

EFFECT OF MATURATION AND GESTATION DELAYS IN A STAGE STRUCTURE PREDATOR PREY MODEL

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ABSTRACT. In this paper, a stage-structured predator prey model (stage structure on prey) with two discrete time delays has been discussed. The two discrete time delays occur due to maturation delay and gestation delay. Linear stability analysis for both non-delay as well as with delays reveals that certain thresholds have to be maintained for coexistence. Numerical simulation shows that the system exhibits Hopf bifurcation, resulting in a stable limit cycle.

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1. Introduction

The study of single population ecological models with stage-structure have started in the 'golden age' of ecology through the works of Alfred Lotka and Vito Volterra [1]. Mackendrick [2] introduced age while describing the dynamics of a one-sex population model. Subsequent research have incorporated the dynamics of interaction into age-structured models. There are numerous ecological examples where size or age plays a dominant role on the dynamics of interacting species. The fact that predators do not consume prey of all ages and sizes indiscriminately is supported by a number of field studies. Most of the existing examples of age-dependent predation are from the fish community [3]. Another example include the wolves on Isle Royale [4] which preferentially hunt very young or very old moose.

The role of time delays on ecosystem models has been investigated by different researchers with variable outcomes. Early work emphasized an inverse

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relationship between time delay and local stability [5,6]. Later research, considering time delays and stage structure established that time delays can have both stabilizing and/or destabilizing effect [7-21]. Aiello and Freedman [15] studied a single species stage-structured model with discrete time delay and obtained the existence of a global attractor around the positive equilibrium which indicates that stage-structure is unable to generate the sustained oscillation in population concentration frequently observed in nature. They further studied the same model with self-dependent maturity time and derived lower and upper bounds of positive solutions [16]. However, from their analysis in [22], Arino et.al. concluded that stage-structured models with stage-dependent maturation delay can explain the phenomenon of periodic oscillation that are often observed in nature. Zhang et.al. [18] studied a predator-prey model with stage structure on prey population and obtained the necessary and sufficient condition for permanence or extinction. Song et.al. [19,20] dealt with two-species competitive models that incorporate optimal harvesting and stage-structure together. Xu et.al. [23] looked after the stability and persistence criteria of a delayed predator-prey model with stage-structure on the predator species. Gourley and Kuang [24] studied a robust predator-prey model with stage-structure and constant maturation delay; they have shown that for a dynamic resource, there exists an interval of the delay parameter which is capable of generating oscillatory dynamics for the system populations.

In the present paper, we study a stage-structured predator-prey model where the prey population have two life stages, namely the juvenile(J) and the adult (A). We incorporate the time required by the juvenile prey to become adult (commonly known as the stage delay) and also the gestation time of the predator species as two discrete time delays. We perform a stability analysis of the model for both non-delay and delay systems and conclude that all three species will coexist provided certain thresholds are achieved. Numerical simulations with hypothetical set of data are carried out to support analytical results.

Section 2 shows the formulation of the mathematical model. Stability analysis for non-delay case, due to maturation time as well as gestation delay are discussed in section 3. The analytical finding are supported by numerical simulations in section 4. The paper ends with a discussion.

2. The model

The pioneering work of Aiello and Freedman [16] on a single species growth model with stage structure have inspired many authors to study different kinds of stage-structured models and some significant work was carried out. Motivated by their work we have proposed a prey-predator model with stage-structure on prey species with the help of delay differential equation as follows:

$$\frac{dJ}{dt} = rA - re^{-d_1 T_1} A(t - T_1) - d_1 J \quad (1)$$

$$\frac{dA}{dt} = re^{-d_1 T_1} A(t - T_1) - d_2 A - \beta AY \tag{2}$$

$$\frac{dY}{dt} = \beta A(t - T_2) Y(t - T_2) - d_3 Y - \eta Y^2 \tag{3}$$

where $J(t)$ and $A(t)$ denote respectively, the densities of Juvenile and Adult individual preys at time t ; $Y(t)$ denote the density of predator population at time t , ($r, d_1, \beta, d_2, \eta, d_3$ are positive constants, T_1, T_2 are non-negative constants). The initial conditions for the system take the form

$$J(\theta) = \phi_1(\theta), A(\theta) = \phi_2(\theta), Y(\theta) = \phi_3(\theta) \tag{4}$$

$$\phi_i(\theta) \geq 0, \theta \in [-\tau, 0], \phi_i(0) > 0 \ (i = 1, 2, 3) \tag{5}$$

where $\tau = \max\{T_1, T_2\}$, $\Phi = (\phi_1, \phi_2, \phi_3) \in C([-\tau, 0], R_{+0}^3)$, the Banach space of continuous functions, mapping the interval $(-\tau, 0)$ into R_{+0}^3 , where we define $R_{+0}^3 = \{(x_1, x_2, x_3) : x_i \geq 0, i = 1, 2, 3\}$ and $R_+^3 = \{(x_1, x_2, x_3) : x_i > 0, i = 1, 2, 3\}$ as the interior of R_{+0}^3 .

The following assumptions have been made to derive the model:

(i) The prey population: At any time t , the birth of the juvenile population are proportional to the existing adult population with proportionality constant r , which explains the first term of the first equation (1). We assume that those juveniles (prey) born at time $t - T_1$, survive to time T_1 , exist from juvenile population and enter the mature population; hence the term $re^{-d_1 T_1} A(t - T_1)$ in the first two equations, namely, (1) and (2); d_1, d_2 are the natural death rates of the juvenile and adult prey population and β is the rate at which predator kills adult prey population.

