho_3)^T e^{i\omega_0\tau_0\theta}$ *and* $q^*(\theta) = D(1, \rho_1^*, \rho_2^*, \rho_3^*)e^{i\omega\tau_0\theta}$ *are eigenvectors of A and A^* corresponding to eigenvalues $i\omega_0\tau_0$ and $-i\omega_0\tau_0$, respectively, and $\langle q^*(s), q(\theta)\rangle = 1$ and $\langle q^*(s), \overline{q}(\theta)\rangle = 0$, where*

$$\rho_1 = \frac{(i\omega_0+\alpha)n_1e^{-i\omega_0\tau_0}}{(i\omega_0+\alpha)i\omega_0 - \alpha n_4}, \quad \rho_2 = \frac{\alpha}{i\omega_0+\alpha}, \quad \rho_3 = \frac{n_1\alpha e^{-i\omega_0\tau_0}}{(i\omega_0+\alpha)i\omega_0 - \alpha n_4},$$

$$\rho_1^* = -\frac{(i\omega_0(\alpha - i\omega_0) + \alpha m_2)}{n_2(\alpha - i\omega_0)e^{i\omega_0\tau_0}}, \quad \rho_2^* = \frac{m_2}{\alpha - i\omega_0}, \quad \rho_3^* = -\frac{\rho_0^* n_3}{i\omega_0 - \alpha},$$

and

$$D = \frac{1}{1 + \overline{\rho_1}\rho_1^* + \overline{\rho_2}\rho_2^* + \overline{\rho_3}\rho_3^* + \tau_0(\overline{\rho_1}m_2 + \rho_1^* n_1)e^{i\omega_0\tau_0}}.$$

As a next step, we use the methodology described in Hassard et al. (1981) (see also Ma et al. (2009), Song amd Yuan (2006) and Xu and Shao (2012)) to compute the coordinates describing centre manifold C_0 at $\sigma = 0$. Let $\overline{x}_t$ be the solution of equation (17) when $\sigma = 0$ and define

$$z(t) = \langle q^*, \overline{x}_t\rangle, \qquad W(t,\theta) = \overline{x}_t(\theta) - 2\mathrm{Re}[z(t)q(\theta)]. \tag{18}$$

On the centre manifold C_0 we have

$$W(t,\theta) = W(z(t),\overline{z}(t),\theta) = W_{20}(\theta)\frac{z^2}{2} + W_{11}(\theta)z\overline{z} + W_{02}(\theta)\frac{\overline{z}^2}{2} + ...$$

where z and $\overline{z}$ are local coordinates for centre manifold C_0 in the directions of q^* and $\overline{q}^*$, respectively. Note that W is a real when $\overline{x}_t$ is real, and we considering only real solution $\overline{x}_t \in C_0$ of equation (17), since $\sigma = 0$, we have

$$\dot{z}(t) = i\tau_0\omega_0 z + g(z,\overline{z}),$$

where

$$g(z,\overline{z}) = g_{20}\frac{z^2}{2} + g_{11}z\overline{z} + g_{02}\frac{\overline{z}^2}{2} + g_{21}\frac{z^2\overline{z}}{2} + \dots. \tag{19}$$

Then,

$$\begin{aligned} g(z,\overline{z}) &= \overline{q^*}^T(0)F(0,z,\overline{z}) \\ &= \tau_0\overline{D}[-a_{11}\phi_1(0)\phi_3(0) - a_{12}\phi_1(0)\phi_2(-1)] \\ &\quad +\tau_0\overline{D\rho_1^*}[a_{21}\phi_2(0)\phi_1(-1) - a_{22}\phi_2(0)\phi_4(0)]. \end{aligned} \tag{20}$$

