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Stability and Bifurcations in Delayed

Three-Species Model

Juancho A. Collera

Department of Mathematics and Computer Science University of the Philippines Baguio Baguio City 2600 Philippines

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Abstract

In this study, a system of delay differential equations arising from a three-species model with two predators feeding on a single prey is considered. It is assumed that the prey population grows logistically in the absence of predators, and both predator populations adapt a Holling type II functional response. Each response term includes a delay time, which reflects the gestation period of each predator. The predator equations are the same except for their delay time. The positive steadystate solution of the form $(\bar{x}, \bar{y}, \bar{y})$ is called the symmetric equilibrium. This work examines the effects of the difference in the gestation period of the two predators. Conditions for the stability and bifurcations of the symmetric equilibrium for both cases when the delay times are equal and when one is larger than the other are provided.

Subject Classification: 37G15, 39A30, 92D25

Keywords: Bifurcations, Delay Differential Equations, Predator-Prey

1 Introduction

Predator-prey system with delay was first introduced by Volterra in 1925, and since then, it has been the topic of numerous research papers (see for example the survey by S. Ruan in [4] and references therein). In this paper, we consider the following system of delay differential equations arising from a three-species model with two predators feeding on a single prey:

$$\dot{x}(t) = rx(t) \left(1 - \frac{x(t)}{K}\right) - \frac{x(t)y(t)}{b + x(t)} - \frac{x(t)z(t)}{b + x(t)},$$

$$\dot{y}(t) = y(t) \left[-d + \frac{x(t - \tau_1)}{b + x(t - \tau_1)}\right],$$

$$\dot{z}(t) = z(t) \left[-d + \frac{x(t - \tau_2)}{b + x(t - \tau_2)}\right],$$
(1)

where $r, K, b, d, \tau_1, \tau_2 > 0$, and x(t), y(t), and z(t) represent 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 $x_0, y_0, z_0 > 0$. In the absence of predators, the prey population follows a logistic growth with intrinsic growth rate r and carrying capacity K. Functional response on both predator populations are of Holling type II [2] with time delay reflecting the gestation period of each predator. For mammals, the gestation period is the time between conception and birth. The parameter brepresents the half-saturation constant in which the per capita predation rate is half when x = b. In the absence of prey, both predator populations decay with the same rate -d.

Our goal is to examine the effects of the difference in gestation periods in (1). This is the rationale why we consider the same predator equations except for their delay time. We assume $\tau_1 \geq \tau_2$. This paper is organized as follows: Sections 2 and 3 discuss the symmetric case ($\tau_1 = \tau_2$) and the case with multiple delays ($\tau_1 > \tau_2$), respectively. Main results are given as theorems. Numerical simulations and discussions of the two cases are presented in Section 4, and the last section summarizes the thoughts in this work.

2 Symmetric Three-Species Model

When $\tau_1 = \tau = \tau_2$, interchanging the predator variables y(t) and z(t) in (1) leaves it unchanged. We call this *the symmetric case* and is given by

$$\dot{x}(t) = rx(t) \left(1 - \frac{x(t)}{K}\right) - \frac{x(t)y(t)}{b + x(t)} - \frac{x(t)z(t)}{b + x(t)},
\dot{y}(t) = y(t) \left[-d + \frac{x(t - \tau)}{b + x(t - \tau)}\right],
\dot{z}(t) = z(t) \left[-d + \frac{x(t - \tau)}{b + x(t - \tau)}\right].$$
(2)

We may reduce (2) into just two equations by letting u(t) = y(t) + z(t). However, we keep (2) as it is to understand some subtleties that symmetry induces.

Each of systems (1) and (2) has 3 equilibrium solutions given by (0, 0, 0), (K, 0, 0), and

$$(\tilde{x}, \tilde{y}, \tilde{z}) = (C, D - s, s), \qquad (3)$$

where

$$C = \frac{bd}{1-d}, \qquad D = \frac{rb(K - dK - bd)}{K(1-d)^2}, \qquad \text{and} \qquad 0 \le s \le D.$$