(ii) The predator population: We assume that the reproduction of predator after predated the prey is not instantaneous but will be mediated by some discrete time lag required for gestation of predator. Let this time be T_2 and we assume that the predator population Y are known in $[-T_2, 0]$. This explains the term $\beta A(t - T_2) Y(t - T_2)$ in the third equation (3), d_3 is the natural death and η is the death rate due to intra-specific competition.

From (1) we get

$$\begin{aligned} \frac{dJ}{dt} + d_1 J(t) &= rA(t) - re^{-d_1 T_1} A(t - T_1) \\ &= re^{-d_1 t} \frac{d}{dt} \left(\int_{t-T_1}^t e^{d_1 \sigma} A(\sigma) d\sigma \right) \\ \Rightarrow J(t) &= r \int_{t-T_1}^t e^{-d_1(t-\sigma)} A(\sigma) d\sigma + e^{-d_1 t} \left(J(0) - r \int_{-T_1}^0 e^{d_1 \sigma} A(\sigma) d\sigma \right) \end{aligned}$$

For $t \geq T_1$, the first integral represents the juveniles that survived and settled in the interval $[t - T_1]$. For $t \geq T_1$, the second integral represents those juveniles that existed initially and have turned into adult at age T_1 and hence must be

zero. This implies

$$\begin{aligned} J(0) - r \int_{-T_1}^0 e^{d_1 \sigma} A(\sigma) d\sigma &= 0 \\ \Rightarrow J(0) &= r \int_{-T_1}^0 e^{d_1 \sigma} A(\sigma) d\sigma \end{aligned}$$

This makes the system ecologically sound and certifies the continuity of the initial conditions. Therefore, we have

$$J(t) = r \int_{t-T_1}^t e^{-d_1(t-\sigma)} A(\sigma) d\sigma \quad (6)$$

Lemma 1. *Solutions of system (1-3) with initial conditions (4) and (5) are positive for all $t \geq 0$.*

Proof. Let $[J(t), A(t), Y(t)]$ be the solution of the system. From (6), it is obvious that $J(t) > 0$ for $t \geq 0$. We now consider $Y(t)$ in the interval $[0, T_2]$. From equation (3) of the system we get

$$\begin{aligned} \frac{dY}{dt} &= \beta \phi_2(t - T_2) \phi_3(t - T_2) - d_3 Y - \eta Y^2 \\ &\geq -d_3 Y - \eta Y^2 \end{aligned}$$

since $\phi_2(\theta), \phi_3(\theta) \geq 0$ for $\theta \in [-T_2, 0]$. Therefore a standard comparison argument shows

$$Y(t) \geq Y(0) e^{-\int (d_3 + \eta Y) dt}$$

That is, $Y(t) > 0$ for $t \in [0, T_2]$. In the similar manner,

$$\begin{aligned} \frac{dA}{dt} &\geq -d_2 A - \beta AY \\ \Rightarrow A(t) &\geq A(0) e^{-\int (d_2 + \beta Y) dt} \end{aligned}$$

That is, $A(t) > 0$ for $t \in [0, T_2]$. In the similar manner we can treat the intervals $[T_2, 2T_2], [2T_2, 3T_2], \dots, [nT_2, (n+1)T_2]$, $n \in \mathbb{N}$. Thus, $J(t), A(t)$ and $Y(t) > 0$ for $t \geq 0$. \square

Lemma 2. *Positive solutions of system (1-3) with initial conditions (4) and (5) are ultimately bounded.*

Proof. Let $[J(t), A(t), Y(t)]$ be the solution of the system (1-3) satisfying the initial condition (4) and (5). Let $\rho(t) = J(t) + A(t) + Y(t)$. Then

$$\begin{aligned} \frac{d\rho}{dt} &= -[d_1 J + (d_2 - r)A + d_3 Y] - \beta AY + \beta A(t - T_2)Y(t - T_2) - \eta Y^2 \\ &\leq -M\rho + \beta A(t - T_2)Y(t - T_2), \text{ where } M = \min\{d_1, (d_2 - r), d_3\} \\ \Rightarrow \frac{d\rho}{dt} + M\rho &\leq \beta \phi_2(\theta) \phi_3(\theta) = M_1 \text{ (say)} \\ \Rightarrow \rho(t) &\leq \frac{M_1}{A} + \left(\rho(0) - \frac{M_1}{A} \right) e^{-Mt} \end{aligned}$$

Hence, the positive solution of the system (1-3) are ultimately bounded. \square

3. Linear stability analysis

By setting $\dot{J} = 0, \dot{A} = 0, \dot{Y} = 0$, in system (1-3), we get the equilibrium solutions as

- (i) $(0,0,0)$
- (ii) $J^* = \frac{r(1-e^{-d_1T_1})\{\beta d_3 + \eta(re^{-d_1T_1} - d_2)\}}{\beta^2 d_1}, A^* = \frac{\beta d_3 + \eta(re^{-d_1T_1} - d_2)}{\beta^2}, Y^* = \frac{re^{-d_1T_1} - d_2}{\beta}$;
provided $r_1 e^{-d_1T_1} > d_2$.

