Stability and Bifurcation in an Age-Structured Model with Stocking Rate and Time Delays

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Abstract. In this paper, a predator-prey model with age structure, stocking rate and two delays is investigated. We show that Hopf bifurcation occurs when one of the time delay \( \tau \) crosses a sequence of critical values, by applying Hopf bifurcation theory for abstract Cauchy problems with non-densely domain. Numerical simulations are included to verify our results and a summary is also given.

1. Introduction. Predator-prey interaction is an important topic in biology. Mathematical model, that describes this interaction, could help to understand its dynamic processes and to make practical predictions. Such model could be various type of differential equations: ordinary differential equations [11, 23, 34], delay differential equations [3, 24, 31, 37], reaction-diffusion equations [4, 7, 32, 36], first order partial differential equations with age-structure [6, 13, 26, 30, 35] and so on. In this paper, we will consider the following model, which is formulated from the one in [26] by incorporating the fertility rate \( \tau_1 \) into the model,

\[
\begin{aligned}
\frac{\partial u(t,a)}{\partial t} + \frac{\partial u(t,a)}{\partial a} &= -\mu(a) u(t,a), \\
\frac{dV(t)}{dt} &= rV(t) \left( 1 - \frac{V(t)}{K} \right) - \frac{V(t) \int_{0}^{\tau_1} u(t,a) \, da}{h + V(t)} + H, \\
u(t,0) &= \eta V(t-\tau_1) \int_{0}^{\tau_1} \beta(a) u(t-\tau_1, a) \, da, \\
u(\theta, \cdot) &\in L^1((0, +\infty), \mathbb{R}), \quad \forall \theta \in [-\tau_1, 0], V_0(\cdot) = \phi \in C([-\tau_1, 0], \mathbb{R}),
\end{aligned}
\]

Here, \( u(t,a) \) is the population density of predator of age \( a \) at time \( t \) and \( V(t) \) represents the density of the prey at time \( t \); \( \mu(a) \) is age-dependent death rate of predator; \( r = b - d \) is the intrinsic growth rate of the prey, where \( b \) and \( d \) are the birth and death rates; \( K \) is the carrying capacity of the environment; \( \eta \) is the birth rate of the predator; \( H \) is the stocking rate and \( \beta(a) \in L^\infty_+(0, +\infty), \mathbb{R}) \) is the fertility rate of predator at age \( a \). We assume that the interaction between predator and prey takes the form of Holling type II functional response.

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Age-structured models have been extensively studied in the literature, see [10,18,22,33], and most of them concentrate on the existence, boundedness and stability of solutions. To deal with an age-structured model, a commonly used method is to transform the original model into a delay differential equation under some proper assumptions. For instance, if we set $\beta(a)$ to be a constant function in (1), then the system will turn into a delay differential equations, which has been investigated in [38]. Another way to study the age-structured model is to rewrite it as an abstract Cauchy problem, for which the integrated semigroup theory will apply. The pioneering work in this field may go back to the references [12,27,28]. In [12], the integrated semigroup theory is developed, and then much of theory for strongly continuous semigroup are extended to the semigroup of this type in [27]. Furthermore, these results are employed to study a semi-linear Cauchy problem with non-dense domain in [28] when the infinitesimal operator is Hille-Yosida, in [14,15,19] when the infinitesimal operator is not. The integrated semigroup are also applicable to other type of differential equations, such as: some partial differential equations with infinite delays [1] and neutral partial differential equations [2].

The main purpose of this note is to determine the stability of positive equilibrium and to examine if the fertility rate $\tau_1$ will induce periodic oscillations of (1) through Hopf bifurcation. It is usually not straightforward to show the existence of the non-trivial periodic solution for age-structured model. In [19], the authors established center manifold theorem for semi-linear equations with non-dense domain, and then applied it to Hopf bifurcation problems in age structured models. Later, a general Hopf bifurcation theorem for this abstract equation is proved in [14], and its normal form theory is also developed in [15], that can be used to compute the direction of Hopf bifurcation and the stability of bifurcating periodic solutions. For applications of these theories, we refer the readers to [5,16,17,21,25,26] and references therein.

For (1), we assume that

\[(H1) \quad \beta(a) := \begin{cases} \beta^* & a \geq \tau_2 \\ 0 & a \in (0, \tau_2) \end{cases}\]

where $\tau_2 > 0$, $\beta^* > 0$ and $\int_0^{\tau_2} \beta(a)e^{-\mu a} da = M < +\infty$, and then show existence of Hopf bifurcation as $\tau_1$ crosses a sequence of critical values, using the Hopf bifurcation theorem in [14]. It is remarked that the method we used in this paper can be applied to more general fertility rate function $\beta(a) \in L^\infty_+((0, +\infty), \mathbb{R})$.

The paper is organized as follows. In Section 2, the Hopf bifurcation theorem in [14] is restated and the model (1) is formulated as a non-densely defined Cauchy problem. In Section 3, the existence of equilibrium is investigated. Then we linearize the system around the positive equilibrium and analyze the spectral properties of the linearized equation. In Section 4, we derive the characteristic equation. By studying the distribution of roots, we obtain the conditions of stability and bifurcation. Numerical simulations to verify our results and a summary are given in Section 5.

2. Preliminary. Consider the following abstract Cauchy problem:

\[ \frac{du(t)}{dt} = Au(t) + F(\mu, u(t)), \quad \forall t \geq 0, \quad u(0) = x \in D(A) := X_0, \tag{2} \]

where $\mu \in \mathbb{R}$, $A : D(A) \subset X \to X$ is a non-densely defined linear operator on a Banach space $X$, and $F : \mathbb{R} \times X_0 \to X$ is a $C^k$ map with $k \geq 4$ such that $F(\mu, 0) = 0$. 
Theorem 2.1. For \( \lambda \in (-\varepsilon, \varepsilon) \) and \( \partial_t F(0, 0) = 0 \). Assume there exist two constants, \( \omega_A \in \mathbb{R} \) and \( M_A \geq 1 \), such that \( \omega_A, +\infty \in \rho(A) \) and

\[
\lim_{\lambda \to +\infty} (\lambda I - A)^{-1} x = 0, \forall x \in X,
\]

\[
\| (\lambda I - A)^{-k} \|_{\mathcal{L}(X_0)} \leq \frac{M_A}{(\lambda - \omega_A)^k}, \forall \lambda > \omega_A, \forall k \geq 1.
\]

Then, \( A \) generates a uniquely determined integrated semigroup \( \{S_A(t)\}_{t \geq 0} \). For \( \{S_A(t)\}_{t \geq 0} \), we assume that there exists a function \( \delta : [0, +\infty) \to [0, +\infty) \) with \( \lim_{t \to 0^+} \delta(t) = 0 \), such that for each \( \tau > 0 \) and \( f \in C([0, \tau], X) \), \( t \to \int_0^t S_A(t - s) f(s) d\sigma \) is continuously differential and

\[
\left\| \frac{d}{dt} \int_0^t S_A(t - s) f(s) d\sigma \right\| \leq \delta(t) \sup_{s \in [0, t]} \| f(s) \|, \forall t \in [0, \tau].
\]

Let \( A_{X_0} \) (also denoted by \( A_0 \)) be the part of \( A \) on \( X_0 \), which is defined by

\[
A_{X_0} x = Ax, \forall x \in D(A_{X_0}) = \{ x \in D(A) \cap X_0 : Ax \in X_0 \}.
\]

Then \( A_0 \) is the infinitesimal generator of a strongly continuous semigroup \( \{T_{A_0}(t)\}_{t \geq 0} \) of bounded linear operators on \( X_0 \). Note that \( \{T_{A_0}(t)\}_{t \geq 0} \) may not be compact for large \( t \). It is also required that the essential growth rate \( \omega_{0, ess}(A_0) \) of \( \{T_{A_0}(t)\}_{t \geq 0} \) is strictly negative. Here

\[
\omega_{0, ess}(A_0) := \lim_{t \to +\infty} \frac{\ln \| T_{A_0}(t) B_{X_0}(0, 1) \|}{t}
\]

where \( B_{X_0}(0, 1) = \{ x \in X_0 : \| x \|_{X_0} \leq 1 \} \), and for each bounded set \( B \subseteq X_0 \), \( \tau(B) \) is the Kuratowski measure of non-compactness and defined by \( \tau(B) = \inf \{ \varepsilon > 0 : B \) can be covered by a finite number of balls of radius \( \varepsilon \} \).

For the occurrence of Hopf bifurcation, we further assume that there exists a pair of conjugated simple eigenvalues of \( A_0 \) for \( \mu \in (-\varepsilon, +\varepsilon) \), denoted by \( \lambda(\mu) \) and \( \overline{\lambda(\mu)} \), such that \( \lambda(\mu) = \alpha(\mu) + i\omega(\mu), \) the map \( \mu \to \lambda(\mu) \) is continuously differentiable, \( \omega(0) > 0, \alpha(0) = 0, \frac{d\alpha}{d\mu} \neq 0, \) and \( \sigma(A_0) \cap i\mathbb{R} = \{ \lambda(0), \overline{\lambda(0)} \} \). The Hopf bifurcation theorem for (2) in [14] is restated as follows.

Theorem 2.1. For (2), there exist \( \varepsilon^* > 0 \) and three \( C^{k-1} \) maps: \( \varepsilon \to \mu(\varepsilon) \) from \( (0, \varepsilon^*) \) into \( \mathbb{R} \), \( \varepsilon \to x_\varepsilon \) from \( (0, \varepsilon^*) \) into \( D(A) \) and \( \varepsilon \to \gamma(\varepsilon) \) from \( (0, \varepsilon^*) \) into \( \mathbb{R} \), such that for each \( \varepsilon \in (0, \varepsilon^*) \), there exists a \( \gamma(\varepsilon) \)-periodic function \( u_\varepsilon \in C^{k}(\mathbb{R}, X_0) \), which is an integrated solution of (2) with the parameter value equals \( \mu(\varepsilon) \) and the initial value equals \( x_\varepsilon \). So for each \( t \geq 0, u_\varepsilon \) satisfies

\[
u_\varepsilon(t) = x_\varepsilon + A \int_0^t u_\varepsilon(l) dl + \int_0^t F(\mu(\varepsilon), u_\varepsilon(l)) dl.
\]

Moreover, we have the following properties

(i) There exist a neighborhood \( N \) of 0 in \( X_0 \) and an open interval \( I \) in \( \mathbb{R} \) containing 0, such that for \( \mu \in I \) and any periodic solution \( \hat{u}(t) \) in \( N \) with minimal period \( \gamma \) close to \( \frac{2\pi}{\omega(0)} \) of (2) for the parameter value \( \mu \), there exists \( \varepsilon \in (0, \varepsilon^*) \) such that \( u_\varepsilon(t) = u_{\hat{\varepsilon}}(t + \theta) \) (for some \( \theta \in [0, \gamma(\varepsilon)] \), \( \mu(\varepsilon) = \hat{\mu}, \) and \( \gamma(\varepsilon) = \check{\gamma} \).

(ii) The map \( \varepsilon \to \mu(\varepsilon) \) is a \( C^{k-1} \) function and we have the Taylor expansion

\[
\mu(\varepsilon) = \sum_{n=1}^{k-1} \mu_{2n} \varepsilon^{2n} + O(\varepsilon^{k-1}), \forall \varepsilon \in (0, \varepsilon^*),
\]

where \( \mu_{2n} \) are real constants.
where \([k-2]\) is the integer part of \(\frac{k-2}{\epsilon}\).

(iii) The period \(\gamma(\epsilon)\) of \(t \to u_\epsilon(t)\) is a \(C^{k-1}\) function and

\[\gamma(\epsilon) = \frac{2\pi}{\omega(0)} \left[ 1 + \sum_{n=1}^{[k-2]} \gamma_{2n} \epsilon^{2n} \right] + O(\epsilon^{k-1}), \ \forall \epsilon \in (0, \epsilon^*).\]

3. Transformation of Cauchy Problems. Let

\[\hat{u} = \frac{a}{\tau}, \ \hat{t} = \frac{t}{\tau}\]

and

\[\hat{V}(\hat{t}) = V(\tau \hat{t}) \quad \hat{u}(\hat{t}, \hat{a}) = \tau u(\tau \hat{t}, \tau \hat{a}).\]

Then, we obtain the following system, by dropping the hat,

\[
\begin{cases}
\frac{\partial u(t,a)}{\partial t} + \frac{\partial u(t,a)}{\partial a} = -\mu \tau u(t,a), \\
\frac{dV(t)}{dt} = \tau \left[ rV(t) \left( 1 - \frac{V(t)}{K} \right) - \frac{V(t) \int_0^{+\infty} u(t,a) da}{h + V(t)} \right] + H, \\
u(t,0) = \tau v\left( t - \frac{\pi}{\tau}, \int_0^{+\infty} \beta(a) u(t-a,\tau) da \right), \\
u_0(\theta, \cdot) \in L^1((0, +\infty), \mathbb{R}), \forall \theta \in \left[ -\frac{\pi}{\tau}, 0 \right], V_0 = \phi \in C([-\frac{\pi}{\tau}, 0], \mathbb{R}),
\end{cases}
\]

(3)

with the function \(\beta(\cdot)\) now defined by

\[\beta(a) = \begin{cases} 
\beta^* & a \geq 1 \\
0 & \text{otherwise}
\end{cases}\]

It also follows from (H1) that \(\beta^* = M \mu e^{\pi\tau_2}\).

We now formulate (3) into an abstract Cauchy problem. Let \(\rho(t,a)\) be the density of prey of age \(a\) at time \(t\). Then, \(V(t) = \int_0^{+\infty} \rho(t,a) da\). From the second equation of (3), we have

\[
\begin{cases}
\frac{\partial \rho(t,a)}{\partial t} + \frac{\partial \rho(t,a)}{\partial a} = -\tau_2 d \rho(t,a), \\
\rho(t,0) = G(u(t,a), \rho(t,a)), \\
\rho(0,a) = \rho_0 \in L^1((0, +\infty), \mathbb{R}),
\end{cases}
\]

where \(G\) is given by

\[
G(u(t,a), \rho(t,a)) = \tau_2 \left[ b \int_0^{+\infty} \rho(t,a) da \left( 1 - \frac{\int_0^{+\infty} \rho(t,a) da}{K} \right) + \frac{d(\int_0^{+\infty} \rho(t,a) da)^2}{K} \right. \left. - \frac{\int_0^{+\infty} \rho(t,a) da \int_0^{+\infty} u(t,a) da}{h + \int_0^{+\infty} \rho(t,a) da} + H \right].
\]

Set \(w(t,a) = \left( \frac{u(t,a)}{\rho(t,a)} \right)\) and \(w(t,\theta,a) = w(t + \theta, a)\) for \(t \geq 0\) and \(\theta \in [-\frac{\pi}{\tau}, 0]\). We have

\[
\begin{cases}
\frac{\partial w(t,a)}{\partial t} + \frac{\partial w(t,a)}{\partial a} = -Dw(t,a), \\
w(t,0) = B(w_0(\theta,a)), \\
w_0(\theta,a) = \left( \frac{u_0(\theta,a)}{\rho_0(\theta,a)} \right) \in C([-\frac{\pi}{\tau}, 0], L^1((0, +\infty), \mathbb{R}^2))
\end{cases}
\]

(4)
Then, with \( x \) integrated semigroup theory will apply. Define parameter. It remains to convert (5) to an ODE on the space \( C \).

Let \( Y := \mathbb{R}^2 \times L^1((0, +\infty), \mathbb{R}^2) \) endowed with the usual product norm \( \|\zeta\|_{\mathbb{R}^2} + \|\varphi\|_{L^1}, \forall \begin{pmatrix} \zeta & \varphi \end{pmatrix} \in Y \). Define the linear operator \( L : D(L) \subset Y \to Y \) by

\[
L \begin{pmatrix} 0 \\ \varphi \end{pmatrix} = \begin{pmatrix} -\varphi(0) \\ -\varphi' - D\varphi \end{pmatrix}
\]

with \( D(L) = \{0\} \times W^{1,1}((0, +\infty), \mathbb{R}^2) \). Let \( C := C \left( \left[ -\frac{\tau_1}{\tau_2}, 0 \right] , Y \right) \) and \( C_A = \left\{ \begin{pmatrix} \zeta(\theta) \\ \psi(\theta) \end{pmatrix} \in C : \zeta(0) = 0 \right\} \). For \( (\zeta(\theta), \psi(\theta))^T \in C_A \), define \( F : C_A \to Y \) by

\[
F \begin{pmatrix} \zeta(\theta) \\ \psi(\theta) \end{pmatrix} = \begin{pmatrix} B(\psi(\theta)) \\ 0_{\mathbb{R}_1} \end{pmatrix}.
\]

Let \( y(t,a) = \begin{pmatrix} 0 \\ w(t,a) \end{pmatrix} \); (4) can be written as

\[
\begin{cases}
\frac{d}{dt} y(t,a) = Ly(t,a) + F(y(t,a), t \geq 0, \\
y_0(\theta,a) = \begin{pmatrix} 0 \\ w_0(\theta,a) \end{pmatrix} \in C_A.
\end{cases}
\]

which is an abstract delay differential equation if the variable \( a \) is regarded as a parameter. It remains to convert (5) to an ODE on the space \( C_A \), and then the integrated semigroup theory will apply. Define \( x \in C \left( (0, +\infty) \times \left[ -\frac{\tau_1}{\tau_2}, 0 \right] ; Y \right) \) by \( x(t,\theta) = y(t+\theta,a) \), for any \( t \geq 0 \) and \( \theta \in \left[ -\frac{\tau_1}{\tau_2}, 0 \right] \). Then, for \( t \geq 0 \),

\[
\begin{cases}
\frac{\partial x(t,\theta)}{\partial t} - \frac{\partial x(t,\theta)}{\partial \theta} = 0, \theta \in \left[ -\frac{\tau_1}{\tau_2}, 0 \right], \\
\frac{\partial x(t,0)}{\partial \theta} = Lx(t,0) + F(x(t,\theta)), \\
x(0,\theta) = y_0(\theta,a) \in C_A.
\end{cases}
\]

Define \( Z = Y \times C \) with the usual product norm \( \begin{pmatrix} f \\ \phi \end{pmatrix} = \|f\|_Y + \|\phi\|_C \), and the linear operator \( A : D(A) \subset Z \to Z \) by

\[
A \begin{pmatrix} 0_Y \\ \phi \end{pmatrix} = \begin{pmatrix} -\phi'(0) + L\phi(0) \\ \phi' \end{pmatrix}, \forall \begin{pmatrix} 0_Y \\ \phi \end{pmatrix} \in D(A),
\]

where

\[
D(A) = \{ 0_Y \} \times \left\{ \phi \in C^1 \left( \left[ -\frac{\tau_1}{\tau_2}, 0 \right] , Y \right) : \phi(0) \in D(L) \right\}.
\]

Then, \( A \) is non-densely defined, since

\[
Z_0 := \overline{D(A)} = \{ 0_Y \} \times C_A \neq Z.
\]
Moreover, if we define $H : Z_0 \to Z$ by
\[
H(y_{\phi}) = \begin{pmatrix} F(\phi) \\ 0_{CA} \end{pmatrix},
\]
and set
\[
z(t) := \begin{pmatrix} 0 \\ x(t) \end{pmatrix}.
\]
Then, (6) turns into
\[
\begin{aligned}
\frac{d}{dt} z(t) &= Az(t) + H(z(t)), \quad t > 0, \\
z(0) &= \begin{pmatrix} 0 \\ y_0 \end{pmatrix} \in Z_0.
\end{aligned}
\tag{7}
\]
Denote
\[
\vartheta := \min \{ \tau_2 d, \tau_2 \mu \} > 0 \quad \text{and} \quad \Omega := \{ \lambda \in \mathbb{C} : \text{Re}(\lambda) > -\vartheta \}.
\]
As a consequence of Theorem 3.5 and Lemma 3.6 in [9], we have

**Theorem 3.1.** For the operators $L$ and $A$, the following statements hold.

(i) If $\lambda \in \Omega$, then $\lambda \in \rho(L)$, and for any $\begin{pmatrix} \delta \\ \psi \end{pmatrix} \in Y$, $(\lambda I - L)^{-1} \begin{pmatrix} \delta \\ \psi \end{pmatrix} = \begin{pmatrix} 0 \\ \phi \end{pmatrix}$ with
\[
\phi(a) = e^{-\int_0^a (\lambda I + D) d\xi} + \int_0^a e^{-\int_\xi^a (\lambda I + D) d\psi(s)} ds;
\]
(ii) $\rho(L) = \rho(A)$. In addition, for each $\lambda \in \rho(A)$ and $\begin{pmatrix} f \\ \psi \end{pmatrix} \in Z$, the formula for the resolvent of $A$ is given by
\[
(\lambda I - A)^{-1} \begin{pmatrix} f \\ \psi \end{pmatrix} = \begin{pmatrix} 0 \\ \phi \end{pmatrix},
\]
where
\[
\phi(\theta) = e^{\lambda \theta} (\lambda I - L)^{-1} [\psi(0) + f] + \int_0^\theta e^{\lambda (\theta - s)} \psi(s) ds;
\]
(iii) The operators $L$ and $A$ are Hille-Yosida operators on $Y$ and $Z$, respectively.

Denote
\[
Y_+ := \mathbb{R}^2_+ \times L^1((0, +\infty); \mathbb{R}^2_+),
\]
\[
Z_+ := Y_+ \times C \left( \left[ \begin{array}{c} -\tau_1 \\ \tau_2 \end{array} \right], Y_+ \right),
\]
and
\[
Z_{0+} := Z_0 \cap Z_+.
\]
Then, the global existence, uniqueness and positive of solutions for system (7) follow directly from [19].

**Theorem 3.2.** There exists a unique continuous semiflow $\{U(t)\}_{t \geq 0}$ on $Z_{0+}$ such that for any $z \in Z_{0+}$, $t \to U(t)z$ is the unique integrated solution of
\[
\begin{aligned}
\frac{dU(t)z}{dt} &= AU(t)z + H(U(t)z), \\
U(0)z &= z,
\end{aligned}
\]
or equivalently,
\[
U(t)z = z + A \int_0^t U(l)z dl + \int_0^t H(U(l)z) dl, \quad t \geq 0.
\]
4. Equilibria and linearization. Assume

\((H2) \eta > \frac{h + K}{MK}\);

The equilibrium \(\tau = \left(\frac{0}{\psi}\right) \in D(A)\), with \(\psi = \left(\frac{\zeta(\cdot)}{\phi(\cdot)}\right) \in C^1\left([-\frac{\tau_2}{2}, \frac{\tau_2}{2}]; Y\right), \psi(0) \in D(L)\) and \(\phi(\cdot) = \left(\frac{\phi_1(\cdot)}{\phi_2(\cdot)}\right)\), must satisfy

\[A\tau + H(\tau) = 0,\]

or equivalently,

\[\begin{cases} -\psi'(0) + L\psi(0) + F(\psi) = 0, \\ \psi' = 0. \end{cases}\]

Solving the above equation, we have the following lemma.

**Lemma 4.1.** The system (7) has always the equilibria

\[\tau_1 = \left(\frac{0}{\psi_1(\cdot)}\right) \quad \text{and} \quad \tau_2 = \left(\frac{0}{\psi_2(\cdot)}\right)\]

with

\[\begin{gathered} \psi_1(\theta) = \psi_2(\theta) = 0_{R^2}, \\
\phi_1(\theta)(a) = 0, \\
\phi_2(\theta)(a) = \left(\frac{1}{2} + \frac{1}{4} + \frac{H}{K^2}\right)\tau_2 dKe^{-\tau_2 da}. \end{gathered}\]

If \((H2)\) holds, then there exists a unique positive equilibrium of (7)

\[\tau = \left(\frac{0}{\psi(\cdot)}\right), \quad \psi(\theta) = 0_{R^2}, \quad \begin{pmatrix} \phi_1(\theta)(a) \\ \phi_2(\theta)(a) \end{pmatrix} = \frac{\tau_2 \mu M [Khr(\eta M - 1) - rh^2 + HK(\eta M - 1)^2]}{\eta M - 1} e^{-\tau_2 da}.\]

Let

\[\bar{z}(t) = z(t) - \tau.\]

Then,

\[\begin{cases} \frac{d\bar{z}(t)}{dt} = A\bar{z}(t) + H(\bar{z}(t) + \tau) - H(\tau), & t \geq 0, \\
\bar{z}(0) = \left(\frac{0}{w_0 - \psi(a)}\right) \triangleq \bar{z}_0 \in D(A). \end{cases}\]

and the linearized equation of (8) at 0 is given by

\[\frac{d\bar{z}(t)}{dt} = A\bar{z}(t) + DH(\tau)\bar{z}(t), \quad t \geq 0, \bar{z}(0) \in D(A),\]
where
\[
DH(\varpi) \begin{pmatrix} 0_Y \\ \psi \end{pmatrix} = \begin{pmatrix} DF(\overline{\psi})(\psi) \\ 0_{C_A} \end{pmatrix}, \forall \begin{pmatrix} 0_Y \\ \psi \end{pmatrix} \in D(A), \psi = \begin{pmatrix} \zeta(\cdot) \\ \phi(\cdot) \end{pmatrix}
\]
with
\[
DF(\overline{\psi})(\psi) = \begin{pmatrix} DB(\overline{\phi})(\phi) \\ 0_{L_1} \end{pmatrix}
\]
and
\[
DB(\overline{\phi})(\phi) = \begin{pmatrix} \frac{\tau_2}{\mu} \cdot 0 \\ 0 \end{pmatrix} \int_0^{+\infty} \beta(a) \phi \left( -\frac{\tau_1}{\tau_2} \right) (a) da
\]
\[
+ \begin{pmatrix} 0 \\ 0 \end{pmatrix} \frac{\tau_2}{\mu} \cdot 0 \int_0^{+\infty} \phi \left( -\frac{\tau_1}{\tau_2} \right) (a) da
\]
\[
+ \begin{pmatrix} -\frac{\tau_2}{\eta M} \\ -\frac{\tau_2}{\eta M} \end{pmatrix} b - \frac{2 r h}{\eta h M} \int_0^{+\infty} \phi \left( -\frac{\tau_1}{\tau_2} \right) (a) da.
\]
Hence, (8) can be written as
\[
\frac{d\tilde{z}(t)}{dt} = \tilde{A}\tilde{z}(t) + \tilde{H}(\tilde{z}(t)), \quad t \geq 0,
\]
where
\[
\tilde{A} := A + DH(\varpi)
\]
and
\[
\tilde{H}(\tilde{z}(t)) = H(\tilde{z}(t) + \varpi) - H(\varpi) - DH(\varpi)\tilde{z}(t)
\]
satisfying \(\tilde{H}(0) = 0\) and \(D\tilde{H}(0) = 0\).

Since \(A\) is a Hille-Yosida operator, it will generate an integrated semigroup \(S(\varpi(t))_{t \geq 0}\) on \(Z\). Let \(A_0\) be the part of \(A\) on \(Z\), then \(A_0\) will generate a \(C_0\)-semigroup \(\{T_{A_0}(t)\}_{t \geq 0}\) on \(Z\) such that \(\|T_{A_0}(t)\| \leq e^{-\delta t}\). Therefore, \(\omega_{0, ess}(A_0) \leq \omega(A_0) \leq -\delta\). Applying Theorem 3 in [29] or Theorem 1.2 in [8], we have
\[
\omega_{0, ess}(A + DH(\varpi))_0 \leq -\delta < 0,
\]
since \(DH(\varpi)\) is a compact bounded linear operator.

**Proposition 1.** The linear operator \(\tilde{A}\) is a Hille-Yosida operator, and its part \(\tilde{A}_0\) in \(Z_0\) satisfies
\[
\omega_{0, ess}(\tilde{A}_0) < 0.
\]

Set \(J := DH(\varpi)\). For \(\lambda \in \Omega\), \((\lambda I - A)\) is invertible, and \(\lambda I - (A + J)\) is invertible if and only if \(I - J(\lambda I - A)^{-1}\) is invertible. Furthermore, we have
\[(\lambda I - (A + J))^{-1} = (\lambda I - A)^{-1}(I - J(\lambda I - A)^{-1})^{-1}.
\]
Now we consider \((I - J(\lambda I - A)^{-1})\frac{\delta_Y}{\phi_{C_A}} = \begin{pmatrix} \gamma_Y \\ \psi_{C_A} \end{pmatrix}, \) with \(\delta_Y = \begin{pmatrix} \delta_1 \\ \delta_2 \end{pmatrix}, \gamma_Y = \begin{pmatrix} \gamma_1 \\ \gamma_2 \end{pmatrix}\)
and \(\psi_{C_A} = \begin{pmatrix} \psi^1(\cdot) \\ \psi^2(\cdot) \end{pmatrix}\) is \(C^1\left(\left[-\frac{T_1}{T_2}, 0\right]; Y\right)\), that is
\[
\begin{cases}
\delta_Y - DF(\overline{\psi}) \left(e^{\lambda Y (\lambda I - L)^{-1}}(\phi_{C_A}(0) + \delta_Y) + \int_0^0 e^{\lambda(0-s)} \phi_{C_A}(s) ds\right) = \gamma_Y,
\varphi_{C_A} = \psi_{C_A},
\end{cases}
\]
or equivalently,
\[
\begin{cases}
[I - DF(\overline{\psi}) \left(e^{\lambda t}(\lambda I - L)^{-1}\right)] \delta_Y \\
= \gamma_Y + DF(\overline{\psi}) \left(\int_0^1 e^{\lambda(t-s)} \varphi_{CA}(s) \, ds + e^{\lambda t}(\lambda I - L)^{-1} \varphi_{CA}(0)\right),
\end{cases}
\]
\[
\varphi_{CA} = \psi_{CA}.
\]
Let
\[
(I - DF(\overline{\psi})(e^{\lambda t}(\lambda I - L)^{-1}))\delta_Y = \left(\begin{smallmatrix} \delta_1 \\ \delta_2 \end{smallmatrix} \right),
\]
that is,

\[
\delta_Y - \left(DB(\overline{\phi}) \left[e^{\lambda t} \left(e^{-\int_0^1 \left[e^{\lambda(t+\delta)}\right] d\delta} + \int_0^1 e^{-\int_0^1 \left[e^{\lambda(t+\delta)}\right] d\delta} (\delta(s) \, ds)\right)\right]\right)
\]

or
\[
\left(I - DB(\overline{\phi}) \left(e^{\lambda t} e^{-\int_0^1 \left[e^{\lambda(t+\delta)}\right] d\delta}\right)\right) \delta_1 = \delta_1 + DB(\overline{\phi}) \left[e^{\lambda t} \int_0^1 e^{-\int_0^1 \left[e^{\lambda(t+\delta)}\right] d\delta} (\delta(s) \, ds)\right] \delta_2.
\]

Denote
\[
\Delta(\lambda) = I - DB(\overline{\phi}) \left(e^{\lambda t} e^{-\int_0^1 \left[e^{\lambda(t+\delta)}\right] d\delta}\right)
\]

and

\[
\gamma(\lambda, \delta_2) = DB(\overline{\phi}) \left[e^{\lambda t} \int_0^1 e^{-\int_0^1 \left[e^{\lambda(t+\delta)}\right] d\delta} (\delta(s) \, ds)\right].
\]

Then \(\Delta(\lambda)\delta_1 = \delta_1 + \gamma(\lambda, \delta_2)\). Whenever \(\Delta(\lambda)\) is invertible, we have

\[
\delta_1 = (\Delta(\lambda))^{-1}(\delta_1 + \gamma(\lambda, \delta_2)).
\]

From the above argument, we arrive at the following conclusion.

**Lemma 4.2.** We have \(\sigma(A + J) \cap \Omega = \sigma_p(A + J) \cap \Omega = \{\lambda \in \Omega : \det(\Delta(\lambda)) = 0\}\), and for each \(\lambda \in \rho(A + J) \cap \Omega\), the resolvent of \(A + J\) is given by

\[
(\lambda I - (A + J))^{-1} \begin{pmatrix} \gamma_Y \\ \psi_{CA} \end{pmatrix} = \begin{pmatrix} 0 \\ e^{\lambda t}(\lambda I - L)^{-1} [\psi_{CA}(0) + \delta_Y] + \int_0^\lambda e^{\lambda(s)} \psi_{CA}(s) \, ds \end{pmatrix},
\]

where

\[
\begin{cases}
\gamma_Y = \begin{pmatrix} \gamma_1 \\ \gamma_2 \end{pmatrix},
\delta_Y = \begin{pmatrix} (\Delta(\lambda))^{-1} \left[\begin{array}{c} \gamma_1 + DB(\overline{\phi}) \left(\int_0^1 e^{\lambda(t+\delta)} \psi_{CA}(s) \, ds\right) + \gamma(\lambda, \gamma_2) \end{array}\right] \end{cases}.
\end{cases}
\]

**Proof.** Let \(\lambda \in \Omega\) and \(\det(\Delta(\lambda)) \neq 0\). Then \((I - DF(\overline{\psi})(e^{\lambda t}(\lambda I - L)^{-1}))\) is invertible, and

\[
(I - DF(\overline{\psi})(e^{\lambda t}(\lambda I - L)^{-1}))^{-1} \begin{pmatrix} \delta_1 \\ \delta_2 \end{pmatrix} = \delta_Y,
\]

where

\[
\delta_Y = \begin{pmatrix} (\Delta(\lambda))^{-1}(\delta_1) + (\lambda, \delta_2) \end{pmatrix}.
\]
Thus, \((I - J(\lambda I - A)^{-1})\) is invertible, and
\[
(I - J(\lambda I - A)^{-1})^{-1} \begin{pmatrix} \gamma_Y \\ \psi_{CA} \end{pmatrix} = \begin{pmatrix} \delta_Y \\ \psi_{CA} \end{pmatrix},
\]
where \(\delta_Y\) is defined in (13). By Theorem 2.1, we obtain (12). Moreover, \(\{\lambda \in \Omega : \det(\Delta(\lambda)) \neq 0\} \subset \rho(A + J) \cap \Omega\), and \(\sigma(A + J) \cap \Omega \subset \{\lambda \in \Omega : \det(\Delta(\lambda)) = 0\}\).
Assume \(\lambda \in \Omega\) and \(\det(\Delta(\lambda)) = 0\). We claim that
\[
(A + J) \begin{pmatrix} 0 \\ \psi \end{pmatrix} = \lambda \begin{pmatrix} 0 \\ \psi \end{pmatrix}
\]
has no solution for \(\begin{pmatrix} 0 \\ \psi \end{pmatrix} \in D(A) \setminus \{0\}\) if and only if we can find \(\begin{pmatrix} \alpha \\ \varphi \end{pmatrix} \in Z \setminus \{0\}\) satisfying \([I - J(\lambda I - A)^{-1}] \begin{pmatrix} \alpha \\ \varphi \end{pmatrix} = 0\). From the above argument, this is also equivalent to find \(\begin{pmatrix} \alpha \\ \varphi \end{pmatrix} \neq 0\) such that
\[
\left\{ \begin{array}{l}
\Delta(\lambda)\alpha = 0, \\
\varphi = 0.
\end{array} \right.
\]
Since \(\det(\Delta(\lambda)) = 0\), the above equation always has non-trivial solution \(\alpha \neq 0\). Therefore, we can find \(\begin{pmatrix} 0 \\ \psi \end{pmatrix} \in D(A) \setminus \{0\}\) satisfying (14) and \(\lambda \in \sigma_p(A + J)\), which completes the proof.

5. Hopf bifurcation. In this section, we assume that \(\tau_1 = \tau_2 = \tau\). Under hypothesis of (H1), the characteristic equation turns into
\[
\det(\Delta(\lambda)) = \frac{\lambda^2 + \tau P \lambda + \tau^2 Q + \tau^2 We^{-\lambda} + (\tau S \lambda + \tau^2 R)e^{-2\lambda}}{\lambda^2 + \tau d} = 0,
\]
where
\[
P = \mu - r + \frac{2hr}{K(\eta M - 1)} + \frac{khr(\eta M - 1) - rh^2 + HK(\eta M - 1)^2}{\eta h MK},
Q = \mu \left[ -r + \frac{2hr}{K(\eta M - 1)} + \frac{khr(\eta M - 1) - rh^2 + HK(\eta M - 1)^2}{\eta h MK} \right],
W = \mu \left[ Khr(\eta M - 1) - rh^2 + HK(\eta M - 1)^2 \right],
S = -\mu, R = -Q
\]
Assume
\((H3)\) \(P + S > 0\);
\((H4)\) \(Q \neq 0\).
Let \(\lambda = \tau \zeta\). Then, \(f_1(\lambda) = 0\) leads to
\[
g(\zeta) = \zeta^2 + P \zeta + Q + We^{-\tau \zeta} + (S \zeta + R)e^{-2\tau \zeta} = 0,
\]
and \(\{\lambda \in \Omega : \det(\Delta(\lambda)) = 0\} = \{\tau \zeta \in \Omega : g(\zeta) = 0\}\). Recall that \(\beta^* = M\mu e^{\mu \tau}\). Then, the coefficient in (16) is delay-dependent. To avoid this, we further assume that \(\beta^* = ce^{\mu \tau}\) for some constant \(c > 0\). Since \(\beta^*\) is not involved in the coefficients in (16), we can employ the method proposed in [4] to seek the purely imaginary roots. When \(\tau = 0\), (16) is reduced to
\[
\zeta^2 + (P + S)\zeta + (Q + W + R) = 0.
\]
Since \( Q + W + R = W > 0 \), all the roots of (16) have strictly negative real parts whenever \( P + S > 0 \).

Suppose that \( \pm i\omega (\omega > 0) \) are a pair of purely imaginary roots of Eq. (16). Then \( \omega \) satisfies
\[
-\omega^2 + P\omega + Q + We^{-i\omega \tau} + (R + Si\omega)e^{-2i\omega \tau} = 0. \tag{17}
\]
Separating the real and imaginary parts, we find that
\[
\begin{align*}
\omega^2 + W - (R + Q) &\quad \theta^2 + 2(S - P)\omega \theta = \omega^2 - W - (R + Q), \\
(P + S)\omega \theta^2 + 2(\omega^2 + R - Q)\theta &\quad = (P + S)\omega.
\end{align*}
\tag{18}
\]
where \( \theta = \tan \frac{\omega \tau}{2} \). Moreover, \( \frac{\omega \tau}{2} \neq \frac{\pi}{2} + j\pi, j \in \mathbb{Z} \), otherwise (17) will implies \( P + S = 0 \), which contradicts to (H3). Let
\[
M = \begin{pmatrix}
\omega^2 + W - (R + Q) & 2(S - P)\omega \\
(P + S)\omega & 2(\omega^2 + R - Q)
\end{pmatrix},
\]
\[
M_1 = \begin{pmatrix}
\omega^2 + W - (R + Q) & 2(S - P)\omega \\
(P + S)\omega & 2(\omega^2 + R - Q)
\end{pmatrix},
\]
\[
M_2 = \begin{pmatrix}
\omega^2 - W - (R + Q) & 2(S - P)\omega \\
(P + S)\omega & 2(\omega^2 + R - Q)
\end{pmatrix},
\]
\[
M_3 = \begin{pmatrix}
\omega^2 + W - (R + Q) & \omega^2 - W - (R + Q) \\
(P + S)\omega & (P + S)\omega
\end{pmatrix},
\]
and
\[
D(\omega) = \det(M_1) = 2 \left[ \omega^4 + (P^2 - S^2 + W - 2Q)\omega^2 + Y(R - Q) + Q^2 - R^2 \right],
\]
\[
E(\omega) = \det(M_2) = 2 \left[ \omega^4 + (P^2 - S^2 - W - 2Q)\omega^2 - (Y + R + Q)(R - Q) \right],
\]
\[
F(\omega) = \det(M_3) = 2(P + S)W\omega > 0.
\tag{19}
\]
Suppose \( i\omega \) is a solution of (17) for some \( \tau \). Then, \( D(\omega) \neq 0 \), otherwise, it concludes that \( F(\omega) = 0 \) which is a contradiction. It follows from (18) that
\[
\theta^2 = \frac{E(\omega)}{D(\omega)}, \quad \theta = \frac{F(\omega)}{D(\omega)}.
\tag{20}
\]
which implies that \( \omega \) satisfies
\[
D(\omega)E(\omega) = F(\omega)^2. \tag{21}
\]
Simplifying (21) gives
\[
\omega^8 + s_1\omega^6 + s_2\omega^4 + s_3\omega^2 + s_4 = 0, \tag{22}
\]
where
\[
\begin{align*}
s_1 &= 2(P^2 - S^2 - 2Q), \\
s_2 &= (P^2 - S^2 - 2Q)^2 - W^2, \\
s_3 &= 4QW^2 - (P + S)^2 W^2, \\
s_4 &= -4Q^2 W^2.
\end{align*}
\]
Lemma 5.1. Assume that (22) has a positive root \( \omega^* \), and (H1)–(H4) hold. Then, (18) has a unique real root \( \theta^* \) when \( \omega = \omega^* \), and \( i\omega^* \) is a root of (16) if and only if
\[
\tau = \tau^j = \frac{2\arctan \theta^* + 2j\pi}{\omega^*}, \quad j \in \mathbb{Z}.
\tag{23}
\]
For θ ∈ (−∞, +∞), define
\[ G(ω, θ) := 2W(1 + θ^2) + 2R(1 - θ^2) + 4Sωθ[W(1 - θ^2) + (P - S)θ] - 2[Sω(1 - θ^2) - 2Rθ][(P + S)(1 - θ^2) - 4ωθ]. \] (24)

The Transversality condition can be verified by applying Lemma 2.10 in [4].

**Lemma 5.2.** Let \( ω^*, θ^* \) and \( τ_j \) be defined in Theorem 5.1. Then,
\[ \left. \frac{d\text{Re}λ(τ)}{dτ} \right|_{τ=τ_j} = \left. \frac{dα(τ)}{dτ} \right|_{τ=τ_j} \begin{cases} > 0, & G(ω^*, θ^*) > 0 \\ < 0, & G(ω^*, θ^*) < 0 \end{cases} \] (25)
for \( j \in \mathbb{Z} \).

**Theorem 5.3.** Assume that (22) has a positive root \( ω^* \), \( β^* = ce^{μτ} \) for some \( c > 0 \), and (H1) – (H4) hold. Let \( τ^* = \min\{τ_j\} \). Then, the following statements hold.
(1) If \( τ \in [0, τ^*) \), then the unique positive equilibrium \( (\bar{u}, \overline{V}) \) of (1) is locally asymptotically stable;
(2) If \( τ \in (τ^*, τ^* + ε) \) for sufficiently small \( ε > 0 \), the equilibrium \( (\bar{u}, \overline{V}) \) of (1) is unstable;
(3) If \( G(ω^*, θ^*) \neq 0 \), then Hopf bifurcation of (1) at \( (\bar{u}, \overline{V}) \) occurs when \( τ = τ^* \).

6. **Summary and numerical simulations.** In this section, numerical simulations are carried out to validate the theoretical results, obtained in Section 4. Choose \( μ = 0.4, r = 1, h = 2.4, K = 3, η = 1.2, M = 2, H = 2 \) and
\[ β(a) := \begin{cases} 0.8e^{0.4τ}, & a \geq τ, \\ 0, & a \in (0, τ). \end{cases} \]

Then, \( η > \frac{h + K}{KM} = 0.9, P + S \approx 1.0734 > 0, Q \approx 0.4294 > 0, \) and \( ω^* \approx 0.496. \) It follows from (23) that \( τ_0 \approx 5.2664 \) and \( τ_1 \approx 18.6464. \) Set \( τ = 3.5 < τ_0, V(0) = 1.5534 \) and \( u(0,a) = 2.6253e^{-0.4a} \). It is observed that the solution starting from \( V(0) \) and \( u(0,a) \) tends to the steady state. If the value of \( τ \) is increased to \( 6 > τ_0, \) then the solution will oscillate and converge to a periodic solution, which is generated through Hopf bifurcation, see Fig 1 and 2.

From Figs.1 and 2, we observe that the age-dependent equilibrium of the model is destabilized, as the maturation period and conception time are increased, leading to the undamped oscillating solutions. This reveals that the model dynamics is sensitive to the threshold \( τ. \)

In this paper, we investigate a predator-prey system with age structure and two delays. The initial model is formulated as an abstract non-densely defined Cauchy problem and the conditions which can guarantee the existence and uniqueness for positive age-dependent equilibrium are obtained. Then, we study the stability of the unique positive age-dependent equilibrium. By applying the theory of integrated semigroup and recently established Hopf bifurcation theory for abstract Cauchy problems, the existence of Hopf bifurcation at the positive steady state is investigated. The results show that a non-trivial periodic solution bifurcates from the positive equilibrium when the bifurcation parameter \( τ \) crosses the critical values \( τ_k (k = 0, 1, 2, \ldots) \). Here the bifurcating parameter \( τ \) might be taken as a measure of a biological maturation period or a time lag between conception and birth.
Figure 1. A solution of (1) that tends to the positive steady states when \( \tau = 3.5 < \tau_0 \)

Figure 2. For \( \tau = 6 > \tau_0 \), the solution will oscillate periodically.

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