A PREY-PREDATOR MODEL WITH MIGRATIONS AND DELAYS

**ISAM AL-DARABSAH**\(^a\), **XIANHUA TANG**\(^b\) AND **YUAN YUAN**\(^a,b,\)†

\(^a\)Department of Mathematics and Statistics
Memorial University of Newfoundland
St. John’s NL, A1C 5S7, Canada
\(^b\)School of Mathematics and Statistics
Central South University
Changsha, Hunan 410083, China

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**Abstract.** In this paper we propose a prey-predator model in multiple patches through the stage structured maturation time delay with migrations among patches. Focus on the case with two patches, we discuss the existence of equilibrium points and the uniform persistence. In particular, when the maturation times are the same in the patches, we study the local and global attractivity of boundary equilibrium point with general migration function and the local stability of the positive equilibrium with constant migration rate. Numerical simulations are provided to demonstrate the theoretical results, to illustrate the effect of the maturation time, the migration rate on the dynamical behavior of the system.

1. **Introduction.** The prey-predator relationship is prevalent in the nature and hence it is one of the major themes in mathematical models. In the 1920s A. Lotka and V. Volterra formulated the original model to describe the prey-predator interactions. Since then, different prey-predator models have been built by incorporating additional biological processes into the classical Lotka-Volterra model \([2, 6, 8–10, 15, 17, 18, 20, 22, 23, 32, 36, 37]\). For instance, in \([8]\), the authors studied the dynamics of a diffusive prey-predator system with Allee effects in the prey growth. In \([15]\), a prey-predator model with a consideration of the prey refuge has been studied. It is well-known that some kind of time delays are unavoidable in prey-predator population and they can affect the stability of equilibrium points \([19]\). In \([6]\), the authors presented a stage-structured predator prey model with gestation delay. A delay prey-predator system without instantaneous negative feedback has been studied in \([32]\). The authors in \([37]\) considered a class of delayed Lokta-Volterra prey-predator model with two delays. Time delay due to maturation of the predator is inescapable since the juvenile predators usually live on their parents until they become mature, or on a resource that is not wanted by adults and available

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\)

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\(^†\) Corresponding author: yyuan@mun.ca.
in abundance. The effect of maturation delay on the behavior of populations has been studied in [12].

In prey-predator system with multi-patch environment, migration occurs when a species moves from its patch to another due to different factors like competition, age, sex, lack of food, climate and the season which make it one of the prevalent phenomena in nature [26]. For example, in aquatic environments, many zooplankton species exhibit vertical movements each day due to light and food. During the day time, some species migrate downwards into the darkness to reduce the risk of predation by fish, while at night time, these species move upward to consume the phytoplankton [4, 24]. Empirical studies have shown that the interaction between patches has important consequences for population stability and persistence e.g. [11, 31, 33]. The influence of such interaction, migration, capture scientists’ attention in the communities. Some researchers considered different migration rates for both predator and prey species. For instance, the authors constructed a two patches model with migration of both the predator and the prey in [10], and assumed the migration of the predator depend on the population of the prey in each patch, while the prey migration is in a constant rate. They found upper and lower bounds for the populations and discussed the stability and instability of the positive and boundary equilibrium points. In [17], a model was provided with two patches where the prey does not migrate and the predator in the patch with a higher density will migrate to the patch with a lower density. In [22], it was assumed that the predator migrates with a constant migration rate, while the prey migration depends on the predator density, the authors proved the existence of a unique strictly positive equilibrium. In [2], it was assumed that the prey (predator) migration rate depend on the predator (prey) density and showed that for a large class of density-dependent migration rules there exists a unique and stable equilibrium for migration.

To the best of our knowledge, there is not so many result in the literature in the research of joined consideration of migration and time delay in biological models. Introducing time delays to prey-predator models usually brings challenges to the mathematical analysis and may change the dynamics. In [36], a model with two prey and one predator population, time delay due to gestation and constant prey migration rate was investigated. The authors discussed the persistence, derived conditions for the existence and local/global stability of the positive equilibrium. All the models studied in [2, 10, 17, 22] have not considered the influence of time delay in any evolution stage although migrations were collaborated. In this paper, we propose a general model with multiple parallel patches which combined the migration interactions among all patches and constant maturation time delay through stage structure. Following the biological feasibility, we take general functional responses with respect to migration rates in both prey and predator classes to allow a unified treatment for all biological important cases. From the viewpoint of dynamics, we analyze the model with proving the positivity and boundedness of the solutions, local stability of the steady states, global attractivity of boundary equilibrium point and uniform persistence of the system. Then, we give numerical simulations to show the theoretical results and to see how the dynamical behavior is sensitive to the maturation time of predator, the migration rates in prey and predator.

The paper is organized as follows: in Section 2, a general model of multiple parallel prey-predator patches with migration of both species is studied. When the model contains two patches, we provide conditions for the uniform persistence, discuss the
A model of multiple parallel prey-predator patches with migration and maturation delays. In previous work [3], we studied a model including multiple parallel food chains, each consisting of a prey species $P_i$ and its dedicated predator $Z_i$, with maturation delay and without interaction between patches. In this paper we consider the interaction between patches, assume all $P_i$ compete for limiting nutrient, only adult predators are capable of preying on the prey species and propose a more complex model for the multi-patch prey-predator system, with prey (predator) migration rates depending on the corresponding predator (prey) density:

\[
\frac{dP_i}{dt} = P_i[\mu_i(N) - Z_i h_i(P_i)] + \sum_{k=1}^{n} P_k f_{ki}(Z_k) - \sum_{k=1}^{n} P_i f_{ik}(Z_i),
\]

\[
\frac{dZ_i}{dt} = b_i e^{-d_i \tau_i} P_i(t - \tau_i) Z_i(t - \tau_i) h_i(P_i(t - \tau_i)) - Z_i \epsilon_i \left( \sum_{k=1}^{n} Z_k \right) + \sum_{k=1}^{n} Z_k g_{ki}(P_k) - \sum_{k=1}^{n} Z_i g_{ik}(P_i),
\]

where $i = 1, \ldots, n$, $\mu_i(N)$ is the growth rate of $P_i$ as a function of nutrient concentration $N = T - \sum_{k=1}^{n} \alpha_k P_k - \sum_{k=1}^{n} \beta_k Z_k \geq 0$, with the coefficients $\alpha_k, \beta_k, (k = 1, \ldots, n)$ related to the efficiency of nutrient consuming for each species. The author in [5] used the form $N = T - \sum_{i=1}^{n} P_i - \sum_{i=1}^{n} Z_i$ which treats the consuming abilities for all the species equally. As we know that in natural world, different species may have different strength in taking nutrient, so to be more realistic, we give different weight on nutrient consumption for the species. The constant parameter $T$ is the internal nutrient supply, $h_i(P_i)$ is the per-prey-per-predator harvest rate of $P_i$ by $Z_i$ and $\epsilon_i \left( \sum_{j=1}^{n} Z_j \right)$ is predation on the $i$th predator by higher trophic levels which is assumed to be proportional to the total predator $\sum_{j=1}^{n} Z_j$ (see [5]); $b_i$ denotes the adult predator’s birth rate, $d_i$ is the mortality death rate of the juvenile (through-stage death rate), $\tau_i$ is time to mature and $f_{ij}(Z_i) (g_{ij}(P_i))$, $j = 1, \ldots, n$ and $i \neq j$, represents the migration rate for prey (predator) from patch $i$ to patch $j$. All the parameters are positive constants. An architecture of the model (1) with 3 patches is given in Fig. 1.

From the biological point of view, we assume all the functions in (1) are continuous and differentiable over $\mathbb{R}_+$, and satisfy the following hypotheses for $i, j = 1, \ldots, n$ with $i \neq j$:

(C1) $\mu_i(0) = 0$, \quad $\frac{d\mu_i}{dN} > 0$ when $N \in (0, T)$;

(C2) $h_i(P_i) \geq 0$, \quad $\frac{d(P_i h_i(P_i))}{dP_i} > 0$, \quad $0 \leq P_i h_i(P_i) \leq M_i$, $M_i$ is a constant;
\[ \frac{\partial \epsilon_i(Z)}{\partial Z_k} \geq 0 \] for each \( Z_k \) in \( Z = \sum_{k=1}^{n} Z_k \);

\( f_{ij}(Z_i) > 0 \) with \( f_{ij}(0) = \gamma_0 \) and \( \frac{df_{ij}}{dZ_i} \geq 0 \) for \( Z_i \in (0, \frac{T}{\beta_i}) \);

\( g_{ij}(P_i) > 0 \) and \( \frac{dg_{ij}}{dP_i} \leq 0 \) for \( P_i \in (0, \frac{T}{\alpha_i}) \).

The assumptions of \((C_1), (C_2)\) and \((C_3)\) are biologically obvious, \((C_4)\) and \((C_5)\) indicate that the preys escape from a patch more actively when more predators are in the same patch, while if more preys stay in a patch, the movement of the predator to other patch is inactive.

The general model (1) can cover several general, partial general and specific models in literature with some particular choice of the functions. To name only a few models with two patches without time delay, the system in [20] is a special model of (1) with \( \mu(N) = \mu(P) \), \( h(P) = \frac{h(P)}{\tau} \), \( g(P) = 0 \); when we take \( \mu(N) = r(1 - \frac{P}{K}) \), \( h(P) = \frac{h(P)}{\tau + P} \), \( g(P) = \frac{d}{\tau + P} \), \( \epsilon(Z) \) and \( f(Z) \) are constant, the model (1) is the same as that in [10]; When one choose \( f_{ij}(Z) = \beta_i Z + \beta_0 \) and \( g_{ij} \) as constant, the migration terms in (1) become the fast model in [22]; while we restrict \( f \) and \( g \) with \( \frac{df}{dZ} > 0 \) and \( \frac{dg}{dP} < 0 \), then the migration terms in (1) become the fast model in [2].

Let \( \tau = \max \{ \tau_i, i = 1, \ldots, n \} \) and define \( C := C([-\tau, 0), \mathbb{R}^{2n}) \). For \( \phi = (\phi_1, \ldots, \phi_{2n}) \in C \), define \( \| \phi \| = \sum_{i=1}^{2n} \| \phi_i \|_\infty \) where

\[ \| \phi_i \|_\infty = \max_{\theta \in [-\tau, 0]} |\phi_i(\theta)|. \]

Then \( C \) is a Banach space and \( C^+ = C([-\tau, 0), \mathbb{R}^{2n}) \) is a normal cone of \( C \) with nonempty interior in \( C \). We have the following result for the positivity and boundedness properties of the system (1).