We now focus on the asymptotic stability of the unique nontrivial steady state of the system, namely, (J^*, A^*, Y^*) and linearize the system (1-3) about (J^*, A^*, Y^*) to determine the associated characteristic equation. The required characteristic equation is

$$\begin{vmatrix} -d_1 - \lambda & r - re^{-d_1T_1}e^{-\lambda T_1} & 0 \\ 0 & re^{-d_1T_1}e^{-\lambda T_1} - re^{-d_1T_1} - \lambda & -\beta A^* \\ 0 & \beta Y^* e^{-\lambda T_2} & \beta A^* e^{-\lambda T_2} - \beta A^* - \eta Y^* - \lambda \end{vmatrix} = 0$$

$$\Rightarrow (\lambda + d_1)[\lambda^2 + (2\eta Y^* + d_3 - \beta A^* e^{-\lambda T_2} + \beta Y^* + d_2 - re^{-d_1T_1}e^{-\lambda T_1})\lambda + \beta Y^*(2\eta Y^* + d_3) + d_2 - re^{-d_1T_1}e^{-\lambda T_1}](2\eta Y^* + d_3 - \beta A^* e^{-\lambda T_2}) = 0$$

Clearly, one of the root of the above equation is $-d_1$ ($d_1 > 0$), so we only concentrate on the roots of the second degree exponential polynomial equation in λ , namely,

$$\lambda^2 + (2\eta Y^* + d_3 - \beta A^* e^{-\lambda T_2} + \beta Y^* + d_2 - re^{-d_1T_1}e^{-\lambda T_1})\lambda + (\beta Y^*(2\eta Y^* + d_3) + d_2 - re^{-d_1T_1}e^{-\lambda T_1})(2\eta Y^* + d_3 - \beta A^* e^{-\lambda T_2}) = 0 \quad (7)$$

Through the study of the sign of the real parts of roots of (7), we can perform the local asymptotic stability analysis of the steady state (J^*, A^*, Y^*) . For that we need to show that (J^*, A^*, Y^*) is locally asymptotically stable iff all the roots of (7) have negative real parts. Also its stability can be lost if roots are purely imaginary, that is, if the roots cross the vertical axis.

We note that the steady state (J^*, A^*, Y^*) depends on the time delay T_1 implicitly, implying that the coefficients of the characteristic equation depend explicitly (the term with $e^{-d_1T_1}$) or implicitly, on T_1 , which creates a complexity to the resolution of (7). Moreover, the analysis of the sign of the real part of the eigenvalues becomes complicated owing to the presence of two delays, namely, T_1 and T_2 in the characteristic equation and hence a direct approach cannot be considered. Working on the line of Ruan [25], we will use a method consisting of determining the stability of the steady state when one delay is equal to zero and go on deducing conditions for the stability of the steady state when both time delays are non-zero by using proper analytical arguments.

3.1 Case I: $T_1 = 0, T_2 = 0$

In this case, the characteristic equation reduces to

$$(\lambda + d_1)[\lambda^2 - (r - d_2 - \beta Y^* + \beta A^* - d_3 - 2\eta Y^*)\lambda + (r - d_2 - \beta Y^*)(\beta A^* - d_3 - 2\eta Y^*) + \beta^2 A^* Y^*] = 0 \quad (8)$$

Proposition 1. *Assume that*

$$P1 \quad \frac{d_2 \eta}{(\beta + \eta)e^{-d_1 T_1} - \beta} < r < \frac{\beta d_3 - \eta d_2}{\eta(1 - 2e^{-d_1 T_1})}$$

Then system (1-3) without delay will be locally asymptotically stable around $E^ = (J^*, A^*, Y^*)$.*

For the values of the parameters taken from Table (1), one can see that condition (P_1) is fulfilled. Biologically it means that the growth rate of prey juveniles lies between two thresholds for the system to be asymptotically stable.

3.2 Case II: $T_1 > 0, T_2 = 0$

We now consider the case $T_1 > 0, T_2 = 0$ which is motivated by the fact there is a maturity time from juvenile to adult which cannot be ignored and hence T_1 cannot be zero. In this case, the characteristic equation will be

$$(\lambda + d_1)[\lambda^2 + (\eta Y^* + r e^{-d_1 T_1})\lambda + \beta Y^*(\eta Y^* + \beta A^*) + d_2 \eta Y^* - e^{-\lambda T_1}(r e^{-d_1 T_1} \lambda + r \eta Y^* e^{-d_1 T_1})] = 0 \quad (9)$$

Clearly, one root has a negative real part and the dynamics of the system will be determined by the quadratic exponential polynomial equation in λ , which is of the form

$$\lambda^2 + A_1 \lambda + A_2 + e^{-\lambda T_1}(A_3 \lambda + A_4) = 0 \quad (10)$$

where

$$\begin{aligned} A_1 &= \eta Y^* + r e^{-d_1 T_1} \\ A_2 &= \beta Y^*(\eta Y^* + \beta A^*) + d_2 \eta Y^* \\ A_3 &= -r e^{-d_1 T_1} \\ A_4 &= -r \eta Y^* e^{-d_1 T_1} \end{aligned} \quad (11)$$

Clearly (7) reduces to (10) when $T_1 = 0$ and the steady state is locally asymptotically stable when $T_1 = 0$, assuming P_1 to be true. Hence, as T_1 increases, the stability of the steady state can only be lost if pure imaginary roots appear. Hence, we look for purely imaginary roots $\lambda = \pm i\omega$, $\omega \in \Re$ of (10). Substituting