On the other hand, equation (18) indicates that

$$\overline{x}_t(\theta) = W(z,\overline{z},\theta) + 2zq(\theta) + 2\overline{z}\overline{q}(\theta),$$

from which we have

$$\begin{aligned} \phi_k(0) &= \rho_{k-1}z + \overline{\rho}_{k-1}\overline{z} + W_{20}^{(k)}(0)\tfrac{z^2}{2} + W_{11}^{(k)}(0)z\overline{z} \\ &\quad +W_{02}^{(k)}(0)\tfrac{\overline{z}^2}{2} + \mathcal{O}(|(z,\overline{z})|^3), \qquad (k=1,2,3,4), \\ \phi_l(-1) &= \rho_{l-1}e^{-i\omega_0\tau_0}z + e^{i\omega\tau_0}\overline{\rho}_{l-1}\overline{z} + W_{20}^{(l)}(-1)\tfrac{z^2}{2} + W_{11}^{(l)}(-1)z\overline{z} \\ &\quad +W_{02}^{(l)}(-1)\tfrac{\overline{z}^2}{2} + \mathcal{O}(|(z,\overline{z})|^3), \qquad (l=1,2), \end{aligned} \tag{21}$$

where $\rho_0 = \overline{\rho}_0 = 1,\ \phi = (\phi_1,\phi_2,\phi_3,\phi_4),\ W = (W^{(1)},W^{(2)},W^{(3)},W^{(4)})$.

Substituting equation (21) into equation (20) and matching the coefficients in this expressions with those in (19) yields

$$\begin{aligned} g_{20} &= 2\tau_0\overline{D}\left[\rho_1\overline{\rho_2}a_{12}e^{-i\omega_0\tau_0} - \rho_1 a_{12}e^{-i\omega_0\tau_0} - \rho_2 a_{11} - \rho_1\overline{\rho_1}a_{22}\right], \\ g_{11} &= \tau_0\overline{D}\Big[\overline{\rho_1}a_{21}(\rho_1 e^{i\omega_0\tau_0} + \overline{\rho_1}e^{-i\omega_0\tau_0}) - a_{12}(\overline{\rho_1}e^{i\omega_0\tau_0} + \rho_1 e^{-i\omega_0\tau_0}) \\ &\quad -a_{11}(\rho_2 + \overline{\rho_2}) - a_{22}(\rho_1\overline{\rho_3} + \overline{\rho_1}\rho_3)\Big] \\ g_{02} &= 2\tau_0\overline{D}[\overline{\rho_1}^2 a_{21}e^{i\omega_0\tau_0} - \overline{\rho_1}a_{12}e^{i\omega_0\tau_0} - \overline{\rho_1}a_{11} - \overline{\rho_1}^2\overline{\rho_3}a_{22}] \\ g_{21} &= \tau_0\overline{D}\Bigg\{\overline{\rho_1}a_{21}\left[2\rho_1 W_{11}^{(1)}(-1) + \overline{\rho_1}W_{20}^{(1)}(-1) + e^{i\omega_0\tau_0}W_{20}^{(2)}(0)\right. \\ &\qquad \left. +2e^{-\omega_0\tau_0}W_{11}^{(2)}(0)\right] \\ &\quad -a_{12}\left[2W_{11}^{(1)}(-1) + W_{20}^{(2)}(-1) + \overline{\rho_1}e^{i\omega_0\tau_0}W_{20}^{(1)}(0) + 2\rho_1 e^{-\omega_0\tau_0}W_{11}^{(1)}(0)\right] \\ &\quad -a_{11}\left[2W_{11}^{(1)}(0) + W_{20}^{(3)}(0) + \overline{\rho_2}W_{20}^{(1)}(0) + 2\rho_2 W_{11}^{(1)}(0)\right] \\ &\quad -\overline{\rho_1}a_{22}\left[2\rho_1 W_{11}^{(4)}(0) + \overline{\rho_1}W_{20}^{(4)}(0) + \overline{\rho_3}W_{20}^{(1)}(0) + 2\rho_3 W_{11}^{(2)}(0)\right]\Bigg\} \end{aligned}$$

