

Stability switch and periodic solutions in delayed three-species model with Holling type III functional response

Juancho A. Collera*

Department of Mathematics and Computer Science, University of the Philippines Baguio

In this paper, a system of delay differential equations that models two predator populations consuming a single prey population is considered. The prey population follows a logistic growth in the absence of predators while each of the predator populations has functional response of Holling type III. Each of these response terms includes a delay time which reflects the gestation period of the respective predator population. The positive equilibrium solution of the form (x, y, y) is called the symmetric equilibrium. This work examines the effects of the difference in gestation periods to the dynamical behaviour of the symmetric equilibrium. Conditions for stability and bifurcations of the symmetric equilibrium are given when the delay times are unequal. Numerical simulations are performed to illustrate stability switch and emergence of periodic solution through Hopf bifurcation.

INTRODUCTION

To explain the dynamics of fish populations in the Adriatic Sea, Volterra (1926) proposed a model which we presently call a predator-prey system. In recent times, delayed predator-prey systems are studied due to their complex dynamical behaviours.

See, for example, the survey by Ruan (2009) and references therein for predator-prey models with discrete delays, the monographs by Brauer and Castillo-Chavez (2012), Gopalsamy (1992), Kuang (1993), and Smith (2011) for general delayed models in biology, and the texts by Guo and Wu (2013) and Hale and Verduyn Lunel (1993) for background on functional differential equations. An example of a predator-prey system with discrete delay is the following (Ruan 2009)

$$\begin{aligned}\dot{x}(t) &= x(t)g(x(t)) - y(t)p(x(t)), \\ \dot{y}(t) &= y(t)[- \mu + cp(x(t - \tau))],\end{aligned}$$

where $g(x)$ represents the per capita growth rate of the prey population $x(t)$ at time t in the absence of the predators, $p(x)$ denotes the functional response for the feeding rate of the predator population $y(t)$, μ is the predator death rate, and the delay time τ is the gestation period of the predators. For mammals, the gestation period is the time between conception and birth. An example of the prey growth rate that is commonly used in modeling is the Verhulstian (logistic growth) with $g(x) = r(1 - x/K)$, where $r > 0$ is the so-called intrinsic growth rate, and K is often referred to as the environment carrying capacity. For the functional response $p(x)$, Holling (1959) proposed the following predator feeding rates:

$$p(x) = ax, \quad p(x) = \frac{ax}{b+x}, \quad p(x) = \frac{ax^2}{b+x^2}.$$

KEYWORDS

delay differential equations, gestation period, Hopf bifurcation, periodic solutions, predator-prey system, population dynamics, stability switch

*Corresponding author

Email Address: jacollera@up.edu.ph

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We call these functional responses as Holling type I, II, and III, respectively. In type I, the feeding rate does not saturate as the prey density increases while in type II, the feeding rate saturates at the maximum feeding rate a and is half maximal at $x = b$. In type III, the feeding rate also saturates at the maximum feeding rate a . However, this functional response has the feature that for small densities prey are able to evade predators by taking refuge. Most researches with delayed models concern two interacting populations such as works in delayed predator-prey system as summarized in Ruan (2009).

In this paper, we consider the following system of delay differential equations arising from a three-species model with two predator populations feeding on a single prey population:

$$\begin{aligned} \dot{x}(t) &= x(t) \left[r \left(1 - \frac{x(t)}{K} \right) - \frac{x(t)y(t)}{b+x^2(t)} - \frac{x(t)z(t)}{b+x^2(t)} \right], \\ \dot{y}(t) &= y(t) \left[-\mu + \frac{cx^2(t-\tau_1)}{b+x^2(t-\tau_1)} \right], \\ \dot{z}(t) &= z(t) \left[-\mu + \frac{cx^2(t-\tau_2)}{b+x^2(t-\tau_2)} \right], \end{aligned} \quad (1)$$