$\lambda = \pm i\omega$ and separating the real and the imaginary parts we get

$$\begin{aligned} A_4 \cos(\omega T_1) + A_3\omega \sin(\omega T_1) + A_2 - \omega^2 &= 0 \\ -A_4 \sin(\omega T_1) + A_3\omega \cos(\omega T_1) + \omega A_1 &= 0 \\ \Rightarrow \cos(\omega T_1) &= \frac{(A_4 - A_1 A_3)\omega^2 - A_2 A_4}{A_3^2 \omega^2 + A_4^2} \\ \sin(\omega T_1) &= \frac{A_3 \omega^3 + (A_1 A_4 - A_2 A_3)\omega}{A_3^2 \omega^2 + A_4^2} \end{aligned}$$

Squaring and adding we get,

$$\omega^4 + (A_1^2 - 2A_2 - A_3^2)\omega^2 + A_2^2 - A_4^2 = 0 \tag{12}$$

Let

$$\psi(W) \equiv W^2 + (A_1^2 - 2A_2 - A_3^2)W + A_2^2 - A_4^2$$

where $W = \omega^2$. The function ψ has positive roots if and only if

$$\begin{aligned} A_2^2 - A_4^2 < 0 \text{ or} \\ (A_1^2 - 2A_2 - A_3^2)^2 \geq 4(A_2^2 - A_4^2) \geq 0 > A_1^2 - 2A_2 - A_3^2 \end{aligned}$$

Without any loss of generality, let W_P be the positive roots of $\psi = 0$ and let $\omega_P = \sqrt{W_P}$.

We note that the unique solution of $\theta \in [0, 2\pi]$ of

$$\begin{aligned} \cos(\omega T_1) &= \frac{(A_4 - A_1 A_3)\omega^2 - A_2 A_4}{A_3^2 \omega^2 + A_4^2} \\ \sin(\omega T_1) &= \frac{A_3 \omega^3 + (A_1 A_4 - A_2 A_3)\omega}{A_3^2 \omega^2 + A_4^2} \end{aligned}$$

is

$$\theta = \cos^{-1}\left[\frac{(A_4 - A_1 A_3)\omega_P^2 - A_2 A_4}{A_3^2 \omega_P^2 + A_4^2}\right]$$

if $\sin(\theta) > 0$, that is, if $A_3\omega^2 + A_1 A_4 - A_2 A_3 > 0$ and

$$\theta = 2\pi - \cos^{-1}\left[\frac{(A_4 - A_1 A_3)\omega_P^2 - A_2 A_4}{A_3^2 \omega_P^2 + A_4^2}\right]$$

if $A_3\omega^2 + A_1 A_4 - A_2 A_3 \leq 0$

We now define the two sequences

$$\begin{aligned} T_{1,P}^{1,i} &= \frac{1}{\omega_P} [\cos^{-1}\left(\frac{(A_4 - A_1 A_3)\omega_P^2 - A_2 A_4}{A_3^2 \omega_P^2 + A_4^2}\right) + 2i\pi] \\ T_{1,P}^{2,i} &= \frac{1}{\omega_P} [2\pi - \cos^{-1}\left(\frac{(A_4 - A_1 A_3)\omega_P^2 - A_2 A_4}{A_3^2 \omega_P^2 + A_4^2}\right) + 2i\pi] \end{aligned}$$

Theorem 1. Let $T_{1,P}^* = T_{1,P}^{1,i}$ or $T_{1,P}^* = T_{1,P}^{2,i}$, that is, $T_{1,P}^*$ represents an element either of the sequence $T_{1,P}^{1,i}$ or $T_{1,P}^{2,i}$, associated with ω_P . Then the equation

$\lambda^2 + A_1\lambda + A_2 + e^{-\lambda T_1}(A_3\lambda + A_4) = 0$ has a pair of simple conjugate roots $\pm i\omega_P$ for $T_2 = T_{1,P}^*$ which satisfies

$$\text{sign}\left\{\frac{d\text{Re}(\lambda)}{dT_1}\Big|_{T=T_{1,P}^*}\right\} = \text{sign}\{\psi'(\omega_P^2)\}$$

Furthermore, assuming the proposition P1 and P2 to be true and denoting $T_1^* = \min_{i \in N} \{T_{1,P}^{1,i}, T_{1,P}^{2,i}\}$, it is concluded that the steady state (J^*, A^*, Y^*) is locally asymptotically stable if $T_1 < T_1^*$ and a Hopf-bifurcation occurs at (J^*, A^*, Y^*) when $T_1 = T_1^*$ iff $\psi'(\omega_P^2) > 0$.

Proof. We prove the theorem by contradiction. Let $\pm i\omega_P$ be a pair of purely imaginary roots of (10) and let $\lambda(T_1) = \phi(T_1) + i\omega(T_1)$ be the branch of roots of (10), with $\phi(T_{1,P}^*) = 0$ and $\omega(T_{1,P}^*) = \omega_P$.

We assume that $\lambda(T_{1,P}^*)$ is not a simple root of (10), then both (10) and derivative of (10) share the same root, which implies

$$\begin{aligned} \lambda^2 + A_1\lambda + A_2 + e^{-\lambda T_1}(A_3\lambda + A_4) &= 0 \\ (2\lambda + A_1 + \{A_3 - T_1(A_3\lambda + A_4)\}e^{-\lambda T_1})\frac{d\lambda}{dT_1} - \lambda(A_3\lambda + A_4)e^{-\lambda T_1} &= 0 \end{aligned} \tag{13}$$

at $\lambda = \lambda(T_{1,P}^*)$. Substituting $\lambda = \lambda(T_{1,P}^*) = \omega(T_{1,P}^*) = \omega_P$ in both the equations and separating real and imaginary parts we get respectively,

$$\begin{aligned} -A_3\omega_P^2 \cos(\omega_P T_{1,P}^*) + A_4\omega_P \sin(\omega_P T_{1,P}^*) &= 0 \\ A_4\omega_P \cos(\omega_P T_{1,P}^*) + A_3\omega_P^2 \sin(\omega_P T_{1,P}^*) &= 0 \end{aligned} \tag{14}$$

and

$$\begin{aligned} -A_3\omega_P \cos(\omega_P T_{1,P}^*) + A_4 \sin(\omega_P T_{1,P}^*) &= A_1\omega_P \\ A_4 \cos(\omega_P T_{1,P}^*) + A_3\omega_P \sin(\omega_P T_{1,P}^*) &= \omega_P^2 - A_2 \end{aligned} \tag{15}$$