In order to determine g_{21}, we need to find W_{11}, W_{20}. The detailed calculation procedure can refer to Appendix 1. Thus, we can compute the following important quantities:

$$\begin{aligned}
c_1(0) &= \frac{i}{2\omega_0\tau_0}\left(g_{11}g_{20} - 2|g_{11}|^2 - \frac{|g_{02}|^2}{3}\right) + \frac{g_{21}}{2}, \\
\mu_2 &= -\frac{\mathrm{Re}\{c_1(0)\}}{\mathrm{Re}\{\lambda^{'}(\tau_0)\}}, \qquad \beta_2 = 2\mathrm{Re}\{c_1(0)\}, \\
T_2 &= -\frac{\mathrm{Im}\{c_1(0)\} + \mu_2\mathrm{Im}\{\lambda^{'}(\tau_0)\}}{\omega_0\tau_0},
\end{aligned} \tag{22}$$

which determine the characteristics of the bifurcating periodic solution at $\tau = \tau_0$. More specifically, μ_2 shows the direction of the Hopf bifurcation, i.e., the periodic solution is supercritical (subcritical) if $\mu_2 > 0$ ($\mu_2 < 0$), and the bifurcating periodic solution exists for $\tau > \tau_0$ ($\tau < \tau_0$); β_2 determines the stability of the bifurcating periodic solution: the bifurcating periodic solutions are stable (unstable) if $\beta_2 < 0$ ($\beta_2 > 0$); T_2 shows the period of the bifurcating periodic solutions: the period increase (decrease) if $T_2 > 0$ ($T_2 < 0$).

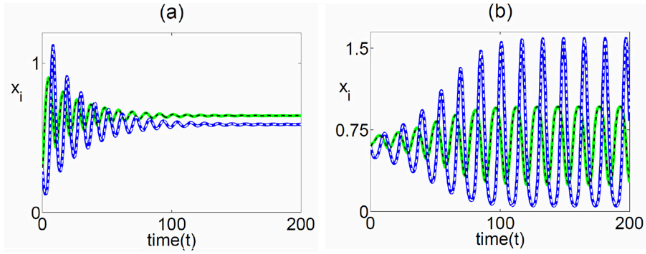
4 Numerical simulations

From the analysis in Section 3, it follows that once the values of $\alpha, r_i, a_{ij}, (i, j = 1, 2)$ and τ_0 are known, it is possible to compute the values of μ_2 and β_2 which show the direction and stability of the periodic solutions bifurcating from the positive equilibrium E^* at the critical value of the time delay $\tau = \tau_0$. Fixing the mean time delay of the gamma distribution as $\tau_m = 0.2$, i.e., $\alpha = 5$, we consider the following system:

$$\begin{aligned}
\dot{x}_1(t) &= x_1(t)[1 - x_3(t) - 0.6x_2(t-\tau)], \\
\dot{x}_2(t) &= x_1(t)[-1 + 2x_1(t-\tau) - 0.5x_4(t)], \\
\dot{x}_3(t) &= 0.5[x_1(t) - x_3(t)], \\
\dot{x}_4(t) &= 0.5[x_2(t) - x_4(t)],
\end{aligned} \tag{23}$$

This system has a positive equilibrium $E^* = (0.6471, 05882, 0.6471, 0.5882)$ that satisfies the conditions of Theorem 3. For the given parameter values, we have $z_0 = 0.728,\ \omega_0 = 0.530,\ h'(z_0) \neq 0,\ \tau_0 = 1.388,\ \lambda^{'}(\tau_0) = -0.498 - 0.053i$. From the formulae (22), it follows that $c_1(0) = 45.666 - 1.370i$, $\mu_2 = 91.570$, $\beta_2 = 91.331$ and $T_2 = 8.505$. Thus, E^* is stable when $\tau < \tau_0$, as shown in Figure 3. When τ passes through the critical value τ_0, E^* loses its stability via Hopf bifurcation, i.e., a family of periodic solutions bifurcates from E^*. Since $\mu_2 > 0$ and $\beta_2 > 0$, the Hopf bifurcation is supercritical, and the bifurcating periodic solution is unstable, as shown in Figure 3.