If s = 0 then $(\tilde{x}, \tilde{y}, \tilde{z}) = (C, D, 0)$, and if s = D then $(\tilde{x}, \tilde{y}, \tilde{z}) = (C, 0, D)$. The positive equilibrium, then, is given by $(\bar{x}, \bar{y}, \bar{z}) = (C, D - s, s)$ with 0 < s < D. We call the positive equilibrium of the form

$$(\bar{x}, \bar{y}, \bar{y}) = (C, D/2, D/2)$$
 (4)

as the symmetric equilibrium, and it exists provided

$$1 - d > 0$$
 and $K - dK - bd > 0.$ (5)

The stability and bifurcations of the equilibria (C, D, 0) and (C, 0, D) are the same as that of $(\bar{x}, \bar{y}, \bar{y})$. Therefore, in the following, we focus only on the equilibria (0, 0, 0), (K, 0, 0), and $(\bar{x}, \bar{y}, \bar{y})$.

Let $X(t) = [x(t), y(t), z(t)]^T$. The linearized system corresponding to (2) about an equilibrium solution (x^*, y^*, z^*) is given by

$$\dot{X}(t) = M_0 X(t) + M_1 X(t-\tau)$$

where

$$M_{0} = \begin{bmatrix} r\left(1 - \frac{2}{K}x^{*}\right) - \frac{b(y^{*} + z^{*})}{(b + x^{*})^{2}} & -\frac{x^{*}}{b + x^{*}} & -\frac{x^{*}}{b + x^{*}} \\ 0 & -d + \frac{x^{*}}{b + x^{*}} & 0 \\ 0 & 0 & -d + \frac{x^{*}}{b + x^{*}} \end{bmatrix},$$
$$M_{1} = \begin{bmatrix} 0 & 0 & 0 \\ \frac{by^{*}}{(b + x^{*})^{2}} & 0 & 0 \\ \frac{bz^{*}}{(b + x^{*})^{2}} & 0 & 0 \end{bmatrix},$$

and the corresponding characteristic equation is

$$\det \Delta(\lambda) = |\lambda I - (M_0 + e^{-\lambda \tau} M_1)| = 0.$$
(6)

For $(x^*, y^*, z^*) = (0, 0, 0)$, the matrix $M_0 + e^{-\lambda \tau} M_1 = M_0$ has eigenvalues r > 0and -d < 0, and therefore the equilibrium point (0, 0, 0) is a saddle point. For $(x^*, y^*, z^*) = (K, 0, 0)$, the matrix $M_0 + e^{-\lambda \tau} M_1 = M_0$ has eigenvalues -r < 0and (K - dK - bd)/(b + K). Thus, if K - dK - bd < 0 then (K, 0, 0) is a stable node. If K - dK - bd > 0 then (K, 0, 0) becomes unstable, and an additional equilibrium point (3) starts to appear. For $(x^*, y^*, z^*) = (\bar{x}, \bar{y}, \bar{y})$, we have

$$M_0 + e^{-\lambda\tau} M_1 = \begin{bmatrix} A & -d & -d \\ (B/2)e^{-\lambda\tau} & 0 & 0 \\ (B/2)e^{-\lambda\tau} & 0 & 0 \end{bmatrix}$$

where

$$A = \frac{rd(K - dK - bd - b)}{K(1 - d)} \quad \text{and} \quad B = \frac{r(K - dK - bd)}{K}.$$
 (7)

The characteristic equation (6) becomes $\lambda^3 - A\lambda^2 + Bd\lambda e^{-\lambda\tau} = 0$ or

$$\lambda(\lambda - A) + Bde^{-\lambda\tau} = 0. \tag{8}$$

From (5), the existence of the symmetric equilibrium (4) requires

$$B > 0. \tag{9}$$

An equilibrium solution is asymptotically stable if all roots of its corresponding characteristic equation have negative real parts [6]. We first discuss the bifurcations of the symmetric equilibrium (4) of system (2) as this is closely tied with our stability results.