Considering the fact that $\omega_P > 0$ and using (14) and (15), we obtain $A_1 = 0$ and $A_2 = \omega_P^2$. Since $A_1 = \eta Y^* + r e^{-d_1 T_1} > 0$ (using 11), we arrive at a contradiction. Hence, we conclude that $\pm i\omega_P$ are simple roots of (10).

From (10) and (13), we get (after simplification)

$$\begin{aligned} e^{\lambda T_1} &= -\frac{A_3\lambda + A_4}{\lambda^2 + A_1\lambda + A_2} \\ \left(\frac{d\lambda}{dT_1}\right)^{-1} &= \frac{(2\lambda + A_1)e^{\lambda T_1} + A_3}{\lambda(A_3\lambda + A_4)} - \frac{T_1}{\lambda} \end{aligned}$$

Eliminating $e^{\lambda T_1}$ we get,

$$\left(\frac{d\lambda}{dT_1}\right)^{-1} = -\frac{2\lambda + A_1}{\lambda(\lambda^2 + A_1\lambda + A_2)} + \frac{A_3}{\lambda(A_3\lambda + A_4)} - \frac{T_1}{\lambda}$$

Then,

$$\left(\frac{d\lambda}{dT_1}\right)^{-1}_{T_1=T_{1,P}^*} = -\frac{-2i\omega - A_1}{i(A_2 - \omega_P^2)\omega_P - A_1\omega_P^2} + \frac{A_3}{-A_3\omega_P^2 + iA_4\omega_P} - \frac{T_{1,P}^*}{i\omega_P}$$

Consequently,

$$Re\left(\frac{d\lambda}{dT_1}\right)^{-1}_{T_1=T_{1,P}^*} = \frac{A_1^2 - 2A_2 + 2\omega_P^2}{(A_2 - \omega_P^2)^2 + A_1^2\omega_P^2} - \frac{A_3^2}{A_3^2\omega_P^2 + A_4^2}$$

Now, $A_3^2\omega_P^2 + A_4^2 = \omega_P^4 + (A_1^2 - 2A_2)\omega_P^2 + A_2^2 = (A_2 - \omega_P^2)^2 + A_1^2\omega_P^2$ (using 12), which gives

$$\begin{aligned} Re\left(\frac{d\lambda}{dT_1}\right)^{-1}_{T_1=T_{1,P}^*} &= \frac{A_1^2 - 2A_2 - A_3^2 + 2\omega_P^2}{(A_2 - \omega_P^2)^2 + A_1^2\omega_P^2} \\ &= \frac{\psi'(\omega_P^2)}{(A_2 - \omega_P^2)^2 + A_1^2\omega_P^2} \end{aligned}$$

Since

$$sign\left\{Re\left(\frac{d\lambda}{dT_1}\right)^{-1}_{T_1=T_{1,P}^*}\right\} = sign\left\{\frac{dRe(\lambda)}{dT_1}\Big|_{T_1=T_{1,P}^*}\right\}$$

we get

$$sign\left\{\frac{dRe(\lambda)}{dT_1}\Big|_{T_1=T_{1,P}^*}\right\} = sign\{\psi'(\omega_P^2)\}$$

If $\psi'(\omega_P^2) > 0$, then $sign\left\{\frac{dRe(\lambda)}{dT_1}\Big|_{T_1=T_{1,P}^*}\right\} > 0$. So the system will be locally asymptotically stable when $T_1 < T_{1,P}^*$ and a Hopf bifurcation occurs at (J^*, A^*, Y^*) at $T_1 = T_{2,P}^*$ iff $\psi'(\omega_P^2) > 0$ □

3.3 Case III: $T_1 > 0, T_2 > 0$

We now state a result regarding the sign of the real parts of the roots of (7) in order to study the local stability of the positive steady state (J^*, A^*, Y^*) of the system (1-3).

Proposition 2. *If all roots of equation (7) have negative real parts for some $T_1 > 0$, then there exists a $T_2^*(T_1) > 0$ such that all roots of equation (7) (that is, with $T_2 > 0$) have negative real parts when $T_2 < T_2^*(T_1)$*

Considering the above proposition we can now state the following theorem:

Theorem 2. *If we assume that all the hypothesis $P_i, i = 1, 2$ hold, Then for any $T_1 \in [0, T_1^*)$ (T_1^* having the same definition as in theorem 1), there exists a $T_2^*(T_1) > 0$ such that the positive steady state (J^*, A^*, Y^*) of the system is locally asymptotically stable when $T_1 \in [0, T_1^*)$*

Proof. Using theorem 1, we can say that all the roots of (7) have negative real parts when $T_1 \in [0, T_1^*)$ and by proposition (2) we can conclude that there exists a $T_2^*(T_1) > 0$ such that all roots of equation (7) have negative real parts when $T_2 < T_2^*(T_1)$. Hence, the steady state (J^*, A^*, Y^*) of system (1-3) is locally asymptotically stable when $T_1 \in [0, T_2^*(T_1))$. \square