**Theorem 2.1**. If the initial condition \((P_1(0), Z_1(0), \ldots, P_n(0), Z_n(0)) \in C^+ \), then the solutions of (1) are nonnegative in \( C \). In addition, if \( \epsilon_i(0) > 0 \) for each \( i = 1, \ldots, n \) then all the solutions are ultimately bounded in \( C \).
Proof. When $n = 2$ the system (1) becomes
\begin{align*}
\frac{dP_1}{dt} &= P_1[\mu_1(N) - Z_1 h_1(P_1)] + P_2 f_{21}(Z_2) - P_1 f_{12}(Z_1), \\
\frac{dZ_1}{dt} &= b_1 e^{-\sigma_1} P_1(t - \tau_1)Z_1(t - \tau_1)h_1(P_1(t - \tau_1)) - Z_1 \epsilon_1(Z_1 + Z_2) \\
&+ Z_2 g_{21}(P_2) - Z_1 g_{12}(P_1), \\
\frac{dP_2}{dt} &= P_2[\mu_2(N) - Z_2 h_2(P_2)] + P_1 f_{12}(Z_1) - P_2 g_{21}(Z_2), \\
\frac{dZ_2}{dt} &= b_2 e^{-\sigma_2} P_2(t - \tau_2)Z_2(t - \tau_2)h_2(P_2(t - \tau_2)) - Z_2 \epsilon_2(Z_1 + Z_2) \\
&+ Z_1 g_{12}(P_1) - Z_2 g_{21}(P_2),
\end{align*}
\tag{2}

with $N = T - \alpha_1 P_1 - \alpha_2 P_2 - \beta_1 Z_1 - \beta_2 Z_2$. It is straightforward that the solution of (2) exists and is unique with initial value in $C^+$ and $P_i(t) \geq 0$ and $Z_i(t) \geq 0$, $i = 1, 2$ for all $t > 0$ (Theorem 5.2.1 in [29]).

Further, from the first and third equations in (2), and the fact that $\mu_i(N)$ is increasing, we have
\[
P'_1 + P'_2 = P_1[\mu_1(N) - Z_1 h_1(P_1)] + P_2[\mu_2(N) - Z_2 h_2(P_2)] \\
\leq (P_1 + P_2) \tilde{\mu}(T - \tilde{\alpha}(P_1 + P_2)),
\]
where $\tilde{\mu}(\cdots) = \max\{\mu_1(\cdots), \mu_2(\cdots)\}$ and $\tilde{\alpha} = \min\{\alpha_1, \alpha_2\}$. In the remain of the paper, we denote $\tilde{\cdot}, \tilde{\cdot}$ as min and max, respectively. Since $\tilde{\mu}(0) = 0$, we know $\lim_{t \to \infty} (P_1 + P_2) \leq T/\tilde{\alpha}$, implying $P_1(t) + P_1(t)$ is ultimately bounded.

Let $P(t) = P_1(t) + P_2(t), Z(t) = Z_1(t) + Z_2(t)$ and
\[
S(t) = \bar{b}^2 e^{-2\sigma t} (P(t + \tau_1) + P(t + \tau_2)) + \bar{b} e^{-\sigma t} Z(t),
\]
we can obtain
\[
S'(t) \leq \bar{b}^2 e^{-2\sigma t} P_1(t - \tau_1) \mu_1(N_1) + \bar{b}^2 e^{-2\sigma t} P_2(t - \tau_1) \mu_2(N_1) \\
+ \bar{b}^2 e^{-2\sigma t} P_1(t - \tau_2) \mu_1(N_2) + \bar{b}^2 e^{-2\sigma t} P_2(t - \tau_2) \mu_2(N_2) \\
- \bar{b} e^{-\sigma t} Z_1(t) \epsilon_1(Z_1(t) + Z_2(t)) - \bar{b} e^{-\sigma t} Z_2(t) \epsilon_2(Z_1(t) + Z_2(t)),
\]
where $N_i = T - \alpha_1 P_i(t - \tau_i) - \alpha_2 P_2(t - \tau_i) - \beta_1 Z_1(t - \tau_i) - \beta_2 Z_2(t - \tau_i), i = 1, 2$. From the hypotheses (C1),(C3), we have $\mu_i(N_j) \leq \mu_i(T)$ and $\epsilon_i(Z_1 + Z_2) \geq \epsilon_i(0)$ for $i, j = 1, 2$. Hence,
\[
S'(t) \leq \bar{b}^2 e^{-2\sigma t} \tilde{\mu}(T)(P(t - \tau_1) + P(t - \tau_2)) \\
+ \bar{b}^2 e^{-2\sigma t} \hat{\epsilon}(0)(P(t - \tau_1) + P(t - \tau_2)) \\
- \hat{\epsilon}(0) \left(\bar{b}^2 e^{-2\sigma t}(P(t - \tau_1) + P(t - \tau_2)) + \bar{b} e^{-\sigma t} Z(t)\right) \\
\leq \frac{T \bar{b}^2 e^{-2\sigma t}}{\hat{\alpha}} (\tilde{\mu}(T) + \hat{\epsilon}(0)) - \hat{\epsilon}(0) S(t).
\]
If $\hat{\epsilon}(0) > 0$ then $\lim_{t \to \infty} S(t) \leq \frac{T \bar{b}^2 e^{-2\sigma t}}{\hat{\alpha}} (\tilde{\mu}(T) + \hat{\epsilon}(0))$. Therefore, $P_1(t), P_2(t), Z_1(t)$ and $Z_2(t)$ are ultimately bounded in $C$.

With general $n$, the idea is similar by using mathematical induction. \hfill \square

**Remark 1.** Theorem 2.1 implies that there exists $t_\ell > 0$, $L_P > 0$ and $L_Z > 0$ such that $0 \leq \sum_{i=1}^n P_i(t) \leq L_P$ and $0 \leq \sum_{i=1}^n Z_i(t) \leq L_Z$ for $t > t_\ell$.  


Obviously the system (1) has a trivial equilibrium point \( E_0 = (0, 0, \ldots, 0, 0) \). In addition, we have

**Proposition 1.** Given the hypothesis \((C_1 - C_5)\), then a unique predator-free equilibrium point

\[
\tilde{E} = \left( \frac{T}{\sum_{i=1}^{n} \alpha_i}, \ldots, \frac{T}{\sum_{i=1}^{n} \alpha_i}, 0 \right)
\]

exists in (1).

**Proof.** When \( n = 2 \) and \( Z_1 = Z_2 = 0 \). A predator-free equilibrium point must satisfy

\[
P_1 \mu_1 (T - \alpha_1 P_1 - \alpha_2 P_2) + f_{21}(0) P_2 - f_{12}(0) P_1 = 0,
\]

\[
P_2 \mu_2 (T - \alpha_1 P_1 - \alpha_2 P_2) + f_{12}(0) P_1 - f_{21}(0) P_2 = 0.
\]

Since \( f_{12}(0) = f_{21}(0) = \gamma_0 \), it is easy to check that \( \tilde{E} \) satisfies (3).

To prove the uniqueness of such \( \tilde{E} \), it’s easy to see that when one of \( P_i, (i = 1, 2) \) is zero, another one must be zero as well, which excludes the case with one prey species can survive and another cannot.

Further, adding two equations in (3) yields

\[
P_1 \mu_1 (T - \alpha_1 P_1 - \alpha_2 P_2) + P_2 \mu_2 (T - \alpha_1 P_1 - \alpha_2 P_2) = 0.
\]

When \( P_1 > 0 \), due to \( \mu_i \geq 0, (i = 1, 2) \), we have \( \alpha_1 P_1 + \alpha_2 P_2 = T \). Substituting into (3), we obtain \( P_1 = P_2 = \frac{T}{\alpha_1 + \alpha_2} := T \). Consequentially, we have \( N = 0 \) at \( \tilde{E} \).

Again, by mathematical induction method the result hold for a general \( n \). \( \square \)

**Remark 2.** With migrations between patches, only one positive predator-free equilibrium point exists for system (1). But without migration, the system has infinite number of predator-free equilibrium points with the form

\[
\hat{E} = \left( \alpha_1 \tilde{P}_1, 0, \alpha_2 \tilde{P}_2, 0, \ldots, \alpha_n \tilde{P}_n, 0 \right)
\]

with \( \sum_{k=1}^{n} \alpha_i \tilde{P}_k = T \) in [3]. The result in Proposition 1 implies the effect of migrations.

To study the stability of each equilibrium point \((x_1, y_1, x_2, y_2, \ldots, x_n, y_n)\), we can obtain the general form of the characteristic equation, which is,

\[
\Delta (\lambda) = \det \left( \lambda I - J^0 - \sum_{k=1}^{n} J^k e^{-\lambda \tau_k} \right) = 0
\]

where \( J^0 = (a_{ij}) \) and \( J^k = (c_{ij}^k) \) are \( 2n \times 2n \) matrices with
Thus one positive real root, implying \( \overline{\lambda} \) exists.

Proof. By Theorem 2.2.

Let \( h(x) = x^{n+1} - \sum_{k=1}^{n} a_{nk} x^k \), where \( n = 1 \text{ or } n = 2 \), and assume all the roots in \( \Delta(\lambda) = 0 \) have negative real parts, then

\[
\Delta(\lambda) = \lambda^n + \sum_{k=1}^{n} a_{nk} \lambda^{n-k} = 0,
\]

where \( \overline{\lambda} = T - \sum_{k=1}^{n} a_{nk} x^k \) and

\[
c_{ij} = \begin{cases} 
0 & \text{if odd, any } j; \text{ or } i \text{ even, } j \neq 2k, j \neq 2k - 1; \\
b_k e^{-\epsilon_k x_k} h_k(x_k) + x_k h'_k(x_k) & \text{if } i = 2k, j = 2k - 1; \\
b_k e^{-\epsilon_k x_k} x_k h_k(x_k) & \text{if } i = 2k, j = 2k.
\end{cases}
\]

Due to the complexity of the construction in the characteristic equation with delay, we only discuss the stability of boundary equilibrium points when \( n = 2 \).