System (2) undergoes a steady-state bifurcation when $\lambda = 0$ is a root of (8). Notice that if $\lambda = 0$, then (8) yields B = 0. By (9), this is not possible and therefore $\lambda = 0$ is not a root of the characteristic equation (8). Meanwhile, Hopf bifurcation occurs when $\lambda = i\omega$, with $\omega > 0$, is a root of (8). In this case, the characteristic equation in (8) becomes $-\omega^2 - iA\omega + Bde^{-i\omega\tau} = 0$. Splitting into real and imaginary parts, we obtain

$$-\omega^2 + Bd\cos\omega\tau = 0$$
, and $-A\omega - Bd\sin\omega\tau = 0$. (10)

Consequently, from equations in (10), we get

$$\cot \omega \tau = \frac{\omega}{-A}.$$
(11)

If A < 0, then (11) has positive roots $\omega_n \in ((n-1)\pi/\tau, (2n-1)\pi/2\tau)$, for $n = 1, 2, \ldots$ For each ω_n , we define

$$B_n = \frac{\omega_n^2}{d\cos\omega_n \tau}.$$
(12)

The above discussion implies that system (2) undergoes a Hopf bifurcation at the symmetric equilibrium (4) when $B = B_n$ (for n = 1, 2, ...).

The following lemmas are needed in the proof of our first result.

Lemma 2.1. Let $\lambda(B) = \alpha(B) + i\omega(B)$ denote the root of (8) with A < 0satisfying $\alpha(B_n) = 0$ and $\omega(B_n) = \omega_n$. Then, sign $\alpha'(B_n) = sign B_n$.

Proof. From (8), we get $2\lambda \frac{d\lambda}{dB} - A \frac{d\lambda}{dB} + de^{-\lambda\tau} - B d\tau e^{-\lambda\tau} \frac{d\lambda}{dB} = 0$. Consequently,

$$\frac{d\lambda}{dB} = \frac{-de^{-\lambda\tau}}{2\lambda - A - Bd\tau e^{-\lambda\tau}} = \frac{\left(\lambda^2 - A\lambda\right)/B}{2\lambda - A - Bd\tau e^{-\lambda\tau}}$$

using (8). At $B = B_n$, that is, at $\lambda(B_n) = i\omega_n$, we have

$$\frac{d\lambda(B_n)}{dB} = \frac{\left(-\omega_n^2 - iA\omega_n\right)/B_n}{i2\omega_n - A - B_n d\tau e^{-i\omega_n \tau}} = \frac{\left(-\omega_n^2 - iA\omega_n\right)/B_n}{\left(-A - B_n d\tau \cos\omega_n \tau\right) + i(2\omega_n + B_n d\tau \sin\omega_n \tau)}$$

So that, for $\Delta = \left[-A - B_n d\tau \cos \omega_n \tau\right]^2 + \left[2\omega_n + B_n d\tau \sin \omega_n \tau\right]^2 > 0$, we have

$$\begin{aligned} \alpha'(B_n) &= \operatorname{Re}\left(\frac{d\lambda(B_n)}{dB}\right) \\ &= \frac{1}{\Delta}\left[-\frac{\omega_n^2}{B_n}\left(-A - B_n d\tau \cos\omega_n \tau\right) - \frac{A\omega_n}{B_n}\left(2\omega_n + B_n d\tau \sin\omega_n \tau\right)\right] \\ &= \frac{B_n d^2}{\Delta}\left[-A\left(\frac{\omega_n^2}{B_n^2 d^2}\right) + \tau\left(\frac{\omega_n^2}{B_n d}\cos\omega_n \tau - \frac{A\omega_n}{B_n d}\sin\omega_n \tau\right)\right] \\ &= \frac{B_n d^2}{\Delta}\left[-A\left(\frac{\omega_n^2}{B_n^2 d^2}\right) + \tau\right] \end{aligned}$$

using (10). Therefore, since $-A, \tau > 0$, we obtain that the sign of $\alpha'(B_n)$ is the same as that of B_n .

The proof of the next lemma uses Corollary 2.4 of [5] 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 2.2. All roots of the characteristic equation (8) with A < 0 have negative real parts if and only if $B \in (0, B_1)$, where B_1 is given in (12) and corresponds to positive root ω_1 of (11) on the interval $(0, \pi/2\tau)$. **Proof.** Suppose A < 0 and $B \in (0, B_1)$. 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 $B = B_n$ for $n \in \mathbb{Z}^+$. Hence, by Corollary 2.4 of [5], the sum of the orders of the roots of (8) in the open right half-plane does not change when $B \in (0, B_1)$. By Lemma 2.1, $\alpha(B_1) = 0$ and sign $\alpha'(B_1) = \text{sign } B_1 > 0$. This means that $\alpha(B) < 0$ whenever $B \in (0, B_1)$. Therefore, all roots of (8) have negative real parts when $B \in (0, B_1)$. Now, if $B > B_1$, then Lemma 2.1 implies that (8) has at least one root with positive real parts. Therefore, all roots of the characteristic equation (8) have negative real parts if and only if $B \in (0, B_1)$. \Box

We now state our first stability result. The proof follows from Lemma 2.2 and the Hopf Bifurcation Theorem [6].