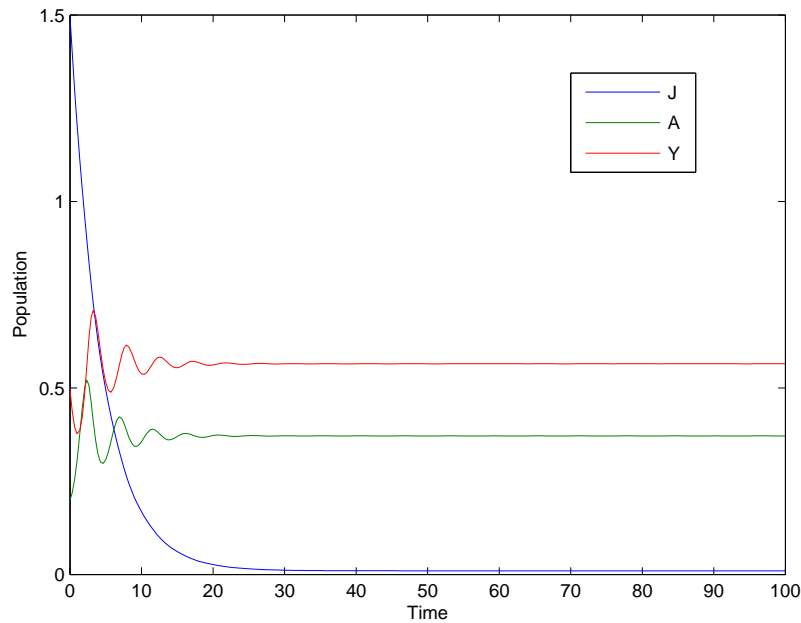


FIGURE 1. *Time evolution of the three populations with $T_1=0.01$ and $T_2 = 0$. The parameter set is taken from Table 1.*

4. Numerical illustration

We now numerically solve the equations with hypothetical set of parameter values obtained, given in tabular form (Table 1).

Figure 1 shows the time evolution of the three populations when time of maturity is very small ($T_1 = 0.01$) and no gestation delay (that is, $T_2 = 0$). The juvenile population goes to extinction in this case. Figure 2A shows that the three populations are asymptotically stable ($T_1 = 4, T_2 = 0$). However, if the maturation time exists a threshold value ($T_1 = 5, T_2 = 0$), all the three population becomes extinct. This is shown in figure 2B. The next three figures

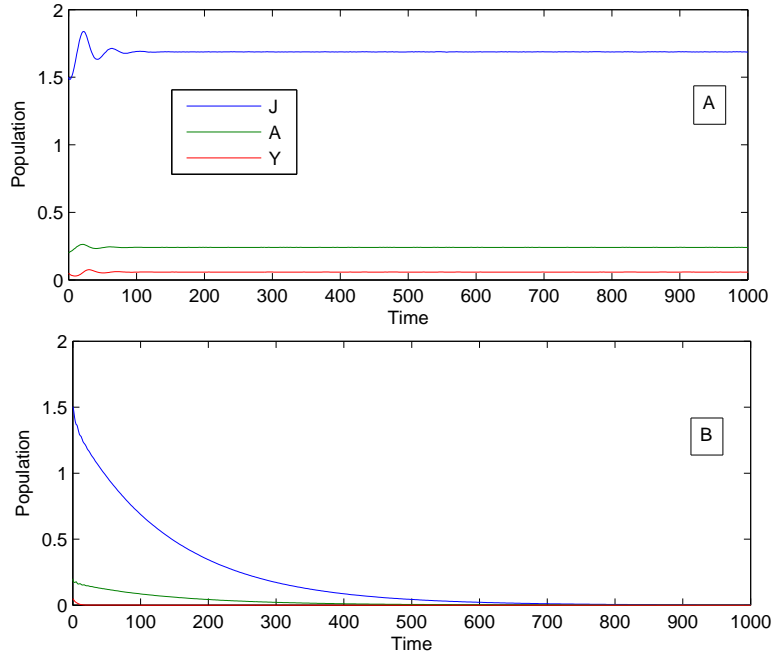


FIGURE 2. Time evolution of the three populations with $T_1 = 4$ and $T_2 = 0$. The parameter set is taken from Table 1.

TABLE 1. Parameter values used for numerical illustration.

Parameters	Values
r (birth rate of juvenile prey population)	2.657
d_1 (natural death rate of juvenile prey population)	0.225
d_2 (natural death rate of adult prey population)	0.9
β (rate at which predator kills adult preys)	3.1
d_3 (natural death rate of predator population)	0.7
η (death rate due to intra-specific competition)	0.8

give the time evolutions of the three populations when gestation delay is taken into account. Figures 3A, 3B, 3C shows that the steady state is asymptotically stable, though damped oscillation can be observed. In figure 3D, the solutions are drawn in the (J,A,Y)-plane. The time delays are $T_1 = 4, T_2 = 4$. Oscillating solutions are observed in figures 4A, 4B, 4C. As T_2 increases through $T_2 = 5.5$, a periodic solution occurs (which is evident from Figure 4) which is the case of Hopf-bifurcation. The importance of Hopf-bifurcation in this context is that at the bifurcation point a limit cycle (Figure 4D) is formed around the fixed