Figure 3 Numerical solution of the system (23) for $\tau = 1.1$ (a), and $\tau = 2$ (b). The critical time delay is $\tau_0 = 1.388$ (see online version for colours)



5 Conclusion

In this paper we have analysed a predator-prey model with discrete and distributed delays. For particular case of a weak gamma distributed delay we have shown that it is not possible for both prey and predators to become extinct, while the single-species steady state is stable independent of time delays whenever the co-existence steady state is not feasible. For the co-existence steady state we have derived conditions for linear stability and Hopf bifurcation in terms of system parameters. Using normal form theory and the centre manifold reduction, we found the direction of Hopf bifurcation and derived the conditions for stability of bifurcating periodic solutions. Numerical simulations have been performed to illustrate different types of the dynamics in the system, and they show perfect agreement with the analytical analysis.

The analysis presented in this paper can be extended in several directions. In the model we considered, the predation term was chosen to be monotonically growing with the delayed prey density, and in some cases it may be more realistic to allow for other non-monotone forms of the response (Hsu et al., 2001; Ruan, 2009). Another possibility is to allow predation terms to be themselves represented by some delay distributions rather than discrete delays, in a manner similar to Song amd Yuan (2006). Besides ecological applications, analysis presented in this paper can also be used for investigating other systems underpinned by a similar type of interactions, such as those arising in mathematical neuroscience (Li and Hu, 2011; Zhou et al., 2009).

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Appendix A

In this section we show how one can compute $W_{20}(\theta)$ and $W_{11}(\theta)$. From equations (17) and (18)

$$\dot{W} = \dot{x_t} - \dot{z}q - \dot{\overline{z}}\overline{q} = \begin{cases} AW - 2\mathrm{Re}[\overline{q^*}(0)F_0 q(\theta)] & \text{for } \theta \in [-1,0), \\ AW - 2\mathrm{Re}[\overline{q^*}(0)F_0 q(\theta)] + F_0 \text{ for} & \theta = 0, \end{cases} \tag{A1}$$

$$\stackrel{\text{def}}{=} AW + H(z, \overline{z}, \theta),$$

where

$$H(z, \overline{z}, \theta) = H_{20}(\theta)\frac{z^2}{2} + H_{11}(\theta)z\overline{z} + H_{02}(\theta)\frac{\overline{z}^2}{2} + ... \tag{A2}$$

On the centre manifold C_0 near the origin we have

$$\dot{W} = W_z \dot{z} + W_{\overline{z}}\dot{\overline{z}}.$$

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

$$(A - 2i\omega_0\tau_0)W_{20}(\theta) = -H_{20}(\theta), \qquad AW_{11}(\theta) = -H_{11}(\theta). \tag{A3}$$

Equation (A1) implies that for $\theta \in [-1, 0)$, one has

$$H(z, \overline{z}, \theta) = -\overline{q^*}(0)F_0 q(\theta) - q^*(0)\overline{F}_0\overline{q}(\theta) = -gq(\theta) - \overline{gq}(\theta).$$

and comparing the coefficients with (A2) gives

$$H_{20}(\theta) = -g_{20}q(\theta) - \overline{g}_{02}\overline{q}(\theta), \tag{A4}$$

and

$$H_{11}(\theta) = -g_{11}q(\theta) - \overline{g}_{11}\overline{q}(\theta). \tag{A5}$$

From equations (A3) and (A4), and the definition of A, one can find the following equation for $W_{20}(\theta)$

$$\dot{W}_{20}(\theta) = 2i\omega_0\tau_0 W_{20}(\theta) + g_{20}q(\theta) + \overline{g}_{02}\overline{q}(\theta)$$