Theorem 2.3. Let B_n be defined by (12) and suppose that A < 0. The symmetric equilibrium (4) of system (2) is asymptotically stable if and only if $B \in (0, B_1)$. When $B = B_n$ (n = 1, 2, ...), then (2) undergoes a Hopf bifurcation at the symmetric equilibrium (4).

3 Three-Species Model with Two Delays

Consider now system (1) with $\tau_1 > \tau_2$. To study the stability and bifurcations of the symmetric equilibrium (4) of (1), we follow the same technique as in the previous symmetric case. Linearizing (1) about the symmetric equilibrium (4) yields the corresponding characteristic equation

$$\lambda(\lambda - A) + \frac{1}{2}Bd\left(e^{-\lambda\tau_1} + e^{-\lambda\tau_2}\right) = 0.$$
(13)

By (9), we see that $\lambda = 0$ is not a root of (13), for if $\lambda = 0$ then (13) gives B = 0. Now, if $\lambda = i\omega$, with $\omega > 0$, then (13) becomes

$$-\omega^2 - iA\omega + \frac{1}{2}Bd\left(e^{-i\omega\tau_1} + e^{-i\omega\tau_2}\right) = 0.$$

Separating into real and imaginary parts, we obtain

$$Bd \ \frac{\cos \omega \tau_1 + \cos \omega \tau_2}{2} = \omega^2, \qquad \text{and} \qquad Bd \ \frac{\sin \omega \tau_1 + \sin \omega \tau_2}{2} = -A\omega, \quad (14)$$

or equivalently,

$$Bd \cdot \cos\left(\frac{\tau_1 + \tau_2}{2}\omega\right) \cos\left(\frac{\tau_1 - \tau_2}{2}\omega\right) = \omega^2,$$

$$Bd \cdot \sin\left(\frac{\tau_1 + \tau_2}{2}\omega\right) \cos\left(\frac{\tau_1 - \tau_2}{2}\omega\right) = -A\omega.$$
 (15)

From equations in (15), we get

$$\cot\left(\frac{\tau_1 + \tau_2}{2}\,\omega\right) = \frac{\omega}{-A}.\tag{16}$$

If A < 0, then (16) has positive roots $\omega_n \in \left(\frac{(2n-2)\pi}{\tau_1+\tau_2}, \frac{(2n-1)\pi}{\tau_1+\tau_2}\right)$, for $n = 1, 2, \ldots$ For each ω_n , we define

$$\beta_n = \frac{\omega_n^2}{d\cos\left(\frac{\tau_1 + \tau_2}{2} \,\,\omega_n\right)\cos\left(\frac{\tau_1 - \tau_2}{2} \,\,\omega_n\right)}.\tag{17}$$

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

The following lemmas are needed in the proof of our second and final result. These are generalization of Lemmas 2.1 and 2.2 to the case when $\tau_1 > \tau_2$.

Lemma 3.1. Let $\lambda(B) = \alpha(B) + i\omega(B)$ denote the root of (13) with A < 0 satisfying $\alpha(\beta_n) = 0$ and $\omega(\beta_n) = \omega_n$. Then, sign $\alpha'(\beta_n) = sign \beta_n$.

Proof. From (13), we get

$$2\lambda \frac{d\lambda}{dB} - A\frac{d\lambda}{dB} + \frac{1}{2}d\left(e^{-\lambda\tau_1} + e^{-\lambda\tau_2}\right) + \frac{1}{2}Bd\left(-\tau_1 e^{-\lambda\tau_1} - \tau_2 e^{-\lambda\tau_2}\right)\frac{d\lambda}{dB} = 0.$$