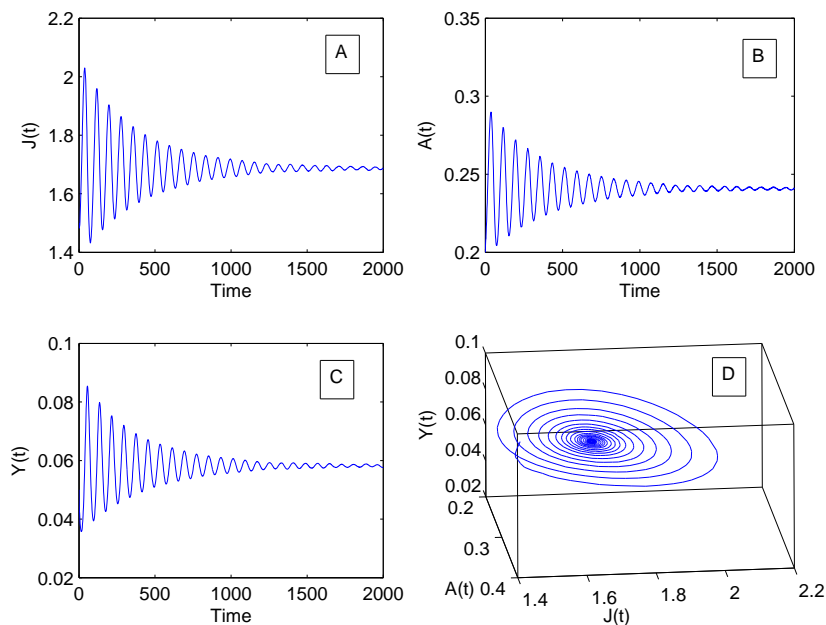


FIGURE 3. Time evolution of the three populations with $T_1 = 4$ and $T_2 = 4$. The parameter set is taken from Table 1.

point, thus resulting in stable periodic solutions. Figure 5 shows that the system becomes unstable when T_2 crosses the value 5.5.

5. Discussion

In this paper, the effect of two time delays on the dynamical behavior of a prey predator system with stage structure for prey has been studied. The two delay term is due to maturity time from juvenile to adult stage for preys and due to gestation delay. For non-delay case, the system is asymptotically stable if the growth rate of the prey juveniles (that is, r) lies between two thresholds. When there is no gestation delay (that is, $T_2 = 0$), the maturity time plays an important role in the dynamics of the system. For small maturity time of the prey species, the juveniles cannot survive and goes to extinction. Also, if the juveniles takes long time to mature, all the three species perish. In presence of gestation delay (along with maturity delay), the system shows interesting dynamics. Because of discrete time delay due to gestation of prey biomass by their predators, an oscillatory behavior of both prey and predator populations is noted. This indicates that seasonal effects on population models often lead to

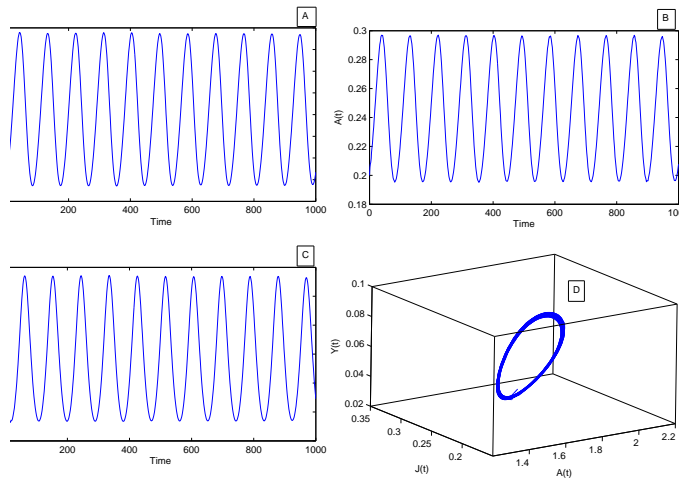


FIGURE 4. Time evolution of the three populations with $T_1 = 4$ and $T_2 = 5.5$. The parameter set is taken from Table 1.

synchronous solutions. However, the seasonality has an upper hand and is often the generating force for the observed oscillatory behavior in population densities [26]. When there is a question of selection between time delays and seasonality, both of which may present in nature.

Inclusion of discrete time delay due to gestation of prey biomass by their predators have ability to capture the oscillatory behavior of both prey and predator populations. This strongly suggests that seasonal effects on population models often lead to synchronous solutions. In addition, we may conclude that when both seasonality and time delay are present and deserve consideration, the seasonality is often the generating force for the often observed oscillatory behavior in population densities [26]. There may be some other causes behind the oscillation of individual population density, but we have made an attempt to understand the oscillatory behavior by incorporating gestation delay in predators growth equation. However, we regret our inability to represent the numerical results with a real field data. The next challenging expansion of this work will be to investigate whether the system (1-3) can admit chaotic behavior under periodic or almost periodic perturbations, especially by theoretical analysis, which we propose as our future work.