where the parameters $r, K, b, c, \mu, \tau_1, \tau_2$ are all positive, and the state variables $x(t), y(t),$ and $z(t),$ denote the populations of a local prey, an alien predator, and a local predator, respectively, with initial condition $(x(t), y(t), z(t)) = (x_0, y_0, z_0)$ for $t \in [-\tau_m, 0]$ where $\tau_m = \max(\tau_1, \tau_2)$ and x_0, y_0, z_0 are all positive. The prey population grows logistically in the absence of predators. Furthermore, we assume that for small densities prey are able to evade predators by taking refuge. Hence, functional response for both predator feeding rates is of Holling type III. These response functions include delay time reflecting the gestation period of each predator. We assume that the alien predator population has longer gestation period than the local predator population, that is, $\tau_1 \geq \tau_2$. Our objective is to examine the effects of this difference in gestation periods to the positive equilibrium solution of the form (x, y, y) . This is the idea behind considering the same predator equations in (1) except for the delay parameters. Recently, the author has examined a system similar to (1) but with predator feeding rates of Holling type II. The model in this recent paper (Collera 2013) differs from (1) in that for Holling type II functional response for small densities prey can no longer evade predators.

This paper is organized as follows. We first examine the equilibrium solutions of (1), and their stability and bifurcations. Results are given in Theorem 1. Numerical simulations are then presented, as well as a discussion of a possible biological interpretation. Lastly, we give a summary of the thoughts and results of this research.

EQUILIBRIUM SOLUTIONS

System (1) has three nonnegative equilibrium solutions given by

$$\begin{aligned} E_0 &= (0,0,0), \\ E_1 &= (K,0,0), \\ E_2 &= (P, Q-R, R), \end{aligned} \quad (2)$$

where

$$P = \sqrt{\frac{b\mu}{c-\mu}}, \quad Q = \frac{r(K-P)(b+P^2)}{KP},$$

and $0 \leq R \leq Q$. If $R = 0$, then E_2 becomes $(P, Q, 0)$, and if $R = Q$, then E_2 becomes $(P, 0, Q)$. The positive equilibrium, then, is given by E_2 where $0 < R < Q$ and with

$$c - \mu > 0 \quad \text{and} \quad K - P > 0. \quad (3)$$

We call the positive equilibrium given by

$$(x_s, y_s, y_s) = (P, Q/2, Q/2) \quad (4)$$

as the *symmetric equilibrium*. The stability and bifurcations of the equilibrium solutions $(P, Q, 0)$ and $(P, 0, Q)$ are similar to that of the symmetric equilibrium (4). Therefore, in the following, we only focus on the equilibrium solutions $(0, 0, 0), (K, 0, 0),$ and (x_s, y_s, y_s) .

Let $X(t) = [x(t), y(t), z(t)]^T$. The linearized system corresponding to (1) about an equilibrium solution (x^*, y^*, z^*) is given by

$$\dot{X}(t) = M_0 X(t) + M_1 X(t - \tau_1) + M_2 X(t - \tau_2), \quad (5)$$

where

$$M_0 = \begin{bmatrix} r - \frac{2rx^*}{K} - \frac{2bx^*(y^*+z^*)}{(b+x_*^2)^2} & \frac{-x_*^2}{b+x_*^2} & \frac{-x_*^2}{b+x_*^2} \\ 0 & \frac{cx_*^2}{b+x_*^2} - \mu & 0 \\ 0 & 0 & \frac{cx_*^2}{b+x_*^2} - \mu \end{bmatrix},$$

$$M_1 = \begin{bmatrix} 0 & 0 & 0 \\ \frac{2bcx_*y_*}{(b+x_*^2)^2} & 0 & 0 \\ 0 & 0 & 0 \end{bmatrix} \quad \text{and} \quad M_2 = \begin{bmatrix} 0 & 0 & 0 \\ 0 & 0 & 0 \\ \frac{2bcx_*y_*}{(b+x_*^2)^2} & 0 & 0 \end{bmatrix}.$$

The linear system (5) has the corresponding characteristic equation

$$\det \Delta(\lambda) = |\lambda I - M| = 0, \quad (6)$$

where $M = M_0 + e^{-\lambda\tau_1} M_1 + e^{-\lambda\tau_2} M_2$. For the trivial equilibrium solution E_0 , the matrix $M = M_0$ has eigenvalues $r > 0$ and $-\mu < 0$, and therefore E_0 is a saddle point. For E_1 , the matrix $M = M_0$ has eigenvalues $-r < 0$ and $(cK^2 - \mu K^2 - b\mu) / (b + K^2)$. Thus, if