**Theorem 2.2.** \( E_0 \) is always an unstable steady state.

**Proof.** The linearization of (2) at \( E_0 \) is

\[
\begin{align*}
x_1'(t) &= (\mu_1(T) - \gamma_0) x_1(t) + \gamma_0 x_2(t), \\
y_1'(t) &= -(\epsilon_1(0) + g_{12}(0)) y_1(t) + g_{21}(0) y_2(t), \\
x_2'(t) &= \gamma_0 x_1(t) + (\mu_2(T) - \gamma_0) x_2(t), \\
y_2'(t) &= g_{21}(0) y_1(t) - (\epsilon_2(0) + g_{21}(0)) y_2(t).
\end{align*}
\]

(4)

The characteristic equation of (4) is

\[
\Delta(\lambda) = (\lambda^2 + \epsilon_1(0) + \epsilon_2(0) + g_{12}(0) + g_{21}(0)) \lambda + \epsilon_1(0) \epsilon_2(0) + g_{12}(0) \epsilon_2(0) + g_{21}(0) \epsilon_1(0).
\]

Let

\[
h(\lambda) = \lambda^2 + (2\gamma_0 - \mu_1(T) - \mu_2(T)) \lambda + \mu_1(T) \mu_2(T) - \gamma_0 (\mu_1(T) + \mu_2(T)).
\]

\( h(\lambda) = 0 \) has real roots since the discriminant of \( h(\lambda) \) is \( 4\gamma_0^2 + (\mu_1(T) - \mu_2(T))^2 > 0 \). Assume all the roots in \( h(\lambda) = 0 \) have negative real parts, then

\[
2\gamma_0 - \mu_1(T) - \mu_2(T) > 0 \text{ and } \mu_1(T) \mu_2(T) - \gamma_0 (\mu_1(T) + \mu_2(T)) > 0,
\]

which is equivalent to

\[
\gamma_0 > \frac{\mu_1(T) + \mu_2(T)}{2} \quad \text{and} \quad \frac{\mu_1(T) \mu_2(T)}{\mu_1(T) + \mu_2(T)} > \gamma_0.
\]

Thus \( \frac{2\mu_1(T) \mu_2(T)}{(\mu_1(T) + \mu_2(T))^2} \) leads to a contradiction. Therefore \( h(\lambda) = 0 \) has at least one positive real root, implying \( E_0 \) is unstable steady state. \( \square \)
Remark 3. We can conjecture that $E_0 = (0, 0, \ldots, 0)$ is unstable when $n \geq 3$, although we can only prove the result when all the functions $\mu_i(N)$ are the same, $\mu_i(N) = \mu(N)$, and all the prey (predictor) migration rates are same constant $f_j(Z_i) = m (g_{ij}(R_i) = s)$. In this case the characteristic equation at $E_0$ is $\Delta(\lambda) = \det(A)\det(B) = 0$ where

$$
A = \begin{vmatrix}
\lambda - \mu(T) + (n - 1)m & -m & \cdots & -m \\
-m & \lambda - \mu(T) + (n - 1)m & \cdots & -m \\
\vdots & \vdots & \ddots & \vdots \\
-m & -m & \cdots & \lambda - \mu(T) + (n - 1)m 
\end{vmatrix}
$$

and

$$
B = \begin{vmatrix}
\lambda + \epsilon_1(0) + (n - 1)s & -s & \cdots & -s \\
-s & \lambda + \epsilon_2(0) + (n - 1)s & \cdots & -s \\
\vdots & \vdots & \ddots & \vdots \\
-s & -s & \cdots & \lambda + \epsilon_n(0) + (n - 1)s 
\end{vmatrix}
$$

It is easy to show that all the roots of $\det(B) = 0$ are negative real roots by using Gershgorin circle theorem in [27] and the symmetry of $B$. While $\det(A) = (\lambda - \mu(T))(\lambda - \mu(T) + nm)^{n-1} = 0$ has a positive real root $\lambda = \mu(T)$, which means $E_0$ is unstable. When $\mu(T) < nm$, $E_0$ is a saddle point; and if $\mu(T) > nm$, it is a source.

To discuss the stability of the predator-free equilibrium point $\tilde{E} = (\mathcal{T}, 0, \mathcal{T}, 0)$, we introduce the following result given in [19] to discuss the global attractivity of $\tilde{E}$.

Lemma 2.3. In a delay system

\[
\begin{cases}
u'(t) = au(t - \tau) - bu(t), \\
u(t) = \phi(t) > 0, \quad -\tau \leq t \leq 0,
\end{cases}
\]

where $a, b, \tau > 0$, the following results hold

(i) if $a < b$, then $\lim_{t \to \infty} u(t) = 0$.

(ii) if $a > b$, then $\lim_{t \to \infty} u(t) = \infty$.

For the special case with $\tau_1 = \tau_2 := \tau$, we know $\tilde{E}$ is globally attractive under certain condition, which is given in the following theorem.

Theorem 2.4. Assume $\tau_1 = \tau_2 := \tau > 0$. When $\dot{b}T\dot{h}(\mathcal{T})e^{-\delta \tau} < \dot{\epsilon}(0)$ then the solutions of (2) satisfy $P_i(t) \to \mathcal{T}$ and $Z_i(t) \to 0$, $i = 1,2$.

Proof. Adding the second and the forth equations in (2), we have

\[
Z_1' + Z_2' = b_1e^{-d_{1\tau}}P_1(t - \tau)h_1(P_1(t - \tau))Z_1(t - \tau) - \epsilon_1(Z_1 + Z_2) + b_2e^{-d_{2\tau}}P_2(t - \tau)h_2(P_2(t - \tau))Z_2(t - \tau) - \epsilon_2(Z_1 + Z_2).
\]

Let $\delta > 0$. Following the hypotheses $(C_1)$ and $(C_3)$, we have $\epsilon_i(Z_1 + Z_2) \geq \dot{\epsilon}(0)$ and $P_i(t - \tau)h_i(P_i(t - \tau)) \leq T h_i(\mathcal{T})$ for any $t > t_0 + \tau$. Thus

\[
Z_1' + Z_2' \leq \dot{b}T\dot{h}(\mathcal{T})e^{-\delta \tau}(Z_1(t - \tau) + Z_2(t - \tau)) - \dot{\epsilon}(0)(Z_1(t) + Z_2(t))
\]
The comparison theory implies that \( Z_1(t) + Z_2(t) \) is bounded above by the solution of
\[
u'(t) = \bar{b} T h(T) e^{-\bar{c} \tau} u(t - \tau) - \dot{\epsilon}(0) u(t), \quad t > t_\delta + \tau
\]
such that \( u(t) = Z_1(t) + Z_2(t) \) for \( t \in [t_\delta, t_\delta + \tau] \). When
\[
\bar{b} T h(T) e^{-\bar{c} \tau} < \dot{\epsilon}(0),
\]
from Lemma 2.3, we have \( \lim_{t \to \infty} (Z_1(t) + Z_2(t)) = 0 \). Since both \( Z_1(t) \) and \( Z_2(t) \) are nonnegative from Theorem 2.1, we have \( \lim_{t \to \infty} Z_i(t) = 0, \ i = 1, 2 \).

By the existences and uniqueness of the predator-free equilibrium point \( \tilde{E} \) in Proposition 1 and Remark 2, we obtain \( \lim_{t \to \infty} P_i(t) = \mathcal{T}, \ i = 1, 2 \).

In general, beyond the strong condition \( \bar{b} T h(T) e^{-\bar{c} \tau} < \dot{\epsilon}(0) \) and/or with two different delays \( \tau_1, \tau_2 \), we can discuss the local stability of \( \tilde{E} \) by setting \( x_1 = P_1 - \mathcal{T}, \ y_1 = Z_1, x_2 = P_2 - \mathcal{T} \) and \( y_2 = Z_2 \). Then the linearization of (2) at \( \tilde{E} \) is
\[
\begin{align*}
x'_1(t) &= a_{11} x_1(t) + a_{12} y_1(t) + a_{13} x_2(t) + a_{14} y_2(t), \\
y'_1(t) &= a_{22} y_1(t) + a_{23} y_2(t) + b_{22} y_1(t - \tau_1), \\
x'_2(t) &= a_{31} x_1(t) + a_{32} y_1(t) + a_{33} x_2(t) + a_{34} y_2(t), \\
y'_2(t) &= a_{42} y_1(t) + a_{44} y_2(t) + c_{44} y_2(t - \tau_2),
\end{align*}
\]
(5)
where
\[
\begin{align*}
a_{11} &= -\alpha_1 \mathcal{T} \mu_1'(0) - \gamma_0 < 0, & a_{12} &= -\beta_1 \mathcal{T} \mu_1'(0) - \mathcal{T} \tau_1 h_1(T) - \mathcal{T} f_{12}'(0) < 0, \\
a_{13} &= -\alpha_2 \mathcal{T} \mu_2'(0) + \gamma_0, & a_{14} &= -\beta_2 \mathcal{T} \mu_1'(0) + \mathcal{T} f_{21}'(0), \\
a_{22} &= -\epsilon_1(0) - g_{12}(T) < 0, & a_{23} &= g_{21}(T) > 0, & b_{22} &= b_1 e^{-\tau_1 d_1} \tau_1 h_1(T) > 0, \\
a_{31} &= -\alpha_1 \mathcal{T} \mu_2'(0) + \gamma_0, & a_{32} &= -\beta_1 \mathcal{T} \mu_2'(0) + \mathcal{T} f_{12}'(0), \\
a_{33} &= -\alpha_2 \mathcal{T} \mu_2'(0) - \gamma_0 < 0, & a_{34} &= -\beta_2 \mathcal{T} \mu_2'(0) - \mathcal{T} h_2(T) - \mathcal{T} f_{21}'(0) < 0, \\
a_{42} &= g_{12}(T) > 0, & a_{44} &= -\epsilon_2(0) - g_{21}(T) < 0, & c_{44} &= b_2 e^{-\tau_2 d_2} \tau_2 h_2(T) > 0.
\end{align*}
\]
The characteristic equation of (5) is
\[
\Delta(\lambda, \tau_1, \tau_2) = G(\lambda) K(\lambda, \tau_1, \tau_2) = 0,
\]
(6)
with
\[
\begin{align*}
G(\lambda) &= \lambda^2 - (a_{11} + a_{33}) \lambda + a_{11} a_{33} - a_{13} a_{31}, \\
K(\lambda, \tau_1, \tau_2) &= (\lambda - a_{22} - b_{22} e^{-\lambda \tau_1}) (\lambda - a_{44} c_{44} e^{-\lambda \tau_2} - a_{44} a_{42}).
\end{align*}
\]

It is easy to check that \( G(\lambda) = 0 \) has two roots with negative real part, since both \(- (a_{11} + a_{33}) > 0 \) and \( a_{11} a_{33} - a_{13} a_{31} - \gamma_0 \mathcal{T} (a_1 + c_2) (\mu_1(0) + \mu_2(0)) > 0 \). So we only need to discuss the distribution of roots in \( K(\lambda, \tau_1, \tau_2) = 0 \).