REFERENCES

1. F. Scudo and J. Ziegler, *The Golden Age of Theoretical Ecology : 1923-1940*, Springer-Verlag, New York, 1978.

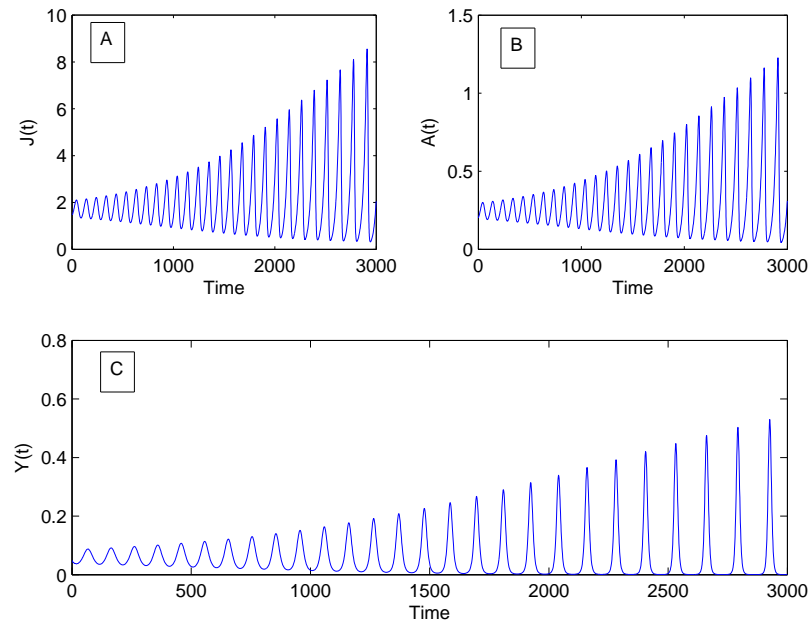


FIGURE 5. Time evolution of the three populations with $T_1 = 4$ and $T_2 = 6.5$. The parameter set is taken from Table 1.

2. A.G. MacKendrick, *Applications of mathematics to medical problems*, Proceedings of Edinburgh Mathematical Society **44**(1926), 98-130.
3. L. Nielsen, Effect of walleye predation on juvenile mortality and recruitment of yellow perch in oneida lake. Canadian Journal of Fish and Aquatic Science **37**(1980), 11-19.
4. D. Mech, *The wolves of Isle Royale*, U.S. Govt. Printing Office, 1966.
5. G.E. Hutchinson, *Circular casual systems in ecology*, Ann. N.Y. Acad. Sci. **50**(1948), 221-246.
6. R.M. May, *Time-delay versus stability in population models with two and three trophic levels*, Ecology **54**, 315-325.
7. S. Blythe, R.M. Nisbet and W. Gurney, *Instability and complex dynamica behaviour in population models with long time delay*, Theoretical Population Biology **22**(1982), 147-176.
8. J. Cushing and M. Saleem, *A predator prey model with age structure*, Journal of Mathematical Biology **14**(1982), 231-250.
9. A. Hasting and D. Wollkind, *Age structure in predator-prey systems. i. a general model and a specific example*, Theoretical Population Biology **21**(1982), 44-56.
10. A. Hasting and D. Wollkind, *Age structure in predator-prey systems. ii. functional response and stability and the paradox of enrichment*, Theoretical Population Biology **21**(1982), 57-68.
11. A. Hasting, *Age dependent predation is not a simple process. i. continuous time models*, Theoretical Population Biology **23**(1983), 347-362.

12. A. Hasting, *Delays in recruitment at different trophic levels : Effects on stability*, Journal of Mathematical Biology **21**(1984), 35-44.
13. L. Nunney, *The effect of long time delays in predator-prey systems*, Theoretical Population Biology **27**(1985), 202-221.
14. L. Nunney, *Short time delays in population models : a role in enhancing stability*, Ecology **66**(1985), 1849-1858.
15. W. Aiello and H. Freedman, *A time delay model of single-species growth with stage structure*, Mathematical Biosciences **101**(1990), 139-153.
16. W. Aiello, H. Freedman and J. Wu, *Analysis of a model representing stage-structured population growth with stage-dependent time delay*, SIAM Journal of Applied Mathematics **52**(1992), 855-869.
17. W. Wang and L. Chen, *A predator-prey system with stage structure for predator*, Comput. Math. Appl. **33** (8)(1997), 83-91.
18. X. Zhang, L. Chen and U.A. Neumann, *The stage-structured predator-prey model and optimal harvesting policy*, Mathematical Biosciences **168**(2000), 201-210.
19. X. Song and L. Chen, *Optimal harvesting and stability for a two-species competitive system with stage structure*, Mathematical Biosciences **170**(2001), 173-186.
20. X. Song and L. Chen, *Optimal harvesting and stability for a predator-prey system with stage structure*, Acta Math. Appl. Sin. **18** (3)(2002), 423-430.
21. M. Bandyopadhyay and Sandip Banerjee, *A stage-structured prey-predator model with discrete time delay*, Applied Mathematics and Computation **182**(2006), 1385-1398.
22. O. Arino, E. Sanchez and A. Fathallah, *State-dependent delay differential equations in population dynamics: modeling and analysis*, Amer. Math. Soc., Providence, RI **29**(2001), 19-36.
23. R. Xu, M.A. Chaplin and F.A. Davidson, *Persistence and stability of a stage-structured predator-prey model with time delays*, Appl. Math. Comp. **150**(2004), 259-277.
24. S.A. Gourley and Y. Kuang, *A stage structured predator-prey model and its dependence on maturation delay and death rate*, Journal of Mathematical Biology **49**(2004), 188-200.
25. M. Adimy, F. Crauste and S. Ruan, *Periodic oscillations in leukopoiesis models with two delays*, Journal of Theoretical Biology **242**(2006), 288-299.
26. Y. Li and Y. Kuang, *Periodic solutions in periodic delayed gause-type predator-prey systems*, Proceedings of Dynamical Systems and Applications **3**(2001), 375-382.

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