$cK^2 - \mu K^2 - b\mu < 0$ then E_1 is a stable node. If $cK^2 - \mu K^2 - b\mu > 0$ then E_1 loses its stability, and by (3), an additional equilibrium solution E_2 appears. For $(x^*, y^*, z^*) = (x_s, y_s, z_s)$, we obtain

$$M = \begin{bmatrix} -A & -\mu/c & -\mu/c \\ (B/2)e^{-\lambda\tau_1} & 0 & 0 \\ (B/2)e^{-\lambda\tau_2} & 0 & 0 \end{bmatrix},$$

where

$$\begin{aligned} A &= \frac{rK(c-2\mu) + 2\mu rP}{cK}, \\ B &= \frac{2r(K-P)(c-\mu)}{K}. \end{aligned} \quad (7)$$

The characteristic equation in (6) then becomes

$$\lambda(\lambda + A) + \frac{B\mu}{2c}(e^{-\lambda\tau_1} + e^{-\lambda\tau_2}) = 0. \quad (8)$$

From (3), the existence of the symmetric equilibrium (4) requires

$$B > 0. \quad (9)$$

Moreover, for the rest of the discussion, we assume that $A > 0$. An equilibrium solution is asymptotically stable if all roots of its corresponding characteristic equation have negative real parts (Smith 2011). We first discuss the bifurcations of the symmetric equilibrium (4) of system (1) as these are closely tied to our stability result.

BIFURCATIONS OF THE SYMMETRIC EQUILIBRIUM

Steady-state bifurcation occurs when M has a zero eigenvalue, that is, when $\lambda = 0$ is a root of the characteristic equation (8). However, by (9), we see that $\lambda = 0$ is not a root of the characteristic equation (8), for if $\lambda = 0$ then (8) yields $B = 0$ which contradicts (9).

Hopf bifurcation is the emergence of a limit cycle or a periodic solution from an equilibrium solution. It occurs when M has a pair of purely imaginary eigenvalues, that is, $\lambda = \pm i\omega$ are roots of the characteristic equation (8). Now, suppose that $\lambda = i\omega$, with $\omega > 0$, is a root of (8). Then,

$$-\omega^2 + iA\omega + \frac{B\mu}{2c}(e^{-i\omega\tau_1} + e^{-i\omega\tau_2}) = 0.$$

Separating into real and imaginary parts, we obtain

$$\begin{aligned} \left(\frac{B\mu}{c}\right) \frac{\cos \omega\tau_1 + \cos \omega\tau_2}{2} &= \omega^2, \\ \left(\frac{B\mu}{c}\right) \frac{\sin \omega\tau_1 + \sin \omega\tau_2}{2} &= A\omega, \end{aligned} \quad (10)$$

or equivalently,

$$\begin{aligned} \left(\frac{B\mu}{c}\right) \cos\left(\frac{\tau_1 + \tau_2}{2}\omega\right) \cos\left(\frac{\tau_1 - \tau_2}{2}\omega\right) &= \omega^2, \\ \left(\frac{B\mu}{c}\right) \sin\left(\frac{\tau_1 + \tau_2}{2}\omega\right) \cos\left(\frac{\tau_1 - \tau_2}{2}\omega\right) &= A\omega. \end{aligned} \quad (11)$$

From equations in (11), we get

$$\cot\left(\frac{\tau_1 + \tau_2}{2}\omega\right) = \frac{\omega}{A}. \quad (12)$$

If $A > 0$, then (12) has positive roots

$$\omega_n \in \left(\frac{(2n-2)\pi}{\tau_1 + \tau_2}, \frac{(2n-1)\pi}{\tau_1 + \tau_2}\right), \quad n = 1, 2, \dots$$

For each ω_n , we define

$$\beta_n = \frac{c\omega_n^2}{\mu \cos\left(\frac{\tau_1 + \tau_2}{2}\omega_n\right) \cos\left(\frac{\tau_1 - \tau_2}{2}\omega_n\right)} \quad (13)$$

The above discussion implies that system (1) undergoes a Hopf bifurcation at the symmetric equilibrium (4) when $A > 0$ and $B = \beta_n$ ($n = 1, 2, \dots$).