Substituting $q(\theta) = (1, \rho_1, \rho_2, \rho_3)^T e^{i\omega_0\tau_0\theta}$ yields

$$W_{20}(\theta) = \frac{ig_{20}}{\omega_0\tau_0}q(0)e^{i\omega_0\tau_0\theta} + \frac{i\overline{g}_{02}}{3\omega_0\tau_0}\overline{q}(0)e^{-i\omega_0\tau_0\theta} + E_1 e^{2i\omega_0\tau_0\theta}, \tag{A6}$$

where $E_1 = (E_1^{(1)}, E_1^{(2)}, E_1^{(3)}, E_1^{(4)}) \in \mathbb{R}^4$ is a constant vector.
Similarly, from equations (A3) and (A5) we can obtain

$$W_{11}(\theta) = -\frac{ig_{11}}{\omega_0\tau_0}q(0)e^{i\omega_0\tau_0\theta} + \frac{i\overline{g}_{11}}{\omega_0\tau_0}\overline{q}(0)e^{-i\omega_0\tau_0\theta} + E_2, \tag{A7}$$

where $E_2 = (E_2^{(1)}, E_2^{(2)}, E_2^{(3)}, E_2^{(4)}) \in \mathbb{R}^4$ is a constant vector.

Explicit expressions for E_1 and E_2 can be found as follows. From the definition of A and the above equations we have

$$\int_{-1}^{0} \mathrm{d}\eta(\theta) W_{20}(\theta) = 2i\tau_0\omega_0 W_{20}(0) - H_{20}(0), \tag{A8}$$

and

$$\int_{-1}^{0} \mathrm{d}\eta(\theta) W_{11}(\theta) = -H_{11}(0), \tag{A9}$$

where $\eta(\theta) = \eta(0, \theta)$. From equation (A3), one can find

$$H_{20}(0) = -g_{20}q(0) - \overline{g}_{02}\overline{q}(0) + 2\tau_0 \begin{pmatrix} -a_{11}\rho_2 - a_{12}\rho_1 e^{-i\omega_0\tau_0} \\ a_{21}\rho_1 e^{-i\omega_0\tau_0} - a_{22}\rho_1\rho_3 \\ 0 \\ 0 \end{pmatrix}, \tag{A10}$$

and

$$H_{11}(0) = -g_{11}q(0) - \overline{g}_{11}\overline{q}(0) + 2\tau_0 \begin{pmatrix} -a_{11}\mathrm{Re}\{\rho_2\} - a_{12}\mathrm{Re}\{\rho_1 e^{-i\omega_0\tau_0}\} \\ a_{21}\mathrm{Re}\{\rho_1 e^{-i\omega_0\tau_0}\} - a_{22}\mathrm{Re}\{\rho_1\rho_3\} \\ 0 \\ 0 \end{pmatrix}. \tag{A11}$$

Using the relations

$$\left(i\omega_0\tau_0 I - \int_{-1}^{0} e^{i\theta\omega_0\tau_0}\mathrm{d}\eta(\theta)\right) q(0) = 0,$$

$$\left(-i\omega_0\tau_0 I - \int_{-1}^{0} e^{-i\theta\omega_0\tau_0}\mathrm{d}\eta(\theta)\right) \overline{q}(0) = 0,$$

and substituting expressions (A6) and (A10) into equation (A8) gives

$$\left(2i\tau_0\omega_0 I - \int_{-1}^{0} e^{2i\theta\omega_0\tau_0}\mathrm{d}\eta(\theta)\right) E_1 = 2\tau_0 \begin{pmatrix} -a_{11}\rho_2 - a_{12}\rho_1 e^{-i\omega\tau_0} \\ a_{21}\rho_1 e^{-i\omega_0\tau_0} - a_{22}\rho_1\rho_3 \\ 0 \\ 0 \end{pmatrix}.$$

This can be written explicitly as the following linear system for E_1:

$$\begin{pmatrix} 2i\omega_0 & -m_2 e^{-2i\omega_0\tau_0} & -m_3 & 0 \\ -n_1 e^{-2i\omega_0\tau_0} & 2i\omega_0 & 0 & -n_4 \\ -\alpha & 0 & 2i\omega_0 + \alpha & 0 \\ 0 & -\alpha & 0 & 2i\omega_0 + \alpha \end{pmatrix} E_1 = 2 \begin{pmatrix} -a_{11}\rho_2 - a_{12}\rho_1 e^{-i\omega_0\tau_0} \\ a_{21}\rho_1 e^{-i\omega_0\tau_0} - a_{22}\rho_1\rho_3 \\ 0 \\ 0 \end{pmatrix}.$$