In the stability analysis, we are more interested in the influence of the key parameters, functions including the migration rates \( f_{ij}, g_{ij} \) and the time delays \( \tau_i \) \( i = 1, 2 \). We notice that \( K(\lambda, \tau_1, \tau_2) \) is independent of the prey migration rates \( f_{ij} \), so the prey migrations do not affect the stability of the predator-free equilibrium point \( \tilde{E} \). On the other hand, if there is no predator migration, i.e. \( g_{ij} = 0 \), \( \tilde{E} \) is locally asymptotically stable if \( b_k T h_k(T) e^{-d_k \tau_k} < \epsilon_k(0) \) \( k = 1, 2 \) in [3]: but with general predator migration, the stability at \( \tilde{E} \) becomes complicated. In the following, we focus on the stability with respect to time delay only and we will investigate the influence of migration rates numerically.
More specifically, \( K(\lambda, \tau_1, \tau_2) \) can be written as
\[
K(\lambda, \tau_1, \tau_2) = \lambda^2 + k_1\lambda + k_2 + e^{-\lambda\tau_1} (k_3\lambda + k_4) + e^{-\lambda\tau_2} (k_5\lambda + k_6) + k_7e^{-\lambda(\tau_1 + \tau_2)},
\]
where
\[
k_1 = -(a_{22} + a_{44}) > 0, \quad k_2 = a_{22}a_{44} - a_{24}a_{42} > 0, \quad k_3 = -b_{22} < 0,
\]
\[
k_4 = b_{22}a_{44} < 0, \quad k_5 = -c_{44} < 0, \quad k_6 = c_{44}a_{22} < 0, \quad k_7 = b_{22}c_{44} > 0.
\]
From \( K(\lambda, 0, 0) = \lambda^2 + (k_1 + k_3 + k_5)\lambda + (k_2 + k_4 + k_6 + k_7) \),
following the Routh-Hurwitz stability criterion we have

**Proposition 2.** At \( \tau_1 = \tau_2 = 0 \), the predator-free equilibrium point \( \tilde{E} \) is locally asymptotically stable if and only if
\[
k_1 + k_3 + k_5 > 0 \land k_2 + k_4 + k_6 > 0. \quad (H_1)
\]

With \( \tau_1, \tau_2 > 0 \), first, we consider a simple case \( \tau_1 = \tau_2 := \tau > 0 \), Eq. (7) becomes
\[
K(\lambda, \tau) = \lambda^2 + k_1\lambda + k_2 + (k_3 + k_5)\lambda e^{-\lambda\tau} + (k_4 + k_6) e^{-\lambda\tau} + k_7 e^{-2\lambda\tau}. \quad (9)
\]
Then, for a pure imaginary root of (9), let \( \lambda = i\omega, \omega > 0 \), then separate the real and imaginary parts to obtain
\[
\begin{align*}
\omega^2 - k_2 &= (k_3 + k_5)\omega \sin \omega \tau + (k_4 + k_6) \cos \omega \tau + k_7 \cos 2\omega \tau \\
\omega \kappa &= -(k_3 + k_5)\omega \cos \omega \tau + (k_4 + k_6) \sin \omega \tau + k_7 \sin 2\omega \tau. \quad (10)
\end{align*}
\]
Squaring and adding both equations of (10) lead to
\[
\omega^4 - \left[2k_2 + (k_3 + k_5)^2 - k_1^2\right] \omega^2 + \left[k_2^2 - (k_4 + k_6)^2 - k_7^2\right] \]
\[
= 2(k_4 + k_6)k_7 \cos \omega \tau - 2\omega (k_3 + k_5)k_7 \sin \omega \tau,
\]
\[
\leq -2(k_4 + k_6)k_7 - 2\tau(k_3 + k_5)k_7 \omega^2, \quad (11)
\]
since \( k_7 > 0, (k_4 + k_6) < 0, (k_3 + k_5) < 0, \omega > 0 \). (11) is equivalent to
\[
\omega^4 - \left[2k_2 + (k_3 + k_5)^2 - k_1^2 - 2\tau(k_3 + k_5)k_7\right] \omega^2 + \left[k_2^2 - (k_4 + k_6 - k_7)^2\right] \leq 0.
\]
From the latter inequality we know that if
\[
2k_2 + (k_3 + k_5)^2 - k_1^2 - 2\tau(k_3 + k_5)k_7 < 0 \quad (12)
\]
and
\[
(k_4 + k_6 - k_7)^2 > 0, \quad (13)
\]
then there is no such \( \omega > 0 \). In addition, if \( K(0, \tau) = k_2 + k_7 + k_4 + k_6 \neq 0 \), then (9) has no roots with zero real part. Related to the time delay, we have,

**Theorem 2.5.** Assume \( \tau_1 = \tau_2 := \tau > 0 \) and
\[
A = \left(\frac{c_2(0) + g_{21}(T)}{\epsilon_1(0)}\right) b_1 T h_1(T) + \left(\frac{c_1(0) + g_{12}(T)}{\epsilon_1(0)}\right) b_2 T h_2(T) + \left(\frac{b_1 b_2 T}{\epsilon_1(0)}\right) h_1(T) h_2(T).
\]
Let
\[
\bar{e} = \left(\frac{c_1(0) + c_2(0) + g_{12}(T) + g_{21}(T)}{4b_2 b_2 T^2 (b_1 T h_1(T) + b_2 T h_2(T))} \right)^2 - 2(b_1 T h_1(T) + b_2 T h_2(T)) h_1(T) h_2(T) > 0,
\]
\[
\bar{e} = \left\{ \begin{array}{ll}
\frac{1}{d} \ln A, & \text{when } A > 1 \\
0, & \text{when } 0 < A < 1,
\end{array} \right.
\]
and \( \bar{\tau} > \bar{\tau} \). If the predator-free equilibrium point \( \hat{E} \) is locally asymptotically stable at \( \tau^* \in (\bar{\tau}, \bar{\tau}) \) then \( \hat{E} \) is locally asymptotically stable for all \( \tau \in (\bar{\tau}, \bar{\tau}) \).

**Proof.** Firstly, we consider the left side of (12). Substituting the expression \( k_1, \ldots, k_7 \) from (8), we have

\[
2k_2 + (k_3 + k_5)^2 - k_2^2 - 2\tau (k_3 + k_5) k_7 \\
< (b_1 T h_1(T) + b_2 T h_2(T))^2 + 2\tau (b_1 T h_1(T) + b_2 T h_2(T)) b_1 b_2 T^2 h_1(T) h_2(T) \\
- ((\epsilon_1(0) + \epsilon_2(0))^2 + (g_{12}(T) + g_{21}(T))^2) \\
< (b_1 T h_1(T) + b_2 T h_2(T))^2 + 2\tau (b_1 T h_1(T) + b_2 T h_2(T)) b_1 b_2 T^2 h_1(T) h_2(T) \\
- \frac{1}{2} (\epsilon_1(0) + \epsilon_2(0) + g_{12}(T) + g_{21}(T))^2.
\]

So if

\[
\tau < \bar{\tau} := \left( \frac{\epsilon_1(0) + \epsilon_2(0) + g_{12}(T) + g_{21}(T))^2 - 2(b_1 T h_1(T) + b_2 T h_2(T))^2}{4 b_2 b T^2 (b_1 T h_1(T) + b_2 T h_2(T)) h_1(T) h_2(T)} \right)
\]

then (12) holds.

Secondly, since \( k_2 - k_4 - k_6 + k_7 \) is always positive, we can see (13) is true if and only if \( k_2 + k_4 - k_6 - k_7 > 0 \). From

\[
k_2 + k_4 - k_6 - k_7 = \epsilon_1(0) \epsilon_2(0) + g_{21}(T) \epsilon_1(0) + g_{12}(T) \epsilon_2(0) - (\epsilon_2(0) + g_{21}(T)) b_1 T h_1(T) e^{-d_1 \tau} \\
- ((\epsilon_1(0) + g_{12}(T)) b_2 T h_2(T) e^{-d_2 \tau} - b_1 b_2 T^2 h_1(T) h_2(T)) e^{-(d_2 + d_1) \tau} > B,
\]

where

\[
B := \epsilon_1(0) \epsilon_2(0) + g_{21}(T) \epsilon_1(0) + g_{12}(T) \epsilon_2(0) \\
- ((\epsilon_2(0) + g_{21}(T)) b_1 T h_1(T) + (\epsilon_1(0) + g_{12}(T)) b_2 T h_2(T) + b_1 b_2 T^2 h_1(T) h_2(T)) e^{-d \tau}
\]

So if \( A > 1 \), then \( B > 0 \) for \( \tau > \bar{\tau} := \frac{1}{A} \ln A \) and when \( 0 < A < 1 \), \( B > 0 \) for all \( \tau > 0 \). Therefore, when \( \tau \in (\bar{\tau}, \bar{\tau}) \), both (12) and (13) hold. Thus, (9) has no pure imaginary roots.

Under the assumption that \( \hat{E} \) is locally asymptotically stable at \( \tau^* \), we have that \( \hat{E} \) is locally asymptotically stable on this interval, since there are no sign changes in roots of \( K(\lambda, \tau) = 0 \) for \( \tau \in (\bar{\tau}, \bar{\tau}) \).

Adapting ideas from [35, 38], we can study the persistence of the system (2), when one of the following assumptions holds:

\[b_1 e^{-d_1 \tau} T h_1(T) > \epsilon_1(0) + g_{12}(T)\] \hspace{1cm} (R_1)

or

\[b_2 e^{-d_2 \tau} T h_2(T) > \epsilon_2(0) + g_{21}(T)\] \hspace{1cm} (R_2)

Let

\[X = \{ \phi = (\phi_1, \phi_2, \phi_3, \phi_4) \in C^+ \}\]

and the solution semiflow \( \Phi(t) \phi = u_1(\phi) \), \( \phi \in X, t \geq 0. \)

The following result shows that system (2) is uniformly persistent if either (R_1) or (R_2) holds.

**Theorem 2.6.** When either (R_1) or (R_2) holds, there is a positive number \( \eta > 0 \) such that every solution \( (P_i(t), Z_1(t), P_2(t), Z_2(t)) \) in system (2) with \( P_i(0) > 0 \) and \( Z_i(0) > 0 \), \( i = 1, 2 \), satisfies

\[\liminf_{t \to \infty} (P_i(t), Z_1(t), P_2(t), Z_2(t)) \geq (\eta, \eta, \eta, \eta).\]
Proof. We prove the theorem under the first assumption of (R1). For the second case, a similar proof works.