MAIN RESULTS

The following lemmas are needed in the proof of our result. Lemma 1 below gives us a way of determining the sign of the real part of the eigenvalues of M , while Lemma 2 gives a necessary and sufficient condition to guarantee that all eigenvalues of M have negative real part.

Lemma 1. Let $\lambda(B) = \alpha(B) + i\omega(B)$ denote the root of (8) with $A > 0$ satisfying $\alpha(\beta_n) = 0$ and $\omega(\beta_n) = \omega_n$. Then, $\text{sign } \alpha'(\beta_n) = \text{sign } \beta_n$.

Proof. From (8), we get

$$2\lambda \frac{d\lambda}{dB} + A \frac{d\lambda}{dB} + \frac{\mu}{2c}(e^{-\lambda\tau_1} + e^{-\lambda\tau_2}) - \frac{B\mu}{2c}(\tau_1 e^{-\lambda\tau_1} + \tau_2 e^{-\lambda\tau_2}) \frac{d\lambda}{dB} = 0.$$

Consequently,

$$\begin{aligned} \frac{d\lambda}{dB} &= \frac{-(\mu/2c)(e^{-\lambda\tau_1} + e^{-\lambda\tau_2})}{2\lambda + A - \frac{B\mu}{2c}(\tau_1 e^{-\lambda\tau_1} + \tau_2 e^{-\lambda\tau_2})} \\ &= \frac{(\lambda^2 + A\lambda)/B}{2\lambda + A - \frac{B\mu}{2c}(\tau_1 e^{-\lambda\tau_1} + \tau_2 e^{-\lambda\tau_2})} \end{aligned}$$

using (8). For ease of notation, we let

$$\begin{aligned} \varphi(\omega) &= \cos \omega\tau_1 + \cos \omega\tau_2, \\ \psi(\omega) &= \sin \omega\tau_1 + \sin \omega\tau_2, \end{aligned} \quad (14)$$

Thus,

$$\begin{aligned} -\varphi'(\omega) &= \tau_1 \sin \omega\tau_1 + \tau_2 \sin \omega\tau_2, \\ \psi'(\omega) &= \tau_1 \cos \omega\tau_1 + \tau_2 \cos \omega\tau_2. \end{aligned} \quad (15)$$

At $B = \beta_n$, that is, at $\lambda(\beta_n) = i\omega_n$, we have

$$\begin{aligned} \frac{d\lambda(\beta_n)}{dB} &= \frac{(-\omega_n^2 + iA\omega_n)/\beta_n}{i2\omega_n + A - \frac{\beta_n\mu}{2c}(\tau_1 e^{-i\omega_n\tau_1} + \tau_2 e^{-i\omega_n\tau_2})} \\ &= \frac{(-\omega_n^2 + iA\omega_n)/\beta_n}{\left[A - \frac{\beta_n\mu}{2c}\psi'(\omega_n) \right] + i\left[2\omega_n - \frac{\beta_n\mu}{2c}\varphi'(\omega_n) \right]} \end{aligned}$$

using (15). Thus, for

$$\Delta = \left[A - \frac{\beta_n\mu}{2c}\psi'(\omega_n) \right]^2 + \left[2\omega_n - \frac{\beta_n\mu}{2c}\varphi'(\omega_n) \right]^2 > 0,$$