Using Cramer's rule, individual components of E_1 can now be found as

$$E_1^{(1)} = \frac{\Delta_{11}}{\Delta_1},\ E_1^{(2)} = \frac{\Delta_{12}}{\Delta_1},\ E_1^{(3)} = \frac{\Delta_{13}}{\Delta_1},\ E_1^{(4)} = \frac{\Delta_{14}}{\Delta_1},$$

In a similar way, substituting (A7) and (A11) into (A9) yields

$$\left(\int_{-1}^{0} d\eta(\theta)\right) E_2 = 2\tau_0 \begin{pmatrix} -a_{11}\mathrm{Re}\{\rho_2\} - a_{12}\mathrm{Re}\{\rho_1 e^{-i\omega_0\tau_0}\} \\ a_{21}\mathrm{Re}\{\rho_1 e^{-i\omega_0\tau_0}\} - a_{22}\mathrm{Re}\{\rho_0\rho_3\} \\ 0 \\ 0 \end{pmatrix},$$

which gives the following system of equations for E_2:

$$\begin{pmatrix} 0 & -m_2 & -m_3 & 0 \\ -n_1 & 0 & 0 & -n_4 \\ -\alpha & 0 & \alpha & 0 \\ 0 & -\alpha & 0 & \alpha \end{pmatrix} E_2 = 2 \begin{pmatrix} -a_{11}\mathrm{Re}\{\rho_2\} - a_{12}\mathrm{Re}\{\rho_1 e^{-i\omega_0\tau_0}\} \\ a_{21}\mathrm{Re}\{\rho_1 e^{-i\omega_0\tau_0}\} - a_{22}\mathrm{Re}\{\rho_1\rho_3\} \\ 0 \\ 0 \end{pmatrix}.$$

The solution can be found as

$$E_2^{(1)} = \frac{\Delta_{21}}{\Delta_2},\ E_2^{(2)} = \frac{\Delta_{22}}{\Delta_2},\ E_2^{(3)} = \frac{\Delta_{23}}{\Delta_2},\ E_2^{(4)} = \frac{\Delta_{24}}{\Delta_2},$$

where

$$\Delta_1 = \begin{vmatrix} 2i\omega_0 & -m_2 e^{-2i\omega_0\tau_0} & -m_3 & 0 \\ -n_1 e^{-2i\omega_0\tau_0} & 2i\omega_0 & 0 & -n_4 \\ -\alpha & 0 & 2i\omega_0 + \alpha & 0 \\ 0 & -\alpha & 0 & 2i\omega_0 + \alpha \end{vmatrix},$$

$$\Delta_{11} = 2\begin{vmatrix} -a_{11}\rho_2 - a_{12}\rho_1 e^{-i\omega_0\tau_0} & -m_2 e^{-2i\omega_0\tau_0} & -m_3 & 0 \\ a_{21}\rho_1 e^{-i\omega_0\tau_0} - a_{22}\rho_1\rho_3 & 2i\omega_0 & 0 & -n_4 \\ 0 & 0 & 2i\omega_0 + \alpha & 0 \\ 0 & -\alpha & 0 & 2i\omega_0 + \alpha \end{vmatrix},$$

$$\Delta_{12} = 2\begin{vmatrix} 2i\omega_0 & -a_{11}\rho_2 - a_{12}\rho_1 e^{-i\omega_0\tau_0} & -m_3 & 0 \\ -n_1 e^{-2i\omega_0\tau_0} & a_{21}\rho_1 e^{-i\omega_0\tau_0} - a_{22}\rho_1\rho_3 & 0 & -n_4 \\ -\alpha & 0 & 2i\omega_0 + \alpha & 0 \\ 0 & 0 & 0 & 2i\omega_0 + \alpha \end{vmatrix},$$