Consequently,

$$\frac{d\lambda}{dB} = \frac{-\frac{1}{2}d\left(e^{-\lambda\tau_{1}} + e^{-\lambda\tau_{2}}\right)}{2\lambda - A - \frac{1}{2}Bd\left(\tau_{1}e^{-\lambda\tau_{1}} + \tau_{2}e^{-\lambda\tau_{2}}\right)} = \frac{\left(\lambda^{2} - A\lambda\right)/B}{2\lambda - A - \frac{1}{2}Bd\left(\tau_{1}e^{-\lambda\tau_{1}} + \tau_{2}e^{-\lambda\tau_{2}}\right)}$$

using (13). For ease of notation, we let

 $\phi(\omega) = \cos \omega \tau_1 + \cos \omega \tau_2$ and $\psi(\omega) = \sin \omega \tau_1 + \sin \omega \tau_2$. (18)

Thus,

$$-\phi'(\omega) = \tau_1 \sin \omega \tau_1 + \tau_2 \sin \omega \tau_2, \psi'(\omega) = \tau_1 \cos \omega \tau_1 + \tau_2 \cos \omega \tau_2.$$
(19)

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

$$\frac{d\lambda(\beta_n)}{dB} = \frac{\left(-\omega_n^2 - iA\omega_n\right)/\beta_n}{i2\omega_n - A - \frac{1}{2}\beta_n d\left(\tau_1 e^{-i\omega_n\tau_1} + \tau_2 e^{-i\omega_n\tau_2}\right)} \\ = \frac{\left(-\omega_n^2 - iA\omega_n\right)/\beta_n}{\left[-A - \frac{1}{2}\beta_n d\psi'(\omega_n)\right] + i\left[2\omega_n - \frac{1}{2}\beta_n d\phi'(\omega_n)\right]}$$

using (19). Thus, for $\Delta = \left[-A - \frac{1}{2}\beta_n d\psi'(\omega_n)\right]^2 + \left[2\omega_n - \frac{1}{2}\beta_n d\phi'(\omega_n)\right]^2 > 0$,

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

using (14) and (18). By (18), $\phi(\omega)/\psi(\omega) = \cot\left(\frac{\tau_1+\tau_2}{2}\omega\right)$, and since

$$\frac{d}{d\omega} \left(\frac{\phi(\omega)}{\psi(\omega)} \right) = \frac{\psi(\omega)\phi'(\omega) - \phi(\omega)\psi'(\omega)}{\psi^2(\omega)} \quad \text{and} \quad \frac{d}{d\omega}\cot\left(\frac{\tau_1 + \tau_2}{2}\omega\right) < 0,$$

we have $\phi(\omega)\psi'(\omega) - \psi(\omega)\phi'(\omega) > 0$. The required result then follows from the fact that -A > 0 and $\phi(\omega)\psi'(\omega) - \psi(\omega)\phi'(\omega) > 0$.

The proof of the next lemma is similar to the proof of Lemma 2.2.

Lemma 3.2. All roots of the characteristic equation (13) with A < 0 have negative real parts if and only if $B \in (0, \beta_1)$, where β_1 is given in (17) and corresponds to ω_1 which is the root of (16) on the interval $(0, \pi/(\tau_1 + \tau_2))$.

We now state our final result whose proof follows from Lemma 3.2 and the Hopf Bifurcation Theorem [6].

Theorem 3.3. Let β_n be defined by (17) and suppose that A < 0. 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, ...), then (1) undergoes a Hopf bifurcation at the symmetric equilibrium (4).

4 Numerical Simulations

Using DDE-Biftool, which is a numerical continuation and bifurcation analysis tool developed by Engelborghs et al [1], we now examine the dynamics of systems (1) and (2). In the following examples, we use the initial condition (x(t), y(t), z(t)) = (24, 18, 18) for $t \in [-\tau_m, 0]$ where $\tau_m = \max(\tau_1, \tau_2)$.

Example 1. System (2) with (r, K, b, d) = (1, 40, 20, 0.5) has the symmetric equilibrium $(\bar{x}, \bar{y}, \bar{y}) = (20, 10, 10)$, and gives A = -0.25 and B = 0.25 using (7). For $\tau = 1.4$, we get $B_1 = 0.376460$ from (12). Hence, by Theorem 2.3,

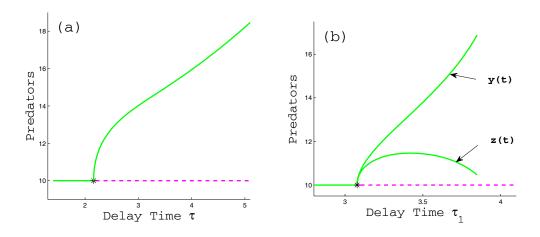


Figure 1: Stability switching and emergence of periodic solutions at a Hopf bifurcation (*) for both cases when $\tau_1 = \tau = \tau_2$ (Left) and $\tau_1 > \tau_2$ (Right).