Define
\[ X_1 = \{ \phi \in X : \phi_i(0) = 0, \ i = 1, 3 \}, \]
\[ X_2 = \{ \phi \in X : \phi_i(0) = 0, \ i = 2, 4 \}, \]
\[ \partial X_0 = X_1 \cup X_2, \]
\[ X_0 = X \setminus \partial X_0 = \{ \phi \in X : \phi_i(0) > 0, \ i = 1, 2, 3, 4 \}, \]
and
\[ M_0 = \{ \phi \in \partial X_0 : \Phi(t)\phi \in \partial X_0, t \geq 0 \}. \]

**Claim 1.** There exists a \( \delta_1 > 0 \), such that for any \( \phi \in X_0 \),
\[ \limsup_{t \to \infty} \| \Phi(t)\phi - E_0 \| \geq \delta_1. \]

By contradiction, suppose that \( \limsup_{t \to \infty} \| \Phi(t)\psi - E_0 \| < \delta_1 \) for some \( \psi \in X_0 \). Thus, there exists \( t_0 > 0 \) such that \( 0 \leq P_i(t, \psi) < \delta_1 \) and \( 0 \leq Z_i(t, \psi) < \delta_1 \) for \( t > t_0, i = 1, 2 \).

Let \( F_i(P_1, Z_1, P_2, Z_2) = \mu_i(N) - Z_i h_i(P_i) - f_{ij}(Z_i), \ i = 1, 2, \ j = 3 - i \). Since \( F_i \) is continuous, \( F_i(P_1, Z_1, P_2, Z_2) \to \mu_i(T) - \gamma_0 \) as \( (P_1, Z_1, P_2, Z_2) \to (0, 0, 0, 0) \), there exists \( \sigma_1 = \sigma_1(\delta_1) \) such that
\[ | F_i(P_1, Z_1, P_2, Z_2) - (\mu_i(T) - \gamma_0) | < \sigma_1. \]

By \( (C_4) \), if \( \phi_1(0) > 0 \) and \( \phi_3(0) > 0 \), then
\[ P_i'(t) = P_i F_i(P_1, Z_1, P_2, Z_2) + P_i f_{ij}(Z_i) \geq \gamma_0 P_i(t) + (\mu_i(T) - \gamma_0 - \sigma_1) P_i(t). \]

Consider the linear system
\[ u_1'(t) = \gamma_0 u_2(t) + (\mu_1(T) - \gamma_0 - \sigma_1) u_1(t), \]
\[ u_2'(t) = \gamma_2 u_1(t) + (\mu_2(T) - \gamma_0 - \sigma_1) u_2(t). \]

From the linearization of (2) at \( E_0 \) in (4), we know that the principle eigenvalue \( \lambda_1 \) and the corresponding eigenfunction are positive. Due to the continuity of \( \lambda_i \), there exists a sufficiently small positive number such that \( \lambda_i(\sigma_1) > 0 \), and a solution of (14) is \( \bar{u}(t) = e^{\lambda_i(\sigma_1)t} \phi_0 \), where \( \phi_0 \) is the positive eigenfunction associated with \( \lambda_i(\sigma_1) \), \( \bar{u} \) and \( \phi_0 \) are vectors with two components. When \( P_i(t, \phi_0) \gg 0 \) for all \( t > 0, i = 1, 2 \), the comparison theory implies that there exists a small \( \xi > 0 \) such that \( (P_1(t, \phi_0), P_2(t, \phi_0)) \geq \xi e^{\lambda_i(\sigma_1)t} \phi_0 \) for all \( t \geq t_0 \) in (14). Since \( \lambda_i(\sigma_1) > 0 \), we have \( \lim_{t \to \infty} (P_1(t, \phi_0), P_2(t, \phi_0))^T = \infty \), which is a contradiction.

**Claim 2.** There exists a \( \delta_2 > 0 \), such that for any \( \phi \in X_0 \),
\[ \limsup_{t \to \infty} \| \Phi(t)\phi - \hat{E} \| \geq \delta_2. \]

Assume the contrary, that \( \limsup_{t \to \infty} \| \Phi(t)\phi - \hat{E} \| < \delta_2 \) for some \( \phi \in X_0 \). Then there exists a large number \( t_1 > 0 \) such that \( \| \Phi(t)\phi - (T, 0, T, 0) \| < \delta_2 \) for all \( t \geq t_1 + \tau \).

Without loss of generality, we assume that (R1) holds. Choose \( \zeta > 0 \) small enough such that
\[ b_1 e^{-d_1 T} (T - \zeta) h_1(T - \zeta) > \epsilon_1(LZ) + g_{12}(0). \]
Let $t_\zeta > t_1 + \tau$ be sufficiently large such that
\[ T - \zeta < P_i(t) < T + \zeta, \text{ for } t > t_\zeta. \]
Thus, by $(C_3)$ and $(C_5)$ for $t > t_\zeta$
\[ Z_i'(t) > b_1 e^{-d_1 \tau_1 (T - \zeta)} h_1(T - \zeta) Z_1(t - \tau_1) - (\epsilon_1(L) + g_{12}(0)) Z_1(t). \]
By the comparison principle and Lemma 2.3, we get $Z_1(t) \to \infty$ as $t \to \infty$, which is a contradiction.

**Claim 3.** $\bigcup_{\phi \in M_0} \omega(\phi) = E_0 \cup \tilde{E}.$

Let $\omega(\phi)$ be the omega limit set of the orbit $\Phi(t)$ through $\phi \in X$. For any $\phi \in M_0$, we have $\Phi(t)\phi \in X_1$ or $\Phi(t)\phi \in X_2$. If $\Phi(t)\phi \in X_1$, i.e. $P_1(t, \phi) = P_2(t, \phi) \equiv 0$, then
\[ (Z_1 + Z_2)' \leq -\min\{\epsilon_1(0), \epsilon_2(0)\}(Z_1 + Z_2). \]
By the comparison theory, we get $Z_1(t, \phi) + Z_2(t, \phi) \to 0$ as $t \to \infty$. Thus, $Z_i(t, \phi) \to 0$ as $t \to \infty$, $i = 1, 2$.

If $\Phi(t)\phi \in X_2$, i.e. $Z_1(t, \phi) = Z_2(t, \phi) \equiv 0$, then
\[ P_i^0 = P_i \mu_i(T - \alpha_1 P_1 - \alpha_2 P_2) + \gamma_0(P_j - P_i) := G_i(P_1, P_2). \tag{15} \]
From the proof Proposition 1, the system $(15)$ has only two equilibrium points $(0,0)$ and $(\frac{\alpha_1}{\alpha_1 + \alpha_2}, \frac{T}{\alpha_1 + \alpha_2})$. It is easy to check that $(0,0)$ is always unstable. Denote $G(P_1, P_2) = (G_1(P_1, P_2), G_2(P_1, P_2))^T$, $E = \{(P_1, P_2) : 0 < \alpha_1 P_1 + \alpha_2 P_2 < T\}$ and $\rho = (P_1 P_2)^{-1}$. Then
\[ \nabla \cdot (\rho G) = \frac{-\alpha_1}{P_2^0} \mu_3(T - \alpha_1 P_1 - \alpha_2 P_2) - \frac{\gamma_0}{P_2^0} \mu_2(T - \alpha_1 P_1 - \alpha_2 P_2) - \frac{\alpha_2}{P_2^0} < 0, \]
for any $P_1, P_2 \in E$. Thus by Dulac’s negative criterion, there is no periodic orbits within $E$. Then we have, $P_i(t, \phi) \to \frac{T}{\alpha_1 + \alpha_2}$ as $t \to \infty$, $i = 1, 2$. Consequently, we have $\bigcup_{\phi \in M_0} \omega(\phi) = E_0 \cup \tilde{E}$. Thus the claim holds.

Define a continuous function $p : X \to \mathbb{R}_+$ by
\[ p(\phi) = \min\{\phi_1(0), \phi_2(0), \phi_3(0), \phi_4(0)\}, \quad \forall \phi \in X. \]
It is clear that $p^{-1}(0,\infty) \subset X_0$ and if $p(\phi) > 0$ then $p(\Phi(t)\phi) > 0$ for all $t > 0$. By Claim 3, we get that for any forward orbit of $\Phi(t)$ in $M_0$ converges to $E_0$ or $\tilde{E}$, by Claim 1 and 2, we conclude that $E_0$ and $\tilde{E}$ are two isolated invariant in $X$, and $(W^s(E_0) \cup W^s(\tilde{E})) \cap X_0 = \emptyset$ and no subset of $\{E_0, \tilde{E}\}$ form a cycle in $\partial X$. By [30], it then follows that there exists $\eta > 0$ such that $\liminf_{t \to \infty} p(\Phi(t)\phi) \geq \eta$ for all $\phi \in X_0$, which implies the uniform persistence. This completes the proof.

3. **With constant migration rates.** After we obtain the conditions for the existence and stability of the boundary equilibrium points $E_0$ and $\tilde{E}$, we simplify the model $(1)$ and assume that all the prey (predictor) migration rates are the same constant $f_{ij}(Z_j) = m \left(g_{ij}(P_i) = s\right)$ to explore the existence and local stability of positive equilibrium solutions for $i = 1, 2, j = 3 - i$. With this simplification, the system $(2)$ becomes
\[ \frac{dP_1}{dt} = P_1 [\mu_1(N) - Z_1 h_1(P_1)] + m (P_2 - P_1), \]
\[ \frac{dZ_1}{dt} = b_1 e^{-d_1 \tau_1} P_1 (t - \tau_1) Z_1(t - \tau_1) h_1(P_1(t - \tau_1)) - Z_1 \epsilon_1 (Z_1 + Z_2) + s (Z_2 - Z_1). \]
\[
\frac{dP_2}{dt} = P_2[\mu_2(N) - Z_2 h_2(P_2)] + m (P_1 - P_2), \tag{16}
\]
\[
\frac{dZ_2}{dt} = b_2 e^{-d_2 \tau_2} P_2(t - \tau_2) Z_2(t - \tau_2) h_2(P_2(t - \tau_2)) - Z_2 \epsilon_2 (Z_1 + Z_2) + s (Z_1 - Z_2).
\]