$$\Delta_{13} = 2\begin{vmatrix} 2i\omega_0 & -m_2 e^{-2i\omega_0\tau_0} & -a_{11}\rho_2 - a_{12}\rho_1 e^{-i\omega_0\tau_0} & 0 \\ -n_1 e^{-2i\omega_0\tau_0} & 2i\omega_0 & a_{21}\rho_1 e^{-i\omega_0\tau_0} - a_{22}\rho_1\rho_3 & -n_4 \\ -\alpha & 0 & 0 & 0 \\ 0 & -\alpha & 0 & 2i\omega_0 + \alpha \end{vmatrix},$$

$$\Delta_{14} = 2\begin{vmatrix} 2i\omega_0 & -m_2e^{-2i\omega_0\tau_0} & -m_3 & -a_{11}\rho_2 - a_{12}\rho_1e^{-i\omega_0\tau_0} \\ -n_1e^{-2i\omega_0\tau_0} & 2i\omega_0 & 0 & a_{21}\rho_1e^{-i\omega_0\tau_0} - a_{22}\rho_1\rho_3 \\ -\alpha & 0 & 2i\omega_0+\alpha & 0 \\ 0 & -\alpha & 0 & 0 \end{vmatrix},$$

and

$$\Delta_2 = \begin{vmatrix} 0 & -m_2 & -m_3 & 0 \\ -n_1 & 0 & 0 & -n_4 \\ -\alpha & 0 & \alpha & 0 \\ 0 & -\alpha & 0 & \alpha \end{vmatrix},$$

$$\Delta_{21} = 2\begin{vmatrix} -a_{11}\mathrm{Re}\{\rho_2\} - a_{12}\mathrm{Re}\{\rho_1e^{-i\omega_0\tau_0}\} & -m_2 & -m_3 & 0 \\ a_{21}\mathrm{Re}\{\rho_1e^{-i\omega_0\tau_0}\} - a_{22}\mathrm{Re}\{\rho_1\rho_3\} & 0 & 0 & -n_4 \\ -\alpha & 0 & \alpha & 0 \\ 0 & -\alpha & 0 & \alpha \end{vmatrix},$$

$$\Delta_{22} = 2\begin{vmatrix} 0 & -a_{11}\mathrm{Re}\{\rho_2\} - a_{12}\mathrm{Re}\{\rho_1e^{-i\omega_0\tau_0}\} & -m_3 & 0 \\ -n_1 & a_{21}\mathrm{Re}\{\rho_1e^{-i\omega_0\tau_0}\} - a_{22}\mathrm{Re}\{\rho_1\rho_3\} & 0 & -n_4 \\ -\alpha & 0 & \alpha & 0 \\ 0 & 0 & 0 & \alpha \end{vmatrix},$$

$$\Delta_{23} = 2\begin{vmatrix} 0 & -m_2 & -a_{11}\mathrm{Re}\{\rho_2\} - a_{12}\mathrm{Re}\{\rho_1e^{-i\omega_0\tau_0}\} & 0 \\ -n_1 & 0 & a_{21}\mathrm{Re}\{\rho_1e^{-i\omega_0\tau_0}\} - a_{22}\mathrm{Re}\{\rho_1\rho_3\} & -n_4 \\ -\alpha & 0 & 0 & 0 \\ 0 & -\alpha & 0 & \alpha \end{vmatrix},$$

$$\Delta_{24} = 2\begin{vmatrix} 0 & -m_2 & -m_3 & -a_{11}\mathrm{Re}\{\rho_2\} - a_{12}\mathrm{Re}\{\rho_1e^{-i\omega_0\tau_0}\} \\ -n_1 & 0 & 0 & a_{21}\mathrm{Re}\{\rho_1e^{-i\omega_0\tau_0}\} - a_{22}\mathrm{Re}\{\rho_1\rho_3\} \\ -\alpha & 0 & \alpha & 0 \\ 0 & -\alpha & 0 & 0 \end{vmatrix}.$$