we have

$$\begin{aligned} \alpha'(\beta_n) &= \operatorname{Re}\left(\frac{d\lambda(\beta_n)}{dB}\right) \\ &= \frac{1}{\Delta} \left[-\frac{\omega_n^2}{\beta_n} \left(A - \frac{\beta_n\mu}{2c}\psi'(\omega_n) \right) + \frac{A\omega_n}{\beta_n} \left(2\omega_n - \frac{\beta_n\mu}{2c}\varphi'(\omega_n) \right) \right] \\ &= \frac{\beta_n\mu^2}{4c^2\Delta} \left[A \left(\frac{4c^2\omega_n^2}{\beta_n^2\mu^2} \right) + \frac{2c\omega_n^2}{\beta_n\mu}\psi'(\omega_n) - \frac{2cA\omega_n}{\beta_n\mu}\varphi'(\omega_n) \right] \\ &= \frac{\beta_n\mu^2}{4c^2\Delta} \left[A \left(\frac{4c^2\omega_n^2}{\beta_n^2\mu^2} \right) + \varphi(\omega_n)\psi'(\omega_n) - \psi(\omega_n)\varphi'(\omega_n) \right] \end{aligned}$$

using (10) and (14). By (14),

$$\frac{\varphi(\omega)}{\psi(\omega)} = \cot\left(\frac{\tau_1 + \tau_2}{2}\omega\right).$$

Since

$$\frac{d}{d\omega} \left(\frac{\varphi(\omega)}{\psi(\omega)} \right) = \frac{\psi(\omega)\varphi'(\omega) - \varphi(\omega)\psi'(\omega)}{\psi^2(\omega)}$$

and

$$\frac{d}{d\omega} \cot\left(\frac{\tau_1 + \tau_2}{2}\omega\right) < 0,$$

we have $\varphi(\omega)\psi'(\omega) - \psi(\omega)\varphi'(\omega) > 0$. This together with the assumption that $A > 0$ gives the desired result.

The proof of the next lemma uses Corollary 2.4 of Ruan and Wei (2003) which states that as the delay parameters vary, the sum of the orders of the roots of the characteristic equation in the open right half-plane can change only if a zero appears on or crosses the imaginary axis.

Lemma 2. All roots of the characteristics equation (8) with $A > 0$ have negative real parts if and only if $B \in (0, \beta_1)$, where β_1 is given in (13) and corresponds to the root $\omega_1 \in (0, p/(\tau_1 + \tau_2))$ of equation (12).

Proof. Suppose $A > 0$ and $B \in (0, \beta_1)$. Recall that $\lambda = 0$ is a root of (8) if and only if $B = 0$, and $\lambda = i\omega$, with $\omega > 0$, is a root of (8) if and only if $B = \beta_n$ ($n = 1, 2, \dots$) given in (13). Hence, by Corollary 2.4 of Ruan and Wei (2003), the sum of the orders of the roots of (8) in the open right half-plane does not change when $B \in (0, \beta_1)$. Since $A > 0$, by Lemma 1, $\alpha(\beta_1) = 0$ and $\operatorname{sign} \alpha'(\beta_1) = \operatorname{sign} \beta_1 > 0$. This means that $\alpha(B) < 0$ whenever $B \in (0, \beta_1)$. Thus, all roots of (8) have negative real parts when $B \in (0, \beta_1)$. Now, if $B > \beta_1$, then Lemma 1 implies that (8) with $A > 0$ has at least one root with positive real part. Therefore, all roots of the characteristic equation (8) with $A > 0$ have negative real parts if and only if $B \in (0, \beta_1)$.

We now state our main result. The proof follows from the above Lemma 2 and the Hopf Bifurcation Theorem (Hale and Verduyn Lunel 1993).

Theorem 1. Let β_n be defined by (13) and suppose that $A > 0$ in (8). The symmetric equilibrium (4) of system (1) is asymptotically stable if and only if $B \in (0, \beta_1)$. When $B = \beta_n$ ($n = 1, 2, \dots$), then (1) undergoes a Hopf bifurcation at the symmetric equilibrium (4).

NUMERICAL SIMULATIONS

We now use DDE-Biftool, which is a numerical continuation and bifurcation analysis tool developed by Engelborghs et al. (2001), to illustrate Theorem 1. In the following examples, we consider system (1) with initial condition $(x(t), y(t), z(t)) = (3.6, 2.8, 2.8)$ for $t \in [-\tau_m, 0]$ where $\tau_m = \max(\tau_1, \tau_2)$. This initial condition is arbitrary. However, we select it so that the two predator populations $y(t)$ and $z(t)$ start with the same number and hence no initial advantage is given to either of them.