 $(\bar{x}, \bar{y}, \bar{y})$ is asymptotically stable. We then use DDE-Biftool to continue this stable equilibrium solution into a branch of equilibria by varying the delay time τ . Figure 1a shows this branch as the horizontal line where green (solid lines) and magenta (dash lines) represent the stable and unstable parts of the branch, respectively. A change of stability occurs at a Hopf bifurcation point marked with (*) where $\tau = \tau_c = 2.160299$. Again, we use DDE-Biftool to continue this Hopf point into a branch of periodic solutions by varying τ . We obtain a stable (solid line) branch of periodic solutions emanating from this Hopf bifurcation point, 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 predators overlap. Note that τ_c can also be recovered by solving for $\omega = \omega_c > 0$ in $\omega^4 + A^2\omega^2 - B^2d^2 = 0$, which is obtained using (10), and then using this ω_c value to get τ_c from (10).

Example 2. Now, consider (1) with $(r, K, b, d, \tau_1, \tau_2) = (1, 40, 20, 0.5, 1.4, 1.4)$. Since $\tau_1 = \tau_2$, we know from Example 1 that $(\bar{x}, \bar{y}, \bar{y})$ is asymptotically stable. We then use DDE-Biftool to continue this stable equilibrium into a branch of equilibria by varying τ_1 . Figure 1b shows this branch as the horizontal line, where a change of stability occurs at a Hopf bifurcation point (*) where $\tau = \tau_{1c} = 3.077528$. The value τ_{1c} can also be obtained by fixing $\tau_2 = 1.4$, and then increasing τ_1 until the condition $B = \beta_1$ in Theorem 3.3 is achieved. Continuing this Hopf bifurcation point into a branch of periodic solutions in DDE-Biftool by varying τ_1 , we obtain a stable bifurcating branch of periodic solutions. Figure 1b shows branches of periodic solutions for predator populations y(t) and z(t) on the same plane. Observe that beyond τ_{1c} , 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 τ_2 . In mammals, specifically elephants [3], the gestation period has a strong relation to neonate brain size. This brain and cognitive capacity then enhances competency and therefore it gives advantage to animals with longer gestation period.

5 Conclusions

The effects of the difference in gestation period of the predators in a threespecies model (1) are examined. When $\tau_1 = \tau_2$, the symmetric equilibrium $(\bar{x}, \bar{y}, \bar{y})$ is asymptotically stable up to some critical delay value $\tau = \tau_c$ where Hopf bifurcations occurs and a stable periodic orbit emerges. The same can be said for the case when $\tau_1 > \tau_2$, by fixing τ_2 and then increasing τ_1 . Stability switching occurs at the critical delay value $\tau_1 = \tau_{1c}$. Furthermore, numerical simulations show that beyond this τ_{1c} , the predator with longer gestation period oscillates higher than the predator with shorter gestation period.

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References

- K. Engelborghs, T. Luzyanina, and G. Samaey DDE-BIFTOOL v. 2.00 User manual: A matlab package for bifurcation analysis of delay differential equations, Dept. of Computer Science, K. U. Leuven, Leuven, 2001.
- [2] C. S. Holling, Some characteristics of simple types of predation and parasitism, *The Canadian Entomologist*, 91(7) (1959), 385 - 398.
- [3] I. Lueders, C. Niemuller, P. Rich, C. Gray, R. Hermes, F. Goeritz and, T. B. Hildebrandt, Gestating for 22 months: luteal development and pregnancy maintenance in elephants, *Proc. R. Soc. B*, **279** (2012), 3687 -3696.
- [4] S. Ruan, On nonlinear dynamics of predator-prey models with discrete delay, Math. Model. Nat. Phenom., 4(2) (2009), 140 - 188.
- [5] S. Ruan and J. Wei, On the zeros of transcendental functions with applications to stability of delay differential equations with two delays, *Dynamics* of Continuous, Discrete and Impulsive Systems, **10** (2003), 863 - 874.
- [6] H. Smith, An Introduction to Delay Differential Equations with Applications to the Life Sciences, Springer, 2011.

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