When the system (16) exists a positive equilibrium point \(E^* = (P_1^*, Z_1^*, P_2^*, Z_2^*)\), then \(P_i^*, Z_i^*, i = 1, 2\) must satisfy
\[
P_1^*[\mu_1(N^*) - Z_1^* h_1(P_1^*)] + m (P_1^* - P_1) = 0,
\]
\[
b_1 e^{-d_1 \tau_1} P_1^* Z_1^* h_1(P_1^*) - Z_1^* \epsilon_1 (Z_1^* + Z_2^*) + s (Z_2^* - Z_1^*) = 0,
\]
\[
P_2^*[\mu_2(N^*) - Z_2^* h_2(P_2^*)] + m (P_1^* - P_2^*) = 0,
\]
\[
b_2 e^{-d_2 \tau_2} P_2^* Z_2^* h_2(P_2^*) - Z_2^* \epsilon_2 (Z_1^* + Z_2^*) + s (Z_1^* - Z_2^*) = 0, \tag{17}
\]
with \(N^* = T - \alpha_1 P_1^* - \alpha_2 P_2^* - \beta_1 Z_1^* - \beta_2 Z_2^* > 0\). Otherwise, it leads to a contradiction with the summation of the first and third equations in (17). From the second and forth equations of (17), we have
\[
\frac{Z_1^* \epsilon_1 (Z_1^* + Z_2^*) + s (Z_2^* - Z_1^*)}{Z_1^*} = b_1 e^{-d_1 \tau_1} P_1^* h_1(P_1^*) \leq b_1 e^{-d_1 \tau_1} T h_1(T),
\]
\[
\frac{Z_2^* \epsilon_2 (Z_1^* + Z_2^*) + s (Z_1^* - Z_2^*)}{Z_2^*} = b_2 e^{-d_2 \tau_2} P_2^* h_2(P_2^*) \leq b_2 e^{-d_2 \tau_2} T h_2(T), \tag{18}
\]
respectively. Since \(\epsilon_i(0) \leq \epsilon_i(Z_i^* + Z_{2}^*)\) for \(i = 1, 2\), we have
\[
\frac{Z_2^*}{Z_1^*} \leq \frac{b_1 e^{-d_1 \tau_1} T h_1(T) + s - \epsilon_1(0)}{s},
\]
\[
\frac{Z_1^*}{Z_2^*} \leq \frac{b_2 e^{-d_2 \tau_2} T h_2(T) + s - \epsilon_2(0)}{s},
\]
provided that \(b_i e^{-d_i \tau_i} T h_i(T) + s > \epsilon_i(0), \ i = 1, 2\). Thus
\[
\frac{s}{b_1 e^{-d_1 \tau_1} T h_1(T) + s - \epsilon_1(0)} \leq \frac{b_2 e^{-d_2 \tau_2} T h_2(T) + s - \epsilon_2(0)}{s},
\]
which leads to
\[
s \leq \frac{(b_1 e^{-d_1 \tau_1} T h_1(T) - \epsilon_1(0))(b_2 e^{-d_2 \tau_2} T h_2(T) - \epsilon_2(0))}{(\epsilon_1(0) - b_1 e^{-d_1 \tau_1} T h_1(T)) + (\epsilon_2(0) - b_2 e^{-d_2 \tau_2} T h_2(T))}. \tag{H_2}
\]

Therefore,

**Lemma 3.1.** When \((H_2)\) does not hold, then \(E^*\) does not exist. In particular, if \(\tau_1 = \tau_2 := \tau\) and
\[
(b_1 T h_1(T) - \epsilon_1(0)) (b_2 T h_2(T) - \epsilon_2(0)) + s (b_1 T h_1(T) + b_2 T h_2(T)) < \epsilon_1(0) + \epsilon_2(0),
\]
\(E^*\) does not exist for any feasible \(\tau > 0\).

The condition \((H_2)\) is necessary for the existence of a positive equilibrium point \(E^* = (P_1^*, Z_1^*, P_2^*, Z_2^*)\) in (17), but is not a sufficient condition in general.

Define \(H_i(P_i) = P_i h_i(P_i)\) for \(i = 1, 2\). From the hypothesis \((C_2)\), \(H_i(P_i)\) is positive and increases in \((0, \frac{T}{\alpha_1 + \alpha_2})\). We can obtain
\[
P_1^* = H_1^{-1} \left( \frac{Z_1^* \epsilon_1 (Z_1^* + Z_2^*) + s (Z_1^* - Z_2^*)}{b_1 e^{-d_1 \tau_1} Z_1^*} \right),
\]
\[
P_2^* = H_2^{-1} \left( \frac{Z_2^* \epsilon_2 (Z_1^* + Z_2^*) + s (Z_2^* - Z_1^*)}{b_2 e^{-d_2 \tau_2} Z_2^*} \right),
\]
from the second and forth equations of (17), respectively, where $Z_i^*$ and $Z_j^*$ are the implicit positive solutions of the following equations:

\[
H_1^{-1}\left(\frac{Z_i'^{e1} + Z_j'^{e1} + s(Z_i'^{e1} - Z_j'^{e1})}{b_1e^{-\tau_1^*}}\right) - \frac{Z_i'^{e1} + Z_j'^{e1} + s(Z_i'^{e1} - Z_j'^{e1})}{b_1e^{-\tau_1^*}} = 0;
\]

\[
H_2^{-1}\left(\frac{Z_i'^{e2} + Z_j'^{e2} + s(Z_i'^{e2} - Z_j'^{e2})}{b_2e^{-\tau_2^*}}\right) - \frac{Z_i'^{e2} + Z_j'^{e2} + s(Z_i'^{e2} - Z_j'^{e2})}{b_2e^{-\tau_2^*}} = 0;
\]

with

\[
N^* = T - \alpha_1H_1^{-1}\left(\frac{Z_i'^{e1} + Z_j'^{e1} + s(Z_i'^{e1} - Z_j'^{e1})}{b_1e^{-\tau_1^*}}\right) - \alpha_2H_2^{-1}\left(\frac{Z_i'^{e2} + Z_j'^{e2} + s(Z_i'^{e2} - Z_j'^{e2})}{b_2e^{-\tau_2^*}}\right) - \sum_{i=1}^2 \beta_iZ_i^*,
\]

which is impossible to find an analytical solution in general.

With fixed parameters, feasible values of delays and certain functions, for instance, choosing the functions given in Table (1) (see [10]), we have $E^*_1 = (0.093, 0.57, 0.048, .56)$ when $\tau_1 = 0.4$ and $\tau_2 = 0.7$.

|          | $h(P)$ | $\mu(N)$ | $\epsilon(Z)$ |
|----------|--------|----------|---------------|
| Patch 1  | $\frac{1}{T^3 + 1}$ | $\frac{N}{T}$ | 0.02          |
| Patch 2  | $\frac{2}{T^3 + 2}$ | $\frac{N}{T}$ | 0.03          |

Table 1. : Existence of $E^*_1$ with $\alpha_1 = \beta_1 = 1$, $d_i = 0.25$, $b_i = 0.01$, $s = 0.1$, $m = 0.6$ and $T = 7$ for $i = 1, 2$.

When the two parallel food chains are symmetric, that is, the growth for all patches have the same functional forms, parameter values and the maturation delay, the system (16) becomes

\[
\begin{align*}
\frac{dP_i}{dt} &= P_i [\mu(N) - Z_i h(P_i)] + m (P_j - P_i), \\
\frac{dZ_i}{dt} &= be^{-d \tau_i P_i (t - \tau)} Z_i (t - \tau) h(P_i (t - \tau)) - Z_i \epsilon(Z_i + Z_j) + s (Z_j - Z_i),
\end{align*}
\]

$i = 1, 2$, $j = 3 - i$ and $N = T - \alpha(P_1 + P_2) - \beta(Z_1 + Z_2)$. Then (H2) becomes

\[
(be^{-d \tau} T h(T) + 2s - \epsilon(0))(be^{-d \tau} T h(T) - \epsilon(0)) \geq 0,
\]

which implies $\tau \leq \tau_{\max} = \frac{1}{d} \ln \left(\frac{bT h(T)}{\epsilon(0)}\right)$.

Let

$\tau_s = \sup \{\tau \in (0, \tau_{\max}) | \text{system (19) has at least a positive equilibrium point}\}$.

When the per-prey-per-predator harvest rate $h(P)$ is increasing, we know the positive equilibrium point $E^*$ exists with the form of $(P^*, Z^*, P^*, Z^*)$.

**Proposition 3.** Assume $h(P)$ is an increasing function on the interval $(0, \frac{T}{30})$. If the positive equilibrium point $E^*$ exists, then it must have the form of $(P^*, Z^*, P^*, Z^*)$. 

Proof. Assume \((P_1^*, Z_1^*, P_2^*, Z_2^*)\) is a positive equilibrium point. We can show \(P_1^* = P_2^*\) and \(Z_1^* = Z_2^*\). Otherwise, we have,
\[
m(P_1^2 - P_2^2) = Z_2^* P_1^* H(P_1^*) - Z_1^* P_2^* H(P_2^*),
\]
\[
s(Z_1^2 - Z_2^2) = be^{-d_r} Z_1^* Z_2^* (H(P_1^*) - H(P_2^*)).
\]
Suppose \(P_1^* > P_2^*\), then by (21) and the hypothesis \((C_2)\), we obtain \(Z_1^* > Z_2^*\). Form the right hand side of (20), we have
\[
Z_2^* P_1^* H(P_2^*) - Z_1^* P_2^* H(P_1^*) < Z_1^* P_1^* P_2^* (h(P_2^*) - h(P_1^*)) < 0
\]
when \(h(P)\) is increasing. Then we arrive to a contradiction. Similar contradiction arrives if \(P_1^* < P_2^*\). Therefore, \(P_1^* = P_2^*\) and \(Z_1^* = Z_2^*\).

Remark 4. When \(h(P)\) is not necessary increasing on the interval \((0, \frac{T}{2a})\), beside the positive equilibrium point \((P^*, Z^*, P^*, Z^*)\), without additional condition, we cannot exclude any other form in \(E^*\). In other words, it is possible to have other positive equilibrium point with different \(P_i^*\) and \(Z_i^*, i = 1, 2\).

When the positive equilibrium point \(E^* = (P^*, Z^*, P^*, Z^*)\) exists, the linearization of (19) at \(E^*\) is
\[
\frac{dx_1}{dt} = a_{11} x_1(t) + a_{12} y_1(t) + a_{13} x_2(t) + a_{14} y_2(t),
\]
\[
\frac{dy_1}{dt} = a_{22} y_1(t) + a_{24} y_2(t) + b_{21} x_1(t - \tau) + b_{22} y_1(t - \tau),
\]
\[
\frac{dx_2}{dt} = a_{13} x_1(t) + a_{14} y_1(t) + a_{11} x_2(t) + a_{12} y_2(t),
\]
\[
\frac{dy_2}{dt} = a_{24} y_1(t) + a_{22} y_2(t) + b_{21} x_2(t - \tau) + b_{22} y_2(t - \tau),
\]
with
\[
a_{11} = -\alpha P^* \mu^* - P^* Z^* h^*_s - m, \quad a_{12} = -\beta P^* \mu^*_s - P^* h^*_s < 0,
\]
\[
a_{13} = -\alpha P^* \mu^* + m, \quad a_{14} = -\beta P^* \mu^*_s < 0, \quad a_{22} = -Z^* \epsilon'_s - \epsilon^* - s < 0
\]
\[
a_{24} = -Z^* \epsilon'_s + s, \quad b_{21} = be^{-d_r} Z^* (P^* h^*_s + h^*) > 0, \quad b_{22} = be^{-d_r} P^* h^*_s > 0,
\]
where \(\mu^*, h^*, \epsilon^*\) denotes the value of the function \(\mu, h, \epsilon\) and \(\mu^*_s, h^*_s, \epsilon'_s\) denotes the value of the derivative of the associated function at \((P^*, Z^*, P^*, Z^*)\) respectively.