Example 1. (Case with $\tau_1 = \tau_2$) System (1) with $(r, K, b, c, \mu) = (1, 20, 10, 0.8, 0.4)$ has the symmetric equilibrium $(3.1623, 2.6623, 2.6623)$ from (4), and gives $A = 0.1581$ and $B = 0.6735$ using (7). For $\tau_1 = \tau_2 = \tau = 0.1$, we get $\beta_1 = 3.1706$ using (12) and (13). By Theorem 1, since $A > 0$ and $0 < B < \beta_1$, we know that the symmetric equilibrium is asymptotically stable. We then follow this stable equilibrium solution in DDE-Biftool to obtain a branch of equilibrium solutions by varying the common delay time τ . Figure 1 shows this branch of equilibrium solutions as the horizontal line where green (solid line) and magenta (dash line) represent the stable and unstable parts of the branch, respectively. Moreover, a change in stability occurs at a Hopf bifurcation point marked with (*) where $\tau = \tau_c = 0.4753$. These numerical results corroborate the results in Theorem 1 when $\tau_1 = \tau_2$. We again use DDE-Biftool to continue the Hopf point into a branch of periodic solutions by varying τ . A stable (green solid curve) branch of periodic solutions emanating from the Hopf bifurcation is obtained, where the vertical axis gives a measure of the amplitude of the oscillation in the predator populations $y(t)$ and $z(t)$. In this case, the bifurcating branches of periodic solutions corresponding to the predator populations overlap. The critical delay value τ_c can also be acquired by solving for the positive

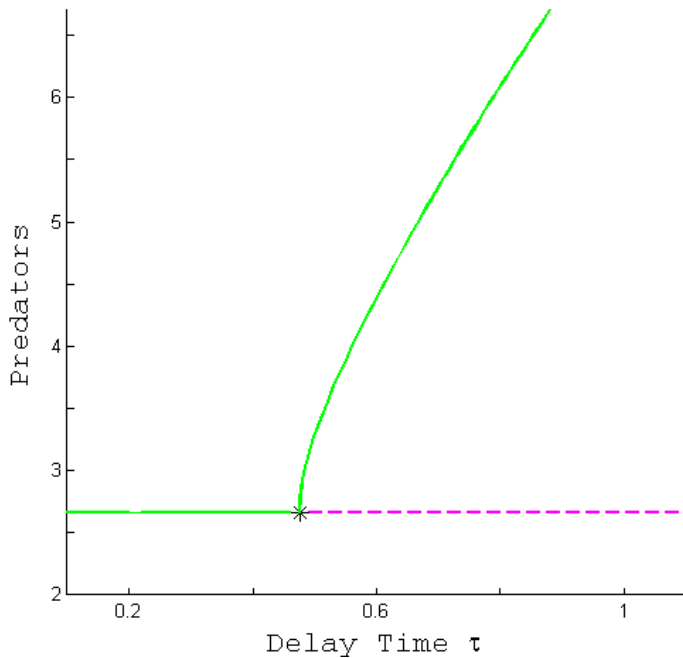


Figure 1. (Case with $\tau_1 = \tau = \tau_2$) Stability switch and emergence of periodic solutions at a Hopf bifurcation (*) at $\tau = \tau_c = 0.4753$.

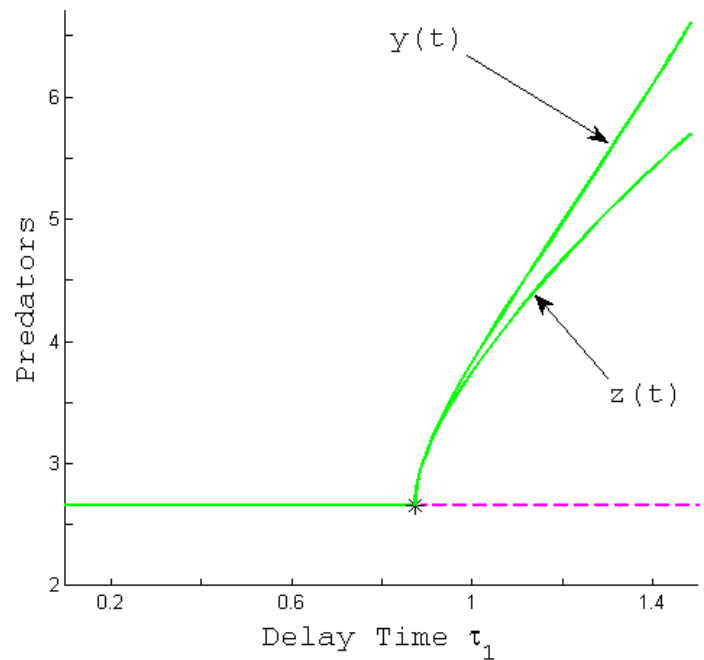


Figure 2. (Case with $\tau_1 \neq \tau_2$) Stability switch and emergence of a branch of periodic solutions at a Hopf bifurcation (*) where $\tau_1 = \tau_{1c} = 0.8739$ and with τ_2 is fixed at 0.1.

root $\omega = \omega_c$ of the equation $\omega^4 + A^2\omega^2 - (B\mu/c)^2 = 0$ obtained from the equations in (10) when $\tau_1 = \tau_2$, and then using this ω_c value to get τ_c using either of the equations in (10).

Example 2. (Case with $\tau_1 \neq \tau_2$) Now, consider system (1) with $(r, K, b, c, \mu, \tau_1, \tau_2) = (1, 20, 10, 0.8, 0.4, 0.1, 0.1)$. Since $\tau_1 = \tau_2$, we know from Example 1 that the symmetric equilibrium $(3.1623, 2.6623, 2.6623)$ is asymptotically stable. We then use DDE-Biftool to continue the symmetric equilibrium into a branch of equilibrium solutions by varying the delay time τ_1 , which is the gestation period of the alien predator population $y(t)$. Figure 2 shows this branch as a horizontal line where a change in stability occurs at a Hopf bifurcation point (*) where $\tau_1 = \tau_{1c} = 0.8739$. The value τ_{1c} is obtained by fixing $\tau_2 = 0.1$ and then increasing τ_1 until the condition $B = \beta_I$ in Theorem 1 is achieved. Again, we use DDE-Biftool to follow the Hopf point into a branch of periodic solutions by varying τ_1 . Stable branches of periodic solutions corresponding to the predator populations $y(t)$ and $z(t)$ are shown in Figure 2. In contrast to Example 1, the bifurcating branches of periodic solutions here do not overlap. Moreover, observe for $\tau_1 > \tau_{1c} = 0.8739$, the alien predator population $y(t)$ with longer gestation period τ_1 oscillates higher than the local predator population $z(t)$ with shorter gestation period $\tau_2 = 0.1$. A recent paper by Lueders et al. (2012) shows that in mammals, specifically in elephants, the gestation period has a strong relation to neonate brain size. This, in turn, translates to brain and cognitive capacity which enhances competency of the species with longer gestation period.

CONCLUSION

The effects of the difference in gestation period of the two predator populations to the dynamical behaviour of the symmetric equilibrium are examined. When $\tau_1 = \tau = \tau_2$, the symmetric equilibrium solution is asymptotically stable if the common delay time τ is less than the critical value τ_c . At $\tau = \tau_c$, a periodic solution emerges via a Hopf bifurcation, and the symmetric equilibrium becomes unstable for $\tau > \tau_c$. Similarly, for the case when $\tau_1 > \tau_2$, stability switching and emergence of a branch of periodic solutions occur at the Hopf bifurcation where $\tau_1 = \tau_{1c}$. These theoretical results are summarized in Theorem 1. Furthermore, beyond the critical delay value τ_{1c} , numerical simulations show that the predator population with longer gestation period oscillates higher than the predator with shorter gestation period. This numerical result corroborates the results in Lueders et al. (2012) that longer gestation period translates to better brain and cognitive capacity making species with longer gestation period more competent.

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CONFLICTS OF INTEREST

There are no conflicts of interest in this study.

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