Lemma 3.2. ([1, 28]) When the block matrices \(A, B\) are square matrices of the same order, then
\[
\det \left( \begin{array}{cc}
A & B \\
-1 & A \\
\end{array} \right) = \det(A - B) \det(A + B).
\]

In our case, \(A = \left( \begin{array}{cc}
\lambda - a_{11} & -a_{12} \\
-b_{21} e^{-d_r} & \lambda - a_{22} - b_{22} e^{-d_r} \\
\end{array} \right)\) and \(B = \left( \begin{array}{cc}
-a_{13} & -a_{14} \\
0 & -a_{24} \\
\end{array} \right)\).
Thus the characteristic equation of (23) is
\[
\Delta(\lambda, \tau) = \Phi(\lambda, \tau) \Psi(\lambda, \tau) = 0,
\]
where
\[
\Phi(\lambda, \tau) = \lambda^2 + \phi_1 \lambda + \phi_2 + \phi_3 e^{-\lambda \tau} + \zeta \lambda e^{-\lambda \tau},
\]
\[
\Psi(\lambda, \tau) = \lambda^2 + \psi_1 \lambda + \psi_2 + \psi_3 e^{-\lambda \tau} + \xi \lambda e^{-\lambda \tau},
\]
\[ \phi_1 = a_{24} + a_{13} - a_{22} - a_{11}, \quad \phi_2 = (a_{24} - a_{22})(a_{13} - a_{11}), \quad \zeta = -b_{22} < 0. \]
\[ \phi_3 = b_{21}(a_{14} - a_{12}) - b_{22}(a_{13} - a_{11}), \quad \psi_1 = -(a_{24} + a_{13} + a_{22} + a_{11}), \]
\[ \psi_2 = (a_{24} + a_{22})(a_{13} + a_{11}), \quad \psi_3 = b_{21}(a_{14} + a_{12}) + b_{22}(a_{13} - a_{11}). \]

As we know that all the roots of \( \Phi(\lambda, \tau) = 0 \) and \( \Psi(\lambda, \tau) = 0 \) with \( \text{Re}(\lambda) \geq 0 \) lie in a bounded domain \([34]\). When \( \tau = 0 \),
\[ \Delta(\lambda, 0) = \Phi(\lambda, 0)\Psi(\lambda, 0) \]
\[ = (\lambda^2 + (\phi_1 + \zeta)\lambda + (\phi_2 + \phi_3))(\lambda^2 + (\psi_1 + \zeta)\lambda + (\psi_2 + \psi_3)) = 0. \]

Parallel to the Proposition 2, we have

**Proposition 4.** At \( \tau = 0 \), the positive equilibrium point \( E^* \) is locally asymptotically stable if and only if
\[ \phi_1 > -\zeta, \quad \phi_2 + \phi_3 > 0, \quad \psi_1 > -\zeta \quad \text{and} \quad \psi_2 + \psi_3 > 0. \quad (H_0^{\Phi, \Psi}) \]

Let \( \tau > 0 \) and suppose \( \lambda = i\omega \) (\( \omega > 0 \)) is a purely imaginary root of \( \Phi(\lambda, \tau) = 0 \) in \((25)\). Substituting it into \( \Phi(\lambda, \tau) = 0 \) and separating the real and imaginary parts, we obtain:
\[ \omega^2 - \phi_2 = \phi_3 \cos \omega \tau + \zeta \omega \sin \omega \tau, \]
\[ \phi_1 \omega = \phi_3 \sin \omega \tau - \zeta \omega \cos \omega \tau. \quad (27) \]

Squaring and adding both equations of \((27)\) lead to
\[ F_\Phi(\omega, \tau) = \omega^4 + q_\Phi(\tau)\omega^2 + \ell_\Phi(\tau) = 0 \]
where
\[ q_\Phi(\tau) = \phi_1^2 - 2\phi_2 - \zeta^2, \quad \ell_\Phi(\tau) = \phi_2^2 - \phi_3^2. \]

Let \( \omega = \omega(\tau) \) be a positive root of \( F_\Phi(\omega, \tau) = 0 \). From \((27)\), for \( i\omega(\tau) \) to be a solution of \( \Phi(\lambda, \tau) = 0 \), \( \omega(\tau) \) needs to satisfy the system
\[ \sin \omega(\tau)\tau = \frac{\zeta\omega^3 + (\phi_1\phi_3 - \zeta\phi_2)\omega}{\zeta^2\omega^2 + \phi_3^2}, \]
\[ \cos \omega(\tau)\tau = \frac{(\phi_3 - \zeta\phi_1)\omega^2 - \phi_2\phi_3}{\zeta^2\omega^2 + \phi_3^2}. \quad (28) \]

Define the function \( \theta_\Phi(\tau) \in [0, 2\pi) \) such that \( \sin \theta_\Phi(\tau) \) and \( \cos \theta_\Phi(\tau) \) are given by \((28)\), and
\[ S_\Phi^n(\tau) = \tau - \frac{\theta_\Phi(\tau) + 2n\pi}{\omega(\tau)}, \quad n \in \mathbb{N}. \quad (29) \]

Following \([7, 21]\), \( i\omega(\tau^*) \) is a root in \( \Phi(\lambda, \tau) = 0 \) if and only if \( \tau^* \) is a zero of a function \( S_\Phi^n \) for some \( n \in \mathbb{N} \).

**Proposition 5.** If \( \tau^* \in (0, \tau_{\text{max}}) \) is a positive root of \( S_\Phi^n \) given in \((29)\) for some \( n \in \mathbb{N} \), then a pair of purely imaginary roots \( i\omega(\tau^*) \) of \( \Phi(\lambda, \tau) = 0 \) exist which crosses the imaginary axis from left to right if \( \frac{dS_\Phi^n}{d\tau}(\tau^*) > 0 \) and crosses the imaginary axis from right to left if \( \frac{dS_\Phi^n}{d\tau}(\tau^*) < 0 \), and
\[ \text{Sign} \left\{ \frac{d\text{Re} (\lambda)}{d\tau} \bigg|_{\lambda = i\omega(\tau^*)} \right\} = \text{Sign} \left\{ \frac{dS_\Phi^n}{d\tau} \bigg|_{\tau = \tau^*} \right\}. \]
Similarly, we can obtain \( F_\Psi(\omega, \tau) = 0 \) and \( S_0^\Psi(\tau) \) to find a pure imaginary roots \( i\omega(\tau^*) \) for \( \Psi(\lambda, \tau) = 0 \) in (26). Then the stability of \( E^* = (P^*, Z^*, P^*, Z^*) \) is just followed:

**Proposition 6.** (i) When \((H_0^\Psi)\) holds and both \( F_\Psi(\omega, \tau) = 0 \), \( F_\Psi(\omega, \tau) = 0 \) have no positive roots, \( E^* \) is locally asymptotically stable for any feasible time delay \( \tau \in (0, \tau^*) \);

(ii) When \((H_0^\Psi)\) holds and \( F_\Psi(\omega, \tau) = 0 \), \( F_\Psi(\omega, \tau) = 0 \) has a positive root, \( E^* \) is locally asymptotically stable for small time delay \( \tau \), say \( \tau < \min\{\tau_n^*\} \) where \( \tau_n^* \) is a zero of a function \( S_n^\Psi \setminus S_n^\Psi \) for some \( n \in \mathbb{N} \);

(iii) When \((H_0^\Psi)\) does not hold and \( F_\Psi(\omega, \tau) = 0 \), \( F_\Psi(\omega, \tau) = 0 \) has a positive root, say \( \tau^* \), \( E^* \) is unstable for small time delay \( \tau \). If \( \frac{dS_\Psi(\tau^*)}{\tau} < 0 \), \( E^* \) can become stable with \( \tau > \tau^* \).

**Remark 5.** We omit the implicit conditions for the existence of positive roots in \( F_\Psi(\omega, \tau) = 0 \) or \( F_\Psi(\omega, \tau) = 0 \), which can be found in [3].

4. **Numerical simulations.** In this section, we fix the parameters

\[
d_i = 0.01, \quad b_i = 0.25, \quad \alpha_i = 1, \quad \beta_i = 1,
\]

(30)

for each \( i \) and choose some different functions from literature, see Table (2), to compliment the theoretical results given previously.

| \( \mu(N) \) | \( Ph(P) \) | \( \epsilon(Z) \) | \( f(Z) \) | \( g(P) \) |
|-------------|-------------|----------------|--------|---------|
| \( \frac{\mu_{\text{max}}N}{N+\lambda} \) Monod function [25] | \( rP \) \( a+bP \) | \( aP^n \) \( b+P^n \), \( n \geq 1 \) | \( \epsilon_o \) constant [20] | \( m \) constant [10] | \( s \) constant [22] |
| \( \frac{N}{T} \) [10] | \( \frac{rP}{a+bP} \) | \( r(1-e^{-nP}) \) | \( aZ + b \) | \( \frac{d}{1+P} \) [10] |

Table 2. Functional responses.

In the following example, we consider a symmetric system with constant migration rates. First, we fix the value of the migration rates and study the dynamic behavior of system (19) as the time delay varies. Then, we fix the time delay and one of the migration rates to explore the affection of another migration rate on the stability of the positive steady state.

**Example 1.** A symmetric system with constant migration rates. Choose

\[
\mu(N) = \frac{N}{1+N}, \quad \mu(P) = \frac{P}{P^2+1}, \quad \epsilon(Z) = 0.15 \quad \text{and} \quad T = 8.
\]

(31)

With constant migration rates, the system has a coexistence equilibrium point \( E^*(\tau) = (P^*(\tau), Z^*(\tau), P^*(\tau), Z^*(\tau)) \), where

\[
P^*(\tau) = \sqrt{\frac{3}{5e^{-0.91\tau}-3}}:
\]

\[
Z^*(\tau) = \frac{9P^* + 2 - \sqrt{16P^* + 64P^* + 97P^* - 28P^* + 4}}{4P^*},
\]

for \( \tau < 45.02 \), which is independent of the constant migration rates.
At $\tau = 0$, $E^*(0) = (1.221, 1.471, 2.211, 1.471)$ is stable by checking the condition ($\mathbf{H}_0^{\Psi}$). With $\tau > 0$ and fixed values $g_{12}(P_1) = g_{21}(P_2) = 0.1$ and $f_{12}(Z_1) = f_{21}(Z_2) = 0.6$, we plot $S_0^\Psi(\tau)$, $S_1^\Psi(\tau)$ and $S_2^\Psi(\tau)$ defined in Eq. (24) in Fig. 2. We can see that the curve of $S_1^\Psi(\tau)$ is negative when $\tau < \tau_1^*$ and then becomes positive as $\tau$ increases up to $\tau_2^* = 24.11$; and return to negative after that, implying for small delay $\tau < \tau_1^*$, the positive equilibrium point $E^*(\tau)$ is stable and loses the stability when $\tau \in (\tau_1^*, \tau_2^*)$ and back to stable for large time delay, i.e $\tau > \tau_2^*$, before it disappears at $\tau = 45.02$. These tell us the occurrence of stability switch, which is confirmed in Fig. 3. Biologically, when the maturation process is too short, both of the prey and the predator move to a certain level with constant concentration; while the maturation time increases, all the species oscillate regularly. Nevertheless, when the predator is mature enough, it behaviors less active which gives a chance to prey to increase. Therefore, the state of coexistence of the predator and the prey is stable, rather than oscillatory.

We notice that the chosen function $h(P)$ in (31) is not a increasing function, from Remark 4 it is possible to have other positive equilibrium point beside $E^*(\tau)$ but we failed to find it although we have tried different choices of the functions and parameters.

![Figure 2. Functions $S_0^\Psi(\tau)$, $S_1^\Psi(\tau)$ and $S_2^\Psi(\tau)$ for $\tau \in (0, 30)$ corresponding to the choice in (31).](image)

![Figure 3. Time series $P_2(t)$ and $Z_2(t)$ of system (19) with parameters and functions given in (30), (31), $g_{12}(P_1) = g_{21}(P_2) = 0.1$ and $f_{12}(Z_1) = f_{21}(Z_2) = 0.6$.](image)

Next, we discuss how the variation of prey and predator migration rates effect the dynamical system. Since the system is symmetric, let $f_{12}(Z_1) = f_{21}(Z_2) = m$, $g_{12}(P_1) = g_{21}(P_2) = s$. In general, the stability is corresponded to the roots in $\Phi(\lambda, \tau) = 0$ given in (25), where $\Phi$ depends on both migration rates $m$, $s$, and $\Psi(\lambda, \tau) = 0$ given in (26) which depends only on $m$. First, we fixed the time delay at $\tau = 0.1$. With the variation of $m$, when $s = 0.1$, we can plot $Re(\lambda)$ v.s $m$ numerically from $\Phi(\lambda, 0.1) = \Psi(\lambda, 0.1) = 0$, see Fig. 4a. Similarly, with the
variation of \( s \), we plot \( Re(\lambda) \) v.s \( s \) in Fig. 4b when \( m = 0.6 \). We can observe, from Figs 4a and 4b, that \( Re(\lambda) < 0 \), so the variation of \( m \) or \( s \) does not change the stability of \( E^s(0.1) \). This gives a good agreement with Fig. 3a. Parallelly, with the large \( \tau = 7 \), we see, from Fig. 4c, that \( Re(\lambda) \geq 0 \), implying the instability, which is consistent with those given in Fig. 3b.

\[ \begin{align*}
\text{(A)} & \quad Re(\lambda) \text{ v.s m for } m \in [0, 20] \text{ with } s = 0.1, \tau = 0.1. \\
\text{(B)} & \quad Re(\lambda) \text{ in } \Phi(\lambda, \tau) = 0 \text{ v.s s for } s \in [0, 20] \text{ with } m = 0.6, \tau = 0.1. \\
\text{(C)} & \quad Re(\lambda) \text{ v.s m for } m \in [0, 20] \text{ with } s = 0.1, \tau = 7.
\end{align*} \]

**Figure 4.** \( Re(\lambda) \) v.s \( m \) and \( s \) for \( \tau = 0.1, 7 \).

In the second example, we consider a non-symmetric system with constant and non-constant migration rates.

**Example 2.** A non-symmetric system. Choose

\[
\begin{align*}
\rho_1(N) &= \frac{N}{T}, \quad \rho_2(N) = \frac{N}{1+N}, \quad h_1(P) = \frac{2(1-e^{-5P})}{P}, \quad h_2(P) = \frac{2P^2}{5P^3+1} \\
\epsilon_1(Z) &= 0.01, \quad \epsilon_2(Z) = 0.1Z + 0.05, \quad T = 10.
\end{align*}
\]

(32)

First, we take a constant migration rates \( f_{12}(Z_1) = f_{21}(Z_2) = m \) and \( g_{12}(P_1) = g_{21}(P_2) = s \). With fixed \( m = 0.6 \) and \( s = 0.8 \), in Fig. 5, we can observe interesting dynamical behavior as \( \tau \) varies. When the maturation time is \( \tau = 5 \), a stable steady state exists (Fig. 5a); with the increasing of the maturation time, the steady state loses the stability and the system becomes oscillatory (Fig. 5b); With further increasing of \( \tau \), it is interested to observe the occurrence of period-doubling (Fig. 5c), and then regain the stability (Fig. 5d) when \( \tau \) is even larger.

To see the influence of the prey migration rate \( m \), we fix \( s = 0.8 \) and \( \tau = 5 \). Fig. 6 shows that the increasing of \( m \) can destabilize the steady state. Corresponding to the remarkable behavior in Fig. 5c, where \( m = 0.6, s = 0.8, \tau = 20 \), we keep all the parameters and delay the same, just slightly change the value of \( m \) around \( m = 0.6 \),

\[ \begin{align*}
\text{(A)} & \quad \tau = 5. \\
\text{(B)} & \quad \tau = 18. \\
\text{(C)} & \quad \tau = 20. \\
\text{(D)} & \quad \tau = 21.
\end{align*} \]

**Figure 5.** Time series \( P_2(t) \) and \( Z_2(t) \) of system (2) with parameters and functions given in (30) and (32).
Fig. 6 shows the affection of the prey migration rate when \( \tau = 5, s = 0.8 \).

Fig. 7 shows the sensitivity of the dynamical behavior with the variation of the prey migration rate \( m \). It is observed that the double-periodic behavior disappears and one period orbit exists at \( m = 0.7 \) and a stable steady state appears at \( m = 0.5 \). More clearly, Figs. 7a-7c show the solution curves with different \( m \) and Figs. 7d-7f depict the associated phase portraits. Same in the following Figs. 8 and 10.

Similarly, we fix \( m = 0.6 \) and vary the value of \( s \). When \( s = 0.6 \), there exists periodic oscillation. Increasing \( s \) from 0.6 to 0.7 or 0.8, another oscillatory behavior appears to form a periodic-doubling. It is very interesting to observe that the stability switch occurs with the further increasing of \( s \), see Fig. 8.

If we choose the migration rates in (31) as non-constant functions,

\[
g_{12}(P) = g_{21}(P) = \frac{0.1}{1+P}, \quad f_{12}(Z) = f_{21}(Z) = \vartheta Z + 0.2;
\]

where \( \vartheta \) is a positive real number. First, we fix \( \vartheta = 0.5 \). Fig. 9 shows the occurrence of stability switch and a periodic-doubling when the time delay varies.

Then we pick the moment shown in Fig. 9c, change the value of \( \vartheta \) slightly around \( \vartheta = 0.5 \). It is surprising that the periodic-doubling is broken when we increase or decrease \( \vartheta \), see Fig. 10, implying that the system may have rich dynamics with the change of migration rate.

In the last example, we consider a non-symmetric system having three patches and with constant migration rates. We compare this system with the model without migration rates which is studied in [3].
Example 3. When $n = 3$, choose

$$\mu_1(N) = \frac{N}{15 + N}, \mu_2(N) = \mu_3(N) = \frac{4N}{10 + N}, \ h_1(P) = \frac{P}{P^2 + 0.1},$$

$$h_2(P) = h_3(P) = \frac{1}{P + 1}, \ \epsilon_1(Z) = 0.05 + 0.31Z, \ \epsilon_2(Z) = \epsilon_3(Z) = 0.15,$$

$$g_{ij}(P_i) = s, \ f_{ij}(Z_i) = m, \ i, j = 1, 2, 3 \ i \neq j, \ T = 9. \ \ (34)$$

If there is no migration, i.e. $m = s = 0$, when the maturation time is very small, a doubly periodic solution exists \[3\], see Figs. 11. While when $m$ and $s$ are very small, then the doubly periodic orbit is disappeared, although a periodic solution still exists, see Fig. 12a. However, when either $m$ or $s$ is relative large, the periodic solution is vanished and the system becomes stable, see Fig. 12b-12d. Therefore the dynamical behavior is sensitive to prey and predator migration rates. Seems the active migration for prey or predator can stabilize the ecosystem.

5. Conclusion. In this paper, we propose a general model with multiple parallel food chains through the stage structured maturation time delay, and consider
predator and prey migrations among all patches. We have carried out mathematical analysis to discuss the existence of the steady states and their stabilities. Taking the system with two patches as an example, we have proved the existence and uniqueness of two boundary equilibrium point $E_0$ and the predator-free equilibrium point $\tilde{E}$. We have shown that $E_0$ is always unstable, provided conditions for the uniform persistence, obtained sufficient condition for the global attractivity of $\tilde{E}$.

Figure 10. The affection of the prey migration rate when $\tau = 32$.

Figure 11. Phase portrait of (16) with parameters and functions given in (30) and (34), $m = s = 0$.

Figure 12. Phase portrait of (16) with parameters and functions given in (30) and (34).
and discussed its local stability with the same time delays. When both patches are symmetric with constant migration rates, we have discussed the existences and local stability of positive equilibrium point; obtained that the time delay can not only destroy the existence, but also destabilize the positive equilibrium even it exists. To complement the analytical results, we have used numerical techniques to examine how the maturation time of predator, the prey and predator migrations affect on the dynamical behavior. The numerical simulations show the rich dynamics including stability switch and periodic-doubling.

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*E-mail address: imaad6@mun.ca*

*E-mail address: tangxh@mail.csu.edu.cn*

*E-mail address: yyuan@mun